BLOAT IN RUMINANTS AS A DYSFUNCTION OF ANIMAL AND PASTURE INTERACTION.

A consideration of the environmental and physiological factors associated with the condition, having particular reference to the grazing animal.

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Dissertation completed under joint tutorship in the departments of Plant and Dairy Husbandry, Massey College. Submitted in part fulfilment for the Plant Husbandry Section of the degree of Master of Agricultural Science, University of New Zealand.

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P R O L O G U E.

It is a simple and yet fundamental biological concept that one of the essential differences between plants and animals lies in their mode of nutrition.

The plant is able to use soil nutrients and synthesize its nutritional requirements in the presence of light by the process of carbon assimilation. The animal is entirely dependent on those synthesized plant products for its nutrition.

In this very essential difference ruminants and herbage plants assume a commensal relationship, becoming increasingly interdependent as systems of pasture and animal production intensify.

This relationship has become a well accepted principle in herbage agronomy as to appear almost a statement of the obvious. Nevertheless the writer submits that progress in this field during the past two decades has been concerned almost solely with the botanical aspects of plant production.

The development of strains of plants for grazing conditions, with the additional benefits of an extended grazing season, and greater herbage bulk per acre, are achievements of the plant breeder which have been making an immeasurable contribution to animal production.

In spite of the ultimate use of herbage plants however, studies of the interaction of animal and plant have lagged behind the advances made by the plant breeder.

The animal has been used almost exclusively either as a measure of plant production in terms of liveweight increase, or as the controllable factor for the purpose of imposing particular environmental conditions upon individual plant species or communities. Bathe 1947 (1).

With this criticism in mind, Stapledon 1948 (2) discussing the subject of grassland management for animal production states that " the school to which I belong has been accused and not without a measmre of justice, of paying insufficient attention to the needs of the animal. It is difficult to-day for any particular school of thought to march in step with all other schools-- but in proportion as knowledge accumulates, so does the need to do so become increasingly urgent. Plant nutrition is not just a matter of Ca, P, K, N, and animal nutrition involves much more than starch equivalent and protein equivalent."

Finally, Stapledon (2) reminds the agronomist that when he advises the farmer either by what he writes or what he says as to seeds mixtures and grassland management, in effect he wears the mantle of the nutritionist, for he prescribes the diet on which alone the animal may be fed for weeks or months on end.

Therein lies the trend of thought which has stimulated the subject of the discourse to follow.

The writer submits that any biological practice which is aimed at stimulating a preferred metabolic process will advance towards a state of imbalance in relation to other processes with an increasing intensity of stimulation.

Muir 1948 (3) subscribes to the widely held opinion that physiological disorders such as bloat, and grass tetany, are more common on leys than on permanent pasture. The difference claimed for the ley as against permanent pasture is one of relatively higher incidence of physiological disorders in animals pastured on leys, it being recognised that both types of pasture are capable at times of disturbing the physiological equilibrium of the grazing animal.

The implication is, therefore, that the temporary sward must tend to possess, at a high level of activity, the factors responsible for physiological aberrations in animals at pasture.

The principle of intensive grassland farming is not necessarily attacked but the present design of pastures under certain conditions of soil and management may be less able to provide a diet for health as well as productivity.

This is borne out by the many reports from those countries of intensive grassland production which indicate an increase in physiological disorders arising from the imbalance of animal nutrition resulting from intensive pastoral management practices. (3). Bennetts 1946 (4), Filmer 1947 (5), and others, (14), (29).

The peculiar seasonal nature of these disorders, and the limitations of our knowledge in respect of seasonal changes in the chemistry of the growing plant, particularly in relation to the grazing animal, have resulted so far in but slow progress towards evolving measures of preventive treatment.

An awareness of the consequences which need to be anticipated from intensive grassland production in New Zealand is expressed by McMeekan, 1947 (86). He considers that it is more than a coincidence that such stock disorders seem to occur at periods of rapid change in pasture growth. McMeekan implicates changes from poverty to plenty, from high fibre to low fibre, from slow growing to rapid growing feed, and suggests that the need for adequate management techniques in this connection is an obvious line of attack.

An approach by means of perfecting our grazing management to overcome grazing disorders is suggested by Johnstone-Wallace 1950.(6), in referring to the bloat problem. At the same time he gives the opinion that the real solution lies perhaps as much with the agronomist and plant breeder as with the grazier.

The concept of breeding plants for bloat-proof pastures is entertained, and already recent literature refers to pasture seeds mixtures recommended for reducing the bloat risk. (33), (34), (35).

It is interesting to note that an agronomic approach, based on the use of pasture having a wider species composition is recommended to overcome a physiological disorder causing serious losses in sheep grazing subterranean clover in Australia. (4).

A new departure then becomes evident, as to those factors which are desirable in pastures and pasture plants. The writer subscribes to the view that the herbage agronomist will be aided in his approach to this new aspect of his work when possessed of an appreciation of the integral relationship between the plant and certain animal physiological processes.

For this reason an exposition of animal pasture interactions will be attempted using bloat in ruminants as the specific example.

Bloat in grazing ruminants is referred to by Johnstone- Wallace 1948 (7) as a problem arising more frequently with improved pasture production methods.

He suggests that it is perhaps the most important factor requiring investigation if a full utilization of improved pastures is to be obtained. McMeekan 1947 (86) states that it is a problem which emphasises the complexity of these animal-pasture interactions and considers that of all of them it is perhaps the most complex.

So far failure to produce the condition in the field has defied the more orthodox methods of experimentation. Any solution however rests more probably upon the integrated efforts of workers in allied rather than in any one field. The growing need for this type of approach in biological studies is keenly appreciated by the writer.

However, the opinion is supported that ultimately measures for the prevention of bloat will take an agronomic form. Further, the agrostologist should bring that thought to bear upon the problem which integrates those many aspects of his work designed to meet the needs of the animal.

An attempt will be made to follow that recommendation in this discourse. Should this dissertation provide also a reference base for constructive thought whatever manner of investigation is adopted for the bloat problem, its purpose will be well served.

Broadly the subject matter will be treated as follows:-

AA. The bloat problem, its manifestations and incidence.

BB.1. The in situ interactions of pasture and animal as phenomena associated with acute bloat. Part I - Plant-conditioned interactions.

BB.2. The in situ interactions of pasture and animal as phenomena associated with acute bloat. Part II - Animal-conditioned interactions.

CC. Ruminant digestion and bloat. The physiological processes involved, particularly as influenced by plant biochemical and physical factors.

AA. THE BLOAT PROBLEM. ITS MANIFESTATIONS AND INCIDENCE.

Bloat or hoven is a digestive disorder in ruminant animals to which cattle, sheep, and goats, are particularly subject. The condition arises from an abnormal distension of the rumen with gas. The essential symptom is a distension of the flank in the left lumbar triangle, although the whole abdomen may distend according to the severity of the condition.

It should be noted that bloat is a very common pathological conditon to which Begg 1912 (8) refers as the outstanding symptom of functional and organic diseased conditions.

Bloat is most frequently classified as "chronic" and "acute". In general, acute bloat usually depends upon the nature of the feed whereas chronic bloat is due to an abnormality in the physiological state of the animal. Cole, Huffman, Kleiber, Olson and Schalk 1945. (9).

Chronic bloat usually extends over a considerable period, such as that caused by obstruction of the oesophagus due to enlarged mediastinal lymph glands Ascott 1946 (10). or that associated with rumenal atony. Stuart and Cross 1946 (11).

Acute bloat usually refers to that condition which occurs within a few hours of pasturing; bloat in ruminants feeding green legumes is termed acute.

Dairy cattle grazing legume pastures in New Zealand have been reported to remain in a tympanic state for several months in certain seasons. Lyons. 1928 (12).

Nevertheless this discourse is primarily concerned with acute bloat as accepted in the general sense and manifest as a tympanic state resulting from abnormal feeding conditions, in particular as associated with pasturing legumes.

Mc Intosh 1941 (48) refers to two types of acute bloat--

a) in which gas is superimposed on the ruminal mass, its escape being impeded by obstruction in the oesophagus and

b) where gas remains admixed in the ruminal ingesta as noted after the engorgement with succulent food.

Whilst published experimental evidence is lacking of the relative susceptibility of the different ruminant species to acute bloat, McCandlish and O'Brien 1933 (13) report from a survey that dairy cows are more susceptible than beef animals or sheep. Quin 1942 (14) suggests that dairy cows and lactating ewes are particularly susceptible owing to an incfeased appetite, and for the same reason Mead, Cole and Regan, 1944 (15) consider that lactating cows are more susceptible than dry cows. According to Bell and Britton 1939 (16) fat lambs are more susceptible than unfinished lambs on ladino clover pastures.

(a) BLOAT: A PROBLEM OF ANIMAL AND GRASSLAND HUSBANDRY.

Bloat in ruminants at pasture is a common disorder reported over a wide dispersal of countries such as New Zealand (12) Australia (42) South Africa (14) England (24) Scotland (13) France (30) Sweden (97) Germany (168) Canada (48) The United States of America (9) Spain (98) and the Argentine (87).

In all reports referred to, particular mention is made of the pasture composed either entirely of leguminous plants or as forming the bulk of the contained species.

Losses are reported in dairy and beef cattle, in mutton and wool sheep, whilst Berg 1950 (17) reports that milking goats are not excepted.

In Great Britain steps have been taken to implement a national survey to obtain field data on the bloat problem (88) (239) The economic importance of bloat, as with other disorders of grazing animals, is not apparent when losses and incidence only are considered.

Ward 1945 (18) indicates that wastage from bloat in dairy herds of the North Island of New Zealand amounts to an average of .22% of all cows, or 1.3% of animals culled annually during the period 1938-43.
Although the culling rate is comparatively low, it is the general experience that incidence is high particularly on individual farms characterised by clover-dominant pastures. Tyrer 1951 (20), (12), (93).
Losses recorded as due to bloat in the Massey College dairy herd in New Zealand, totalled 30 animals between 1940 and 1949. Although the actual milk production and management time losses are a matter of conjecture, they were none the less experienced. A general report of production losses in New Zealand was received from Johnson (personal communication). Referring to the Kairanga area this observer reports that throughout the district bloat causes an appreciable loss in production in individual herds, and causes the dairy farmers and occasionally the sheep farmer some concern. The incidence of bloat in dairy herds during the spring

months of 1949 was instanced as being so severe in some areas that production fell rapidly, and paddocks carrying what should have been ideal pasture for dairy stock were barred from grazing.

There is a paucity of information in the literature concerning milk production losses from bloat, but such losses are in evidence. In England, Wooldridge 1947 (21) refers to the lowering of milk production in individual cows for several weeks after recovery from bloat. In one dairy herd in England known to the writer, total milk yields dropped from a daily average of 200 gallons before the severe outbreak of acute bloat to 110 gallons daily average immediately after and in the ten days following the attack. Longman (personal communication).

Cole et al. (9) comment on the fact that very few surveys of the losses attributable to bloat have been made. They quote Welch, Marsh, and Tuncliffe. 1929 (22) who state that on the basis of a survey in Montana, cattlemen may expect a loss from bloat on sweet clover pasture of less than 1 per cent, and sheepmem about 0.5 per cent.

Mc Candlish (13) reports bloat on 34 per cent of the dairy farms in the South West of Scotland, this figure being obtained in replies from 152 livestock producers.

Hanson and Boyd 1943 (23). made a survey of 1,106 herds with nearly 30 000 head of cattle in Minnesota. A total of 11,205 head were pastured on sweet clover and alfalfa in approximately equal numbers. From May to October 182 cases of bloat were reported, and of these 50 were fatal. Alfalfa caused 28 deaths, sweet clover 20. Six cases of non fatal bloat were reported on non-legume pasture.

In California, Bell and Britton (16) made a survey over seven weeks during July and August of losses on ladino clover pasture. These observations were confined to six ranches with a livestock population of 47,000 lambs and 3,200 cattle. Twenty lambs, representing about 50 per cent of the total losses during the period, died of bloat. Two steers died from this cause,more deaths from bloat occurred in pastures with a stand of pure clover, or with a very high percentage of clover, and bloat was not a problem in certain pastures covered with more than 50 per cent grasses. Bathe 1948 (24) investigated the occurrence of bloat over 53 dairy farms totalling 1,160 animals, in the South West of England during the spring and summer months of 1944 and 1945. Losses amounted to only 3 and 4 cows respectively in each year, but animal and pasture management practices were seriously hampered by the incidence and risk of bloat.

There are a number of reports which indicate the incidence of bloat occurring in particular districts associated with environmental conditions conducive to rapid and lush herbage growth. (24), (13). In New Zealand, Hawkes Bay, Bay of Plenty, and Manawatu districts are known as particularly troublesome areas, (19), (18), (93). Similarly, irrigated pasture areas especially where lucerne is cultivated are known to stimulate pasturing conditions conducive to bloat. Cole, Mead, and Regan 1943 (25), Beruldsen and Morgan 1936 (26).
It is in the various management aspects of pasturing animals that the most serious inconvenience can result when acute bloat occurs. Due to its insidious nature it is difficult to predict the onset of bloat. Quin 1943 (27), whilst according to Ferguson 1950 (28), there is no way except by grazing to tell if a pasture will cause bloat. This uncertainty necessitates constant vigilance of animals at pasture which wholly uneconomic practice is reported by McIntosh 1937 (29), to be responsible for some stockowners selling their herds due to bloat trouble. In South Africa, Quin (14), refers to the fact that stockowners are compelled to use lucerne in hay form with resultant nutritive losses and increased production costs.

The risk of bloat on lucerne pastures in France is a particular hazard to night grazing. Davis 1950 (30). This will be appreciated when it is realised that such pastures are usually unfenced and free grazing is practised. Similar difficulties will be expected to prevail when cattle are extensively grazed in ranching countries. (86).

The feeding of hay to animals prior to grazing pastures on which there is a bloat risk is a preventive measure generally recommended, Olson 1940 (31), and practiced Candy 1947 (32). Apart from being uneconomic, particularly under all pasture systems of farming, there is no conclusive evidence that such a practice is effective, although it has been claimed on the basis of experimental findings that feeding hay will reduce bloat. (25

Recommendations are made for the compilation of seeds mixtures in which legume species are reduced or excluded to lessen the risk of bloat Butler 1949 (33), Jones, Burle and Brown 1942 (34), Mead, Britton and Cole. Generally the inclusion of a greater percentage of grass species

is recommended; This is an entirely empirical agronomic approach for which there is a need to investigate experimentally. Legume pasture plants are usually implicated in the etiology of bloat, and it is reported that bloat will not occur or is reduced on pasture in which grass species are over 50 per cent dominant (16).
This is not the experience of the writer who has observed under New Zealand conditions the onset of bloat in dairy cows severely rationed on pasture containing over 80 per cent grass species.

Reports from dairymen in England indicate that severe bloat incidence with fatalities has occurred on pasture with cocksfoot dominant, Young 1947 (36), Shook 1947 (37).
The exclusion of legumes from pastures would be a practice detrimental both to herbage production and soil fertility, and is a recommendation to be questioned, on the basis of present knowledge concerning the incidence of bloat.

A number of observers report the incidence of bloat as being high during flushes of clover growth in pastures (12), (13), (14), (22), (44). Pasture management to maintain a balance between grass and legume species is considered to reduce bloat risk (93). But even under constant weather conditions, this requires such highly skilled grazing management, often at difference with animal production, as to throw doubt on its economic value under farm conditions.

Measures have been adopted for dairy cow grazing to restrict pasture available at a herbage growth stage when bloat is anticipated (19) and Adams 1950 (38), for which some success is claimed. The system of rationed grazing to prevent bloat remains to be proved however, and its effects on animal production, and pasture composition need to be assessed before this system can be confidently recommended for general practice. Its adoption is strictly limited to intensive systems of pasture and management.

(b) FEED AND ENVIRONMENTAL CONDITIONS ASSOCIATED WITH BLOAT.

According to Muir (3) it is evident that bowel inhibitory substances in forage plants reach threshold levels for the appearance of clinical symptoms only under certain conditions of soil, weather, stage of growth, and botanical composition of pasture. Accordingly intensive study of these factors is considered even more necessary for the prevention of bloat than the identification of the toxic agents which may be involved. It is important then to be familiar with the feed and environmental conditions under which bloat occurs.

Cattle and sheep at pasture were reported to suffer from bloat over eight decades ago. Large 1863 (99). Acute bloat did not become a serious problem according to Niborg 1795 (39), until the middle of the eighteenth century when the pasturing of clover and lucerne became a common practice. The condition is now known as a common sequel to grazing on clover or other leguminous crops when it is often termed "clover blown" Phillipson 1942 (40). The following leguminous crops have been reported as promoting bloat: lucerne (25) white clover (26) red clover (13) ladino clover (16) sweet clover (44) peas (42) and trefoil. (90)

Other green feeds are known to give rise to bloat; the writer has observed bloat in dairy cattle feeding Kale, grass lawn trimmings in which legume species were absent, pasture comprised of over 80 per cent grass species, and in sheep grazing rape, turnip tops, growing wheat and barley. Shanks 1946 (41) states that bloat may occur in sheep during the winter if they have access to the green cereals wheat and barley; rapidly growing green cereals are reported by Ohman 1938 (42) in Australia to cause bloat in cattle. In the same country Veech 1937 (43) refers to travelling cattle becoming blown when excess green feed is available, such as variegated thistle and the leaves of the Kurrajong and willow trees.

The rate and stage of growth at which herbage plants are pastured is reported widely as being an important contributory factor in the onset of bloat. Cole. et. al. (25) claim to produce bloat on lucerne pasture in any season of the year and under varying environmental conditions provided the pasture is in the pre-bloom stage of growth, succulent, and thick enough to allow for rapid ingestion.

Kephart 1929 (44) surveying the occurrence of bloat on sweet clover concluded that incidence was highest when the clover was succulent.

Rapid, succulent growth of sufficient quantity would seem to be the general pasture conditions for inducing bloat. Dixon 1938 (45), 1939 (46) and others (41), (42), (35), (13).

Reference to particular parts of the plant is made by Quin (27) who states that bloat in sheep was associated with the ravenous consumption of the green leafy tops of lucerne. In this connection it is worth noting a dairyman's observation on dairy cows grazing a dominantly cocksfoot pasture on which severe attacks of acute bloat were experienced: "the cattle were curling their tongues around the top of the cocksfoot (which included the flower). The tug then given to sever each mouthful caused the cocksfoot stem to break off some way below, with the result that the unbleached centre stalk was pulled out of its sheath, and this was consumed as well as that which the cattle had already taken into their mouths". Young (36).

The stall feeding of lucerne tops has induced severe bloat in cattle (15) although lucerne tops sampled from the same pasture at the same time and fed in the same dry matter proportions did not cause bloat. The writer under New Zealand conditions has induced bloat in two dairy cows by cutting and feeding random samples from a pasture of mixed grass and clover species, on which bloat regularly occurred. In this manner it is possible to determine the amounts of pasture consumed causing the onset of bloat. Similarly more controlled studies regarding the time interval to the onset of the condition can be made, as well as certain reactions of the rumen motility cycles.

The feeding of cattle on grain alone is reported as causing bloat, Mead and Goss 1935 (47). In this case continuous feeding on the same ration gave rise to the condition which could not be considered the same as acute bloat arising from legume pasturing.

Where soil conditions are conducive to lush pasture growth the risk of bloat is generally considered to be increased (20) (13) and it is not uncommon for the top dressing of pastures to be implicated (8) (93). In this respect McIntosh 1941(48) in Canada makes the contrary statement that bloat is less frequently encountered on lucerne pastures where fertilisation and irrigation have been well maintained, than is the case on neglected pastures growing on poor soil. This is not in accord with the report of Beruldsen and Morgan (26) in Australia who instance bloat as one of the problems associated with lush clover growth under irrigated conditions. Similarly Cole et al (25) state that irrigation of lucerne is necessary to promote the succulent growth conducive to the experimental production of bloat. Alway 1927 (49) reports a wide variation in the Sulphur content of legumes depending upon the sulphur content of the soil.

Doak 1929 (100) in New Zealand has found that the sulphur content of lucerne is decidedly increased in many cases by soil treatment with sulphur or

Sulphur compounds. He found that untreated lucerne on analysis showed a range in sulphur of 0.26 per cent to 0.3 per cent. The lucerne leaves contained a higher percentage of sulphur than the stems. To what extent soil factors affect the chemical composition of the plant subsequently influencing the level of hydrogen sulphide gas production in the rumen is a matter for conjecture at our present state of knowledge.

Weather factors no doubt have a very important if somewhat indirect influence on bloat by affecting those pasture conditions associated with a high incidence. Rainfall and temperature variations may have the following primary effects on a pasture.

a) Increases quantity of herbage per acre.

b) Conditions palatability of the herbage.

c) Influences the dominant production of any one or group of herbage species in a pasture.

Superimposed on and accentuating the influences of c) will be those influences resulting from the defoliation effected by the grazing animal.

It will follow that those quantitative etiological factors in bloat will operate as a) and b) reach optimum conditions in respect of the grazing animal. The qualitative factors will be determined by the nature of the species dominance in c) all other factors being equal.

This temperature, rainfall, and pasture growth relationship as it may be contributory to the incidence of bloat will be developed further in the following section.

At this stage it is pertinent to note that Cole et al (25) claim to produce bloat at will in any season on lucerne pastures where plant water requirements are under control by irrigation. Bathe (24) in England reports that weather favouring bursts of succulent non fibrous herbage seems liable to cause risk of bloat during the seasons of optimum plant growth. High rainfall effecting excessive growth of sweet clover in Iowa was considered by Pammel 1930 (50) to give rise to an unusually high incidence of bloat.

This role of humidity as it may affect bloat in grazing animals is far from being understood. The writer submits however that severe bloat in dairy cattle rarely occurs in much less than one hour after pasturing provided they have not been pre fed on a bloat provoking feed. This is in accord with the findings of Cole et al (25) and referred to by others. (6), (51). In view of this fact it is not unreasonable to assume that primarily a herbage quantitative factor operates to promote the onset of acute bloat whatever the subsequent qualitative reaction. Given this assumption, plant palatability insofar as it influences herbage consumption is an important factor for consideration. The role of humidity then may be implicated in its influence upon plant palatability at those times when risk of bloat incidence is high.

Already the complexity of those interactions involved in the bloat problem become apparent, hence brief recapitulation will lend perspective to further development of the subject.

a) It is evident that acute bloat as a problem of grazing ruminants is world wide.

b) Economic losses from bloat whilst difficult to measure are in evidence from the many reports cited. Such losses are primarily concerned with bloat as a managerial problem.

c) The legume species of herbage plants are those most strongly implicated as inducing bloat in grazing animals. It is not uncommon for other green fodder plants to give rise to the condition.

d) That development stage attained by herbage plants which presents conditions for optimum consumption by the animal is implicated in acute bloat.

Under conditions of active growth, that stage of plant development will be expected to fluctuate according to variations in natural and induced environment.

It will be noted that this section has been concerned with the more general aspects of bloat in ruminants. This approach has enabled the resolving of scattered information into the above generalisations. A more particular examination of the questions posed in c) and d) will follow.

BB1. THE IN SITU INTERACTIONS OF PASTURE AND RUMINANT ANIMAL AS PHENOMENA ASSOCIATED WITH ACUTE BLOAT.

PART. I. PASTURE-CONDITIONED INTERACTIONS.

The many complex plant animal interactions expressed in acute bloat pose numerous problems for research. But one of the greatest deterrents to pursuing a close study of the etiology of bloat is presented by the difficulty of producing the condition with feeding procedures.

As a result, the literature is seriously limited in specific reference, to the interactions in the micro-environment existent between pasture plants and the grazing animal, as they may be associated with bloat. The importance of such interactions should not be overlooked for bloat in grazing ruminants follows upon the initial act of herbage ingestion. It is further associated with pasture plants at a particular stage of growth and development.

The writer submits that according to the efficiency of grazing in terms of pasture intake, so will be determined the amount of herbage entering the rumen in any one period of grazing.

There is evidence that gas production in the rumen is proportionately related to the amount of food consumed Cole, Kleiber and Mead, 1942 (51), Washburn and Brodie 1937 (52), and that the rate of gas formation varies with different foods (52), (53). It follows then that those differences which bring to bear on the type and amount of pasture herbage consumed in a given unit of time, should come under examination when considering the etiology of bloat.

Measurement of in situ herbage consumption, selectivity, and knowledge of food intake regulatory factors in grazing animals, are highly controversial fields still in the early stages of investigation.

Better known is the effect on pastures of the grazing animal as a factor of induced environment, in so far as it influences the social order of herbage species and thereby partly contributes to the conditioning of its own diet.

Whilst an attempt will be made to examine such evidence in those fields as are relevant to this section, the limitations set by the availability of conclusive experimental data should be borne in mind when conjectural aspects are considere d.

A. PASTURE GROWTH AND DEVELOPMENT AS IT MAY INFLUENCE FEED CONSUMPTION.

The concept of pasture as a biotic community Davies 1948 (54) immediately suggests variation in the manner whereby both the community and different species within it respond to environmental conditions. Pasture quantity and quality will be expected to vary considerably throughout the seasons of active growth. Consequent upon such changes will be the diet of the grazing animal.

Against that background pasture will probably influence the quantitative level of ruminant herbage consumption in a given period of grazing as it varies in the following characteristics:-

a) Herbage density and length per unit area grazed.

b) Palatability of the herbage.

c) Herbage quantity and type per unit area grazed.

a) HERBAGE DENSITY AND LENGTH.

Seasonal variation in quantitative pasture production is a characteristic of temperate grassland regions. In New Zealand for example the two periods of lowest production are during the winter and late summer months, Hudson et al. 1933 (55), spread of seasonal production being largely determined by climatic influences.

Various pasture plant species however reach their peak production at different times within the seasonal fluctuations of total production; in turn wide quantitative differences occurring between species varieties, Corkill 1950 (56). A combination then of conditions conducive to optimum growth, and herbage plants having a comparatively high growth rate and vegetative development should provide a micro-environment having herbage density favourable to optimum intake by the grazing animal.

This point is best illustrated by an extreme situation referred to by Du Toit et al. 1940 (57) under free range conditions in South Africa. These workers cite Pole-Evans 1936 (122) describing desert regions where pasture plants are widely spaced in bare soil; under such conditions of low pasture density animals may starve, but will survive in areas having a uniform sward even though excessively deficient in essential mineral and nutrient requirements.

Under intensive pasture conditions Johnstone-Wallace 1944 (58) has indicated that variations in density and height of a pasture probably influence the quantitative level of herbage intake in nursing beef cows. This is illustrated in his data summarised in Table 1.

Table 1.

The influence of pasture height and density on daily herbage consumption.

Condition of herbage.	Available herbage		Estimated daily herbage consumption	
	Green lb	Dry lb	Green lb	Dry lb
Dense sward 4 - 5 inches high	4,500	1,000	150	32
Sward after few days grazing	2,200	500	90	20
Sward after further period of grazing	1,100	250	45	10
Open sward 10 - 12 inches high	5,000	1,200	70	20

The amount of herbage consumed was determined by measuring the difference between herbage from strips mown immediately prior to grazing and similar parallel strips mown at intervals of 1 to 4 days after grazing commenced. The data quoted is therefore subject to the limitations of the method as well as failure to replicate the experiment. Johnstone-Wallace further noted that the cows observed showed no inclination to extend their grazing period beyond 8 hours even when the amount of herbage recorded as consumed fell to 45 pounds per day.

A mechanical factor was conceived in grazing management, and it was submitted that pastures should be in a condition to permit livestock to gather the optimum amount of food within a normal 8 hour period of grazing. According to Woodward 1936 (59) stock were able to gather maximum amount of herbage when the sward was about 6 inches high, with a yield of 915 pounds of dry matter per acre. Consumption fell off when the amount of herbage was less than this; and it also decreased when the herbage was allowed to reach a height of 8-10 inches.

Commenting on the influence of pasture conditions on the grazing behaviour of dairy cows Hancock 1950 (60) states that it seems clear that cows must and do work longer hours under adverse grazing conditions, in that the time periods spent in grazing, ruminating, or both, are longer.

than when the pasture quantity and quality are optimal.

There are indications then that pasture reaches a stage of development most conducive to optimum intake by the grazing animal. It is not necessarily a stage where pasture attains its maximum production potential. For that reason, quantitative pasture production in terms of dry matter available for grazing purposes, means very little without reference to the vegetative state of the herbage, particularly in relation to ground cover.

Both the length and density of pasture are probably of importance, in so far as those factors contribute to accessability for grazing.

b). HERBAGE PALATABILITY.

Ruminant animals are known to show preference for different types of green herbage and fodder when given a choice.

Evidence of this is to be found in the work of Schalk and Amadon 1928 (61) who weighed food boli collected through a rumen fistula at the cardia, or point of entry from the oesophagus into the bovine ruminant stomach. The greater number and weight of boli ingested in a given time being recorded when eating palatable foods. Complete refusal of unpalatable feeds being instanced in some cows even after being without food for 24 hours.

According to Stapledon 1947 (62), in one sense palatability is clearly more important than nutritive value, for unless a plant is eaten abundantly and with something akin to relish, its nutritive value is of little avail. Stapledon further considers that palatability and nutritive value in plants are influenced profoundly by the conditions under which a plant grows, and by the actual stage of growth at which a plant or parts of a plant is eaten.

It is necessary to distinguish between two aspects of palatability. One is a standard of appeal sufficient to hold animals to the grazing of perhaps a single species, or a very limited number of species or strains of plants for days or weeks on end.

The other is a standard of tastiness that will attract animals to particular plants when the scope for selection is comparatively wide.

Palatability then is both intrinsic and relative. Pasture conditions can now be readily conceived whereby palatability influences quantitative food intake levels, owing to differences in intrinsic palatability between component species of different pastures, and as relative palatability changes either within or between pastures, as the result of changes in herbage development.

Numerous factors influence palatability and these present extreme difficulty for study with precision and accuracy in the case of in situ pasture.

Stapledon (62) considers the only safe criterion for pasture palatability is the proportion of the amount eaten to that actually offering. In this respect he states that it is almost impossible to get accurate evidence by any method of sampling.

Nevertheless, attempts have been made to measure palatability. Davies et al. 1950 (63) in experiments to determine the productivity of different pasture plots grazed by sheep, also gave results which they considered indicated relative levels of palatability between pastures. Palatability was measured by the mean quantities of uneaten grass in grams per square yard left at the end of the grazing periods.

On improved pasture in which perennial ryegrass, cocksfoot, and white clover were dominant a mean quantity of 70 grams of herbage remained, with 184 grams and 165 grams respectively on manured and unmanured permanent pastures. These workers concluded that the sheep found reseeded grass more palatable and grazed it more thoroughly than permanent pasture.

Earlier work which attempts to obtain information on the relative palatability of miscellaneous herbage plant species is described by Milton 1938 (64) in Wales. A method of subjective observation was adopted, 10 marks being given to those species which were hardest grazed in a sward by different types of stock. It was considered that certain species were definitely palatable to stock and they coincided very closely with the species mentioned by Cockayne 1919 (65) in New Zealand investigations. Grasses and clovers in their early growth stages during Spring were found to be most palatable to free grazing stock.

The relative palatability of the miscellaneous species was approximately the same over different types of land. Grasses showed variation chiefly due to stage, and type of growth and the presence of burn. These findings being generally in accord with those of other workers. Beaumont et al. 1933 (66). Davies 1925 (67) Stapledon and Jones 1927 (68), Stapledon and Milton 1932 (69), Sheehy 1932 (70).

Later work by Milton 1934 (71), using the same method arrived at an investigation of the relative palatability of simple seeds mixtures in conjunction with single species plots under sheep grazing. It was found that of the grasses, Timothy formed the basis of the most palatable mixtures although it was not the hardest grazed species among the pure plots. There was an indication that grazing was increased in uniformity among contrasting mixtures in proportion to the addition of species to their composition: sheep on the mixture plots selected mixtures as such rather than individual species from mixtures. Red and White clover were found to be more highly palatable than the grasses, red clover being the most highly palatable. Similar conclusions were arrived at by Davies (67) concerning the relatively high palatability of red and white clovers. This worker states that one reason why clover maintains a much more uniform palatability than the grasses is probably that under more or less constant grazing they never produce much stemmy growth, but continue all the time to produce a relative abundance of fresh and succulent leaves.

Cockayne 1920 (123) found that the palatability of White clover in New Zealand varies with the season, most being eaten by sheep in September. Davies (67) concluded that the chief factors influencing palatability would seem to be the relative succulency of the herbage offered by any particular species at any particular time, this being largely due to the stage of growth of the plants.

Shaw and Atheson 1942 (72) recognise the importance of palatability in pasture crops as contributing to maximum food intake for high producing cows, but they admit that the effect palatable food has on the level of food consumption is not known. These workers used the time spent grazing by dairy cows to assess the comparative palatability of green cereal pastures. Fully fed cows were used, kept from pasture and stall fed during the grazing trial, as it was assumed their behaviour would then better reflect the true palatability of each plot.

The following results were obtained:---

	Average Grazing Time over 6 days.	
	Mins.	% of Time.
Balbo Rye Pasture	45	52
Common Rye Pasture	21	24
Turkey Wheat Pasture	15	18
Reno Barley Pasture	5	6

The four plots were laid down in the same five acre field; all plots were stated to be ideal for grazing averaging 4--6 inches in height with good stands.

Although Balbo rye was the longest this factor was not considered the measure of palatability, as barley ranked second in height and appeared the most uniformly good pasture. It should be noted that the data were procured over 6 days only, and can only refer to comparative palatability at a particular growth stage of the pastures, which are subject to wide variation in that respect arising from environmental influences. Further it is an open question as to how far the time spent grazing by an animal on a particular plot reflects the palatability of the herbage, without some indication of the comparative grazing activity which influences the proportion of the food eaten to that offering. (61). None the less these workers suggest a comparatively higher palatability for Balbo Rye to that of Reno Barley.

Watson et al. 1933 (73) suggest that palatable foods will increase the dry matter intake of sheep from the estimated optimum average figure of 2.5 pounds to 3 pounds per 100 pounds live weight.

Woodman et al. 1937 (74) consider that any attempts to measure the so called normal appetite of sheep at different live-weights are essentially arbitrary having no absolute significance. They state that the appetite of any given individual on a constant diet may vary very widely from day to day. Changes in nature of diet, "balance" of ration, palatability and digestibility, and the proportion of coarse or succulent fodder in a ration may cause abrupt changes in the appetite of the individual.

It would be expected then that changes of that nature entering into the seasonal production of herbage would influence the level of quantitative intake by the grazing animal.

Woodman et al. (74) demonstrated that changes from a diet of chaffed lucerne hay to one of the same hay in a long condition occasioned a depression of appetite in sheep. The average depression of 0.42 pounds of dry matter per day amounting to 11.4 per cent of the mean daily dry matter consumption. Improved hay quality (fed unchaffed) in all cases led to increased consumption. Further work by Woodman et al. 1937 (75) implicates increased palatability values in striking increases in the food consumption of sheep when changed from typical English winter fodder rations to spring grazing.

They present the following data;----

Table 2.

Appetites in terms of lb. dry matter, of sheep on (a) pasture and (b) a typical winter ration.

Sheep No:	GRAZING TRIAL (MAY 1934) Mean daily Consumption on Grass 10-17 May lb dry matter.	18-24 May lb D.M.	Mean live weight of sheep. 10-24 May lb.	ON TYPICAL WINTER RATION (MARCH 1934) Mean daily Consumption. 1-20 March lb.D.M.	Mean live weight of sheep. lb.
1.	4.66	5.06	146	3.36	125
2.	4.66	5.17	137	3.23	120
8.	4.99	4.92	166	3.70	157
9.	6.23	6.13	201	4.39	181
Digestion coefficient of organic matter of grass.	81.7%	80.4%			

The food consumption of grazing sheep was calculated on the basis of the digestion coefficient of the organic matter in the herbage. These workers state:-- "The observed increase in appetite could not be attributed to the stimulating influence of being in the open air after a period of indoor confinement, since the sheep had been kept in pens on the same field throughout the entire duration of the winter feeding trials. Neither could it have been induced by the tonic effect of passing suddenly from winter feeding to grazing, for the sheep had become well accustomed to the grass having been grazing the plots for more than 3 weeks before the actual measurement of appetite was begun. It must be ascribed in the writer's opinion to the high palatability of the young spring herbage. The results support the contention that farm animals in general tend to over eat when first put out to grass in spring...."

It was further found that a depressed dry matter intake of sheep at pasture followed upon a marked increase in stemminess of pasture herbage and reduction in pasture quality as the season advanced. The influence of these factors as they lowered herbage palatability were implicated in depressing herbage intake.

There is evidence from Percival 1950 (76) in New Zealand that seasonal changes in pasture may influence the daily dry matter intake of grazing animals. Three methods of measurement compared, showed a progressive increase in dry matter intake between August and December corresponding with the seasonal increases in quantity and quality of pasture.

(See FIG: 2 PAGE 30A).

Any assumption that an increasing dry matter intake of grazing animals on the same pasture is related to an increase in herbage palatability needs to take into account the work of Smuts et al. 1940 (77) in South Africa. These workers demonstrated that the average daily weight of sheep increases or decreases according to the protein content of the pasture and the season of the year.

The dry matter excretion in faeces voided appeared to bear no relationship to growth and seasonal fluctuations in the protein content of pasture ; in fact the lowest values were attained when the grazing was presumably most palatable. These findings being in contradistinction to those in dairy cows demonstrated by Percival (76). Furthering their investigations Smuts et al. calculated the dry matter consumption of sheep, from the daily dry matter of the faeces and the digestibility of the dry matter. On this basis they claim a strong relationship between dry matter consumption and live weight of animals, a decrease in weight resulting in a decrease in dry matter consumption.

Using Kleibers 1932 (78) equation for relating dry matter consumption to body weight they found that while the average daily dry matter consumption varies with the season of the year, and consequently with the protein content of the pasture, it is extremely constant when expressed per unit of weight per $\frac{3}{4}$ power function of the weight or square metre of body surface. In the light of this finding they state:--" The capacity for dry matter consumption then would appear related as in the same manner as the basal metabolism, to the surface area or $\frac{3}{4}$ power function of the weight. This would mean that there is no justification to assume that sheep eat proportionately more per unit of weight of the summer grazing than of the winter grazing. In fact it appears as if the weight of the animal is the dominating factor and not the condition of the grazing."
From this statement it would follow that the feeding capacity of a grazing animal is regulated by the $\frac{3}{4}$ power function of body weight. If, as according to the experiment quoted , the nutritive value of the pasture

herbage determines body weight, then as these factors increase or decrease, so dry matter consumption will vary accordingly.

Under the same pasture conditions then an increased nutritive value of the herbage would provide a live-weight increase, upon which would follow an increased dry matter intake. The same pasture, comprised of those species intrinsically palatable, as conceived by Stapledon (62), as it increased in nutritive value would thereby increase in palatability. According to this reasoning palatability and nutritive value would be related where palatability in this case is recognised as the standard of appeal holding animals to the grazing that same pasture postulated. This would accord with the widely held view that pasture is most palatable when rapidly growing, particularly in its early stages of development when nutritive value is high, (67), (64), (71), (75).

It is emphasised that this section is concerned with herbage palatability as an interacting factor between plant and animal in so far as it may influence quantitative herbage consumption. That there may be no foundation for assuming that sheep and cattle eat proportionately more per unit of weight on young as against mature pasture is of no significance to the discussion.

Of the utmost importance where bloat is concerned is the probability of an increase of dry matter intake occurring relative to the potential capacity or volume of the rumen in the mature animal, as the level of herbage palatability increases. In this respect, the evidence presented so far (75), (77), gives good reason for considering the probability of a close relationship existing between palatability of pasture and the amount eaten by the grazing animal.

To this stage the question of herbage palatability has been without particular reference to these plant changes associated with advancing maturity generally implicated as depressing both palatability and herbage intake. (7). (76). (124).

According to Forbes and Garrigus 1948, (79). palatability as judged by dry matter intake of a wide species range of grasses and clover by sheep and cattle, tended to decrease as maturity and lignin content of the forage increased. It should be noted that large variation was found in intakes between forages that was not apparently related to lignin content. Nevertheless, this work finds general accord with the results of a number of investigators (77), (75), and would account for the seasonal depression in herbage consumption in cattle and sheep (76), (77), (75), associated with the increasing ligno - cellulose percentage Baskett 1948 (80), Patton 1943 (82), (58), and depression in protein (77), (80), in pasture herbage as it advances towards maturity.

It would not be unreasonable to expect that an increasing fibre content of pasture with a consequent lowered digestibility value would depress appetite and herbage intake in grazing animals when the effects of mature herbage on ruminant digestion are examined.
Norman and Fuller 1942 (81), have indicated that the presence of lignin in the cell wall of plants markedly affects the availability of cellulose for digestion. The lignification process in herbage plants is one of maturation, associated also with a reduction in protein content and water soluble constituents. Even allowing for this reduction in available nutrients, it is found that the cellulose of material containing a low percentage of lignin, is more readily decomposed by rumen digestive processes than the cellulose of mature herbage with a high percentage of lignin. Loun et al. 1948. (83).

That highly lignified plant material requires a longer time for cellulose digestion in the rumen of sheep has been shown by Hoflund et al. 1948 (84). These workers concluded from in vitro and in vivo studies that the rate of cellulose digestion was markedly influenced by the diet. The appetite for either lucerne or grass hay being directly affected by the rate of cellulose digested. Of particular interest in this work was the fact that on a basic diet of poor quality grass hay both cellulose digestion and appetite were stimulated by small amounts of sugar, but markedly depressed by excessive amounts. More sugar being tolerated if protein was also given; optimal cellulose digestion necessitating a balance between readily available carbohydrate and protein.

In conjunction with investigations of the effect of diet on ruminal gas formation in dairy cows Cole and Kleiber (53), attempted to determine if palatability varied in different fields of lucerne. The influence of maturity on palatability was a further objective. Whilst no conclusive results were obtained, these workers indicated that alfalfa increased in palatability with maturity. The occurrence of bloat in the animals used depressed herbage consumption so making a true estimate of palatability impossible.

The writer submits that the extent to which ruminal distension following feeding is likely to affect quantitative intake and thereby confuse palatability studies should not be overlooked in experimental work endeavouring to determine the comparative palatability of pastures and herbage species.

One other aspect of palatability associated with advanced herbage maturity and likely to influence dry matter intake is referred to by Johnstone-Wallace (58). Attention is drawn to the fact that immature herbage low in lignin, requires less effort in collection than older lignified material, and this may influence selective grazing in cattle. Tribe 1949 (85), makes a similar observation with sheep, noting that small easily torn plants, or parts of plants, will tend to be preferred by the grazing animal for merely mechanical reasons, physiological and psychological factors being recognised as always potentially limiting factors in selection of herbage for grazing.

Herbage palatability, whilst a somewhat intangible plant and animal interacting factor, is none the less apparent when the evidence is summarised in the following manner,

a). It is certain that foods differ in palatability for ruminants.

b). Upper and lower palatability limits doubtless exist, bounded respectively by excessive consumption or complete refusal of food by the animal.

c). There are indications that certain pastures having different constituent species are preferred to others under free grazing, and that preference is marked by a greater consumption of the preferred pasture.

d). Investigations of an empirical nature strongly suggest differences in palatability existent between pasture herbage species, the high palatability of clover species being particularly noted at certain stages of growth.

e). The available means of investigation, (and subject to their limitations), support the general observation that young and active growing pasture is particularly palatable.

f). It would seem that increasing lignification of herbage plant cells depresses palatability and accessability for consumption.

g). There is good reason to believe that the level of quantitative herbage intake in grazing animals will be raised or lowered accordingly as conditions in e) and f) obtain.

The writer would draw attention to an interesting parallel existent between those conditions when pasture is considered to be highly palatable and pasture conditions associated with acute bloat.

It is known that pasture having different constituent species vary in their bloat producing effects (25), bloat being most often associated with clover dominant pastures (40).
Different pastures of the same species composition also vary in their bloat producing effects. (53).
The same pastures are known to vary in the incidence and severity with which acute bloat occurs upon them during the same season of growth (24).

Bloat is rarely associated with pastures at a mature stage of growth, and most often with young actively growing pasture.

There is then reason to suppose that where a pasture will induce bloat so also will conditions obtain for optimum herbage intake.

c) HERBAGE QUANTITY AND TYPE.

The role of herbage density, length, and palatability, in so far as these factors influence consumption by the grazing animal, has been indicated. In turn, the degree of that influence is likely to be consequent upon the quantity of herbage available for grazing.
All of these factors are the ultimate expression of the pasture type as identified with its constituent species. Under intensive grassland conditions the overall type of herbage made available is largely under control. Thus the nutritional environment is conditional upon those species selected for a pasture seeds mixture. The simpler that mixture the more nearly will the sward type represent the average vegetative character of its constituents.
It will be appreciated that in terms of quantity the vegetative habit of different pasture plants species will vary, and at different times of the year Corkill (56). Inter-specific competition in a mixed pasture may also result in dominance of the most strongly competitive species and the pasture type would be characterised accordingly.
However, the quantity of herbage that pasture species will produce relative to each other, or as between particular pasture types, is beyond

the scope of this section.

The primary consideration is the more general aspects of pasture quantity and type as they may relate to herbage consumption by the animal under conditions conducive to bloat.
Our knowledge is seriously limited in respect of the precise pasture conditions under which bloat becomes manifest, and it will remain so until detailed field studies are available.

The association of pasture quantity and type with bloat can be considered therefore only from a circumstantial aspect. That they may be contributory factors is borne out by the often reported seasonal incidence of bloat (24), (13), (16), (19), its association with lush pasture herbage (45), (46), (41), (42), (35) and with herbage type conducive to optimum herbage consumption Jacobsen. Espe, and Cannon 1942 (89).

The quantitative level of herbage available is implicated in the etiology of bloat by Viljoens 1922 (90), who suggests that the condition arises from too rapid and too large a consumption of lucerne or kaffir corn. Espe et al. 1946 (91), imply that the type of herbage consumed is not of such import as the rate of ingestion, coupled with quantity of herbage consumed, whilst Scales 1946 (92), states that bloat in cattle is caused by eating too much too fast.

Detailed observations made by the writer, illustrated graphically in the following section, indicate that the time to onset of bloat in dairy cattle is increased as the quantity of herbage available becomes less. Similarly, the writer has controlled both the onset of bloat and its degree of severity under pasture conditions conducive to optimum intake in dairy cattle, by intermittent pasturing throughout the day, thereby restricting the quantity of herbage available for consumption at any one time. The pasture conditions prevailing were conducive to the onset of bloat in cows shortly after pasturing where free grazing was permitted.

It will be noted in FIG:10 day 21 and in FIG:13 day 22 in the following section that where grazing on a pasture conducive to bloat was restricted within a certain time limit, bloat did not occur in the ~~first~~ SECOND example and was reduced in the ~~second~~ FIRST example. It would not be un-reasonable to assume that a reduction in the quantitative level of herbage intake was effected, relative to those other grazing periods in which bloat occurred.

It is of interest to further record, that striking differences in bloat incidence in dairy cows associated with a large difference in area of the same pasture available for grazing, were observed by the writer under the conditions of an experiment at the New Zealand Dairy Research Institute farm during the spring of 1950.

Two groups of lactating Monozygotic Twin cattle were restricted by an electric fence to a high and low plane grazing area on the same pasture. The area of the high plane group was adjusted after morning and evening milking to allow that amount of grass which would reasonably suffice without waste between each new pasture break.

The low plane group grazing area was similarly adjusted to approximately 40 per cent of that of the high plane area. Generally insufficient grass was available to prevent intense competition between cows for the grazing, in some cases the herbage was grazed to soil level within the hour of first grazing.

A number of different paddocks were grazed in this manner and periodic observations were made by the writer. Varying degrees of bloat on different pastures were frequently observed in the high plane group; no bloat was observed in the low plane group.

Slight bloat was frequently recorded during August in the high plane group on a pasture earlier top-dressed with nitrogen and having the following species composition :--

Species	Per Cent Dry Weight.
Ryegrass	42
Cocksfoot	3
Poa trivialis	26
Brown Top	9
Yorkshire Fog	6
White clover	13
Sweet Vernal	1

During September one very severe attack of bloat was recorded in all cows of the high plane group with no sign of bloat in the low plane group.

The area grazed was composed of the following species:---

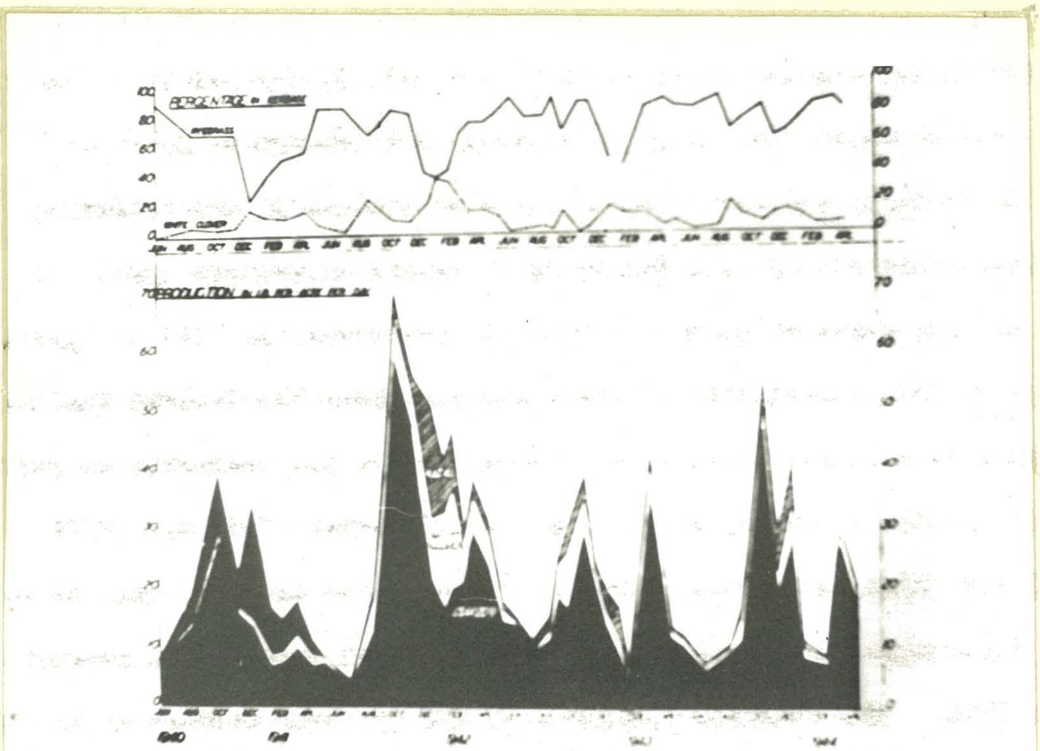
SPECIES	PER CENT Dry weight
Perennial Ryegrass	11
Cocksfoot	33
Goosegrass	1
Prairie Grass	5
Poa Annua	1
White clover	49

These conditions of restricted pasturing were conducive to rapid ingestion by the cows on receiving the new break of pasture, this behaviour as measured by bites per minute, being particularly apparent in the low plane group. As rapid ingestion is so widely reported as being the characteristic behaviour associated with the onset of bloat, (8), (14), (15), (16), (42), (45), (46), (90), (92), (120), (121), it would seem that pasture quantity was the limiting factor in the cases cited. The very high percentage of grass species in the first example quoted is of interest in view of bloat incidence being generally associated with legume dominant pastures. Bloat has been previously reported in New Zealand in cattle grazing pastures which were mainly ryegrass in composition, and stimulated to active growth by nitrogenous manuring Taylor 1940 (93).

The reduction in quantity of herbage available for consumption is the primary difference from free grazing which underlies the system of rationed grazing, recommended as a measure for reducing the incidence of bloat, but as yet to be proved. (19), (38).

If the quantity of pasture available per unit of area grazed should be an etiological factor in bloat, then a high incidence would be expected during the seasonal grand period of herbage growth.

Taylor (93) in New Zealand reports that the September--October period is probably the most anxious time in the year for bloat incidence in the Bay of Plenty region. In the same country Johnson 1950 (94) indicates that the first outbreak of bloat in the Kairanga area occurs with the spring flush of grass during mid- August and continues through September, October,



Graph 2. Ryegrass and white clover. Seasonal changes in growth rate and percentage in herbage. Trial O. Marton.

Fig.I. Note production peaks Sept/Oct.period.
After Lynch (95).

Intake Measurements (Figure 3).

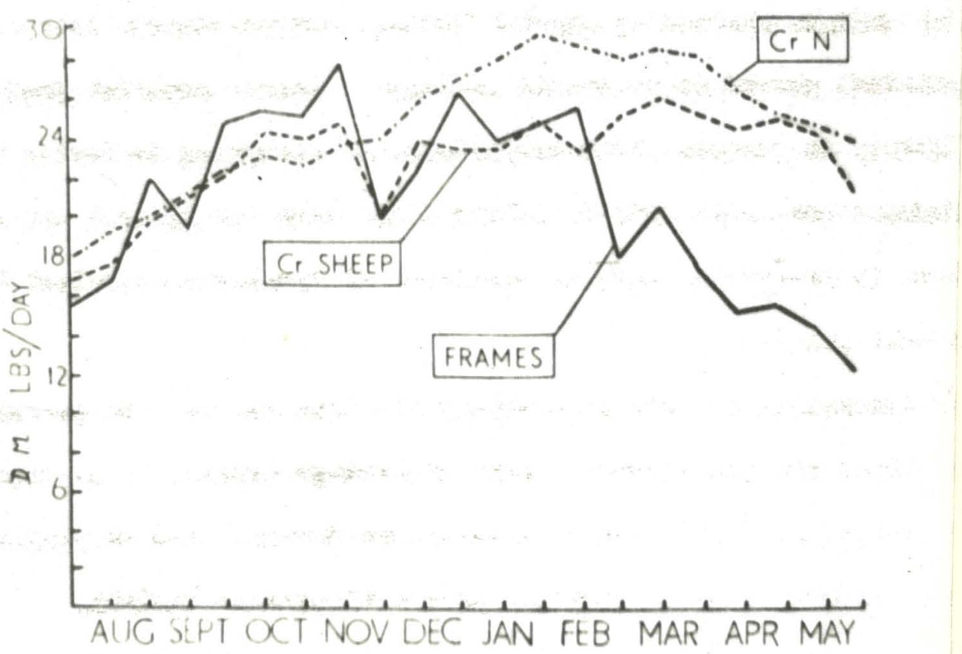


Figure 3 shows the intake of dry matter in pounds per cow per day

Fig.2. After Percival(76).

and sometimes November.

Hudson (55) and Lynch 1949 (95), demonstrate that in general herbage production in New Zealand rises sharply to a peak in the months of September, October, and November, declining in December and January to rise less sharply in February and March before a steady decline in the following months, variation within this depending of course on pasture type. An example of this seasonal growth pattern is illustrated in FIG: 1. Opposite. Pertinent to this association of phenomena are those New Zealand findings which indicate a rising level of dry matter intake for ruminants at pasture during the months of September, October, and November (76). See (FIG: 2). Seasonal variations in pasture quantity available at any one time, in so far as such variations are dependent on the constituent species, is demonstrated by Lynch (95). The evidence presented in the previous section on herbage palatability would suggest that as pastures varied in seasonal growth, and where such variation induced the dominance of palatable species, so conditions conducive to optimum herbage intake would obtain for the grazing animal.

It could reasonably be expected then that those very conditions would be provided by pasture containing species having a comparatively large and rapid vegetative growth of palatable herbage. Legume dominant pastures would be likely to provide those conditions, as according to Davies (67), they maintain a much more uniform palatability than the grasses and continue all the time to produce a relative abundance of fresh and succulent leaves under constant grazing.

This discussion of herbage quantity and type per unit of grazing area, as it may affect the quantitative level of herbage intake, is necessarily of conjectural nature. It seems to emphasise further need of perfecting a technique for measuring the herbage intake of grazing animals.

However, in summarising this discussion, no attempt will be made to criticise either pasture production or herbage intake measurement techniques. Those are self-contained problems which would detract from the main discussion; Their limitations in so far as they affect this summary should be borne in mind.

a) There will be little need for failure to acknowledge that under optimum conditions of pasture growth the quantity of herbage available will depend on the vegetative habit of the contained species.

b) Bloat is most often reported as occurring under optimum /

conditions

of vegetative herbage production and consumption.

c) Where the quantity of herbage available for consumption has been reduced by management factors such as pasture rationing, or restricted grazing time, there have been cases of a reduction in bloat incidence and severity.

d) There is evidence that seasonal peaks exist for the production of herbage, which vary with the vegetative growth of the species components of a pasture.

e) The seasonal incidence of bloat in New Zealand is reported as being highest during the months of peak pasture production. Coincident with this is evidence of rising pasture consumption by ruminants in the same months.

COROLLARY. PART 1.

To this stage pasture has been considered in so far as its various characteristics are likely to be important inter-acting factors with the grazing animal. For this reason an examination has been made of pasture herbage density, coupled with length, its palatability, and the type and quantity of pasture available.

In the micro-environment existent between herbage plants and the grazing animal, the most important single consequence of these interactions is resolved into the amount of herbage removed and consumed by the animal in a given pasturing time.

Evidence of absolute significance is not available to permit a conclusive statement that either of the aforementioned pasture conditioned interactions inhibit or stimulate a particular quantitative level of herbage intake. Nevertheless such evidence presented is convincing in the impression that where optimum conditions of herbage palatability and quantity obtain, compatible with the fully efficient mechanical act of ingestion, then optimum herbage intake in the normal grazing animal will most likely result.

Next, gas formation in the rumen of the grazing animal is a normal biochemical reaction consequent upon the microbial disintegration of the herbage consumed. Quin 1943 (96).

Accordingly then, under the same pasture conditions, those interactions conditioned by the pasture which inhibit or stimulate the optimum level of herbage consumed would be expected to indirectly inhibit or stimulate both the optimum rate and volume of gas produced in the rumen of the normal grazing animal.

In this connection it should be borne in mind that there is strong evidence to indicate that the quantitative level of food consumed in sheep Quin (96), and cattle Cole et al. (51), Washburn and Brodie, (52), is proportionately related to the rate and volume of gas produced in the rumen of the normal stall-fed animal.
Cole et al. (51) have demonstrated that a higher quantitative level of feeding results in a greater rate and volume of rumen gas production than a lower level of feeding.

Such being the case an increasing eructation of gas would be necessary to prevent the building up of gas pressure in the rumen. It would be expected that the onset of bloat would be consequent upon a failure of eructation to cope with gas formation.
Should herbage from different pastures vary in its gas producing potency, then it would be expected that different rates and volumes of rumen gas would be produced in a given time, following the consumption of the same amounts of herbage. That these conditions may prevail is indicated in the work of Quin (96), and Cole and Kleiber (53); These latter workers have found that the same volume of rumen gas, produced by a certain quantity of grass in a given time, is produced by one-third the quantity of lucerne in the same time.

Assuming this phenomenon to be general for all legume and grass species then the same consumption level of herbage on legume dominant pastures, would result in a greater build up of rumen gas pressure in a given time than on a grass dominant pasture.

A situation can therefore be conceived whereby any failure in eructation to keep pace with the removal of rumen gas formed would result in the onset of bloat and the association of its greater incidence with legume pastures.

Further, let it be assumed that those pastures whether grass or legume dominant, having high potency for rumen gas production, attained optimum conditions of palatability, density, and quantity, compatible with the fully efficient mechanical act of ingestion. On such pastures it would then be expected for the optimum level of herbage intake to obtain for the grazing animal, with a minimum time approach to optimum rumen gas production.

The time in which rumen gas production would reach its peak would depend on either the rate or duration of herbage ingestion, in so far as these factors determine the quantity of herbage intake under the conditions assumed. Failure of eructation to remove rumen gas under such conditions would conceivably result in the onset of bloat.

The rumen gas pressure would determine the severity of the condition (25), (115), which would vary from slight to severe bloat, depending on how far the quantity of herbage consumed approached the optimum level.

An examination will follow of the extent to which those interactions conditioned by the grazing animal will be likely to contribute to acute bloat.

BB2. **THE IN SITU INTERACTIONS OF PASTURE AND RUMINANT ANIMAL AS PHENOMENA ASSOCIATED WITH ACUTE BLOAT.**

PART. 2. ANIMAL CONDITIONED INTERACTIONS.

Cattle and sheep are the ruminant animals most widely used under intensive systems of grassland management. Each of these species has habits of grazing peculiar to it.

The difference between and within ruminant species, which constitutes the most important in situ interaction of animal and pasture, lies in the performance of the ingestion act.

It is not unreasonable to assume that the functional nature, efficiency and duration of the ingestion act will determine the quantitative, and in part qualitative level of herbage intake in grazing ruminants.
In turn the intensity of the ingestion act or grazing will determine the degree of defoliation of the pasture or herbage. Thereby an environment will be imposed to which the pasture species may react socially or vegetatively in such manner as to completely change the nutritional environment of the grazing animal.
This is better visualised in the following description of the ingestion act in grazing cattle by Johnstone-Wallace (58),...." It is a mechanical process involving the severing of the leaves and stems of grasses, legumes, and weeds, with the two jaws of the animal measuring on an average about 2½ inches across and having one row of teeth in the front on the lower jaw. A muscular pad on the upper jaw pressing against these teeth enables the tearing action to take place. The tongue is in constant action during grazing usually being protruded with great rapidity alternately from either side of the mouth. Its function would seem to simplify the collecting process as well as the swallowing process. The procedure differs between short and tall herbage; in the latter case it is much slower because of the mechanical difficulties associated with collection, the time being increased by selection and manipulation".

According to Tribe (85) the ingestion act in sheep involves less of a tongue and more of a biting action by the jaws which together work very close to the ground, providing a functional aperture of 1¼ inches in diameter.

Under constant pasture and unrestricted grazing conditions, differences either of duration or rate of the ingestion act performed by the normal ruminant may be fairly attributed to variable underlying physiological causes.

Most important to this discussion are the variations in the ingestion act arising from the systems of animal grazing management imposed, particularly as those variations may influence the quantitative level of herbage intake. The implications of herbage quantity in contributing to rate and volume of rumen gas production have been previously intimated.

A further factor which needs now to be considered is that the grazing ruminant may also influence the qualitative level of pasture intake by reason of herbage selection. In addition, dominance in a pasture of one or a number of herbage species varying in carbohydrate and protein content may be induced by grazing.

This qualitative factor arising from animal pasture interaction is of considerable importance, for, as will be shown later, the carbohydrate and protein level of the diet most probably stimulates the fermentation activity of rumen micro-organisms.

Therefore those animal pasture interactions conditioned by the animal and pertinent to this discussion will be treated in the following manner:----

B. Ruminant grazing behaviour as it may influence feed consumption.

C. The grazing ruminant's influence on pasture composition.

B. RUMINANT GRAZING BEHAVIOUR AS IT MAY INFLUENCE FEED CONSUMPTION.

At the outset it will be as well to reiterate that no known technique is available whereby an exact measurement of herbage intake by the grazing animal can be made.

Nevertheless Hancock (60), considers that while feed intake probably provides the best single index of a grazing animal's reaction to its environment, it seems certain that studies of the grazing behaviour of an animal can help to explain in rational terms its health and productive performance.

Although there is a paucity of literature dealing with grazing behaviour particularly of detailed nature, the importance of such studies is stressed by a number of animal and grassland authorities. Stapledon (62), and (101), Hammond (102), McMeekan (103).

Generally the technique adopted for grazing behaviour studies involves the recording of the various activities of the animal over a certain time period.

The main concern in this discussion are those aspects of behaviour most closely associated with herbage intake and liable to be predisposing factors in the onset of bloat. They will be considered as follows:-

a) Grazing activity, its duration and rate.

b) Herbage selection by the grazing animal.

c) Grazing activity and the onset of acute bloat, with an example.

d) Seasonal grazing activity.

a) GRAZING ACTIVITY.

The grazing activity of ruminants at pasture is expressed in the ingestion act, which may be measured as time employed in the act, or grazing time, as well as in terms of bites per time unit.

Limited studies have been concerned with the first measurement, and less with the second. Most of the investigations have been carried out with grazing cattle.

Hodgson, 1933 (105) reported that Holstein cattle under a system of rotational grazing grazed for $6\frac{1}{2}$ to 7 hours daily, whereas under continuous pasturing they spent 7 to $7\frac{1}{2}$ hours grazing. His observations were made only during daylight from 6 a.m. onwards.

Atkeson et al. 1942 (104) used a limited number of dairy cows and made their observations only during the 12 daylight hours. They found that milking cows on good pastures grazed for a shorter time than cows on poor or medium pastures; dry cows and heifers grazed for 7 hours.

Johnstone-Wallace et al. (58) observed in detail 4 nursing cows of a beef breed on four 24 hour periods and concluded that they grazed on an average for approximately $7\frac{1}{2}$ hours.

Seath and Miller 1946 (106) investigated the influence of temperature on the grazing habits of diary cows and concluded that hot weather (85 - 86° F maximum) lowered the grazing time by one hour compared with cool weather (72° F maximum). Such conditions also altered the ratio of $\frac{\text{day grazing}}{\text{night grazing}}$ from approximately $\frac{1}{1}$ during the cool days to approximately

1/3 during the hot days.

Hancock and Wallace 1947 (107) observed the grazing behaviour of 6 sets of Monozygotic Twins for six complete 24 hour periods at monthly intervals, through the main lactation season and found that on an average 34 per cent of the available time was spent in grazing, or 7 hours in each period of 24 hours. Hancock 1950 (60), more recently states that given a fresh pasture each day lactating dairy cows graze if necessary up to 10 hours as an average for a herd while individual animals may reach 12 hours per day.

Referring to the time distribution of grazing activity Hancock (108), (in press) found that slightly less than 60 per cent of the grazing time was spent between 7.a.m. and 3.p.m. and slightly more than 40 per cent between 5.p.m. and 4.45.a.m. This ratio being fairly constant under all weather conditions. Grazing time was measured as a minute in which 15 or more bites were taken, and this data was obtained in six sets of monozygotic twins over 8 days at approximately monthly intervals.

When available time was divided into day and night periods, 85 per cent of the total grazing time was spent in daylight and 15 per cent in darkness. It was noticed that cows were conditioned to stop grazing soon after darkness fell. This habit was broken when the hours of day-light became so short that the cows did not have time to satisfy their appetites during the period, and therefore extended their afternoon grazing beyond nightfall.

Hancock (60), concluded that poor pasture conditions induce longer grazing and ruminating times in cows than when conditions are optimal for quantity and quality of herbage. When cows are grazing good pasture in the same enclosure during the day and night, the day / night grazing ratio averages 60: 40; on a quantitatively poor pasture the ratio becomes 75: 25.

Warm weather (temperature of 75° F or over) caused discomfort to the cows and was considered to effect a break in afternoon grazing periods before milking.

Time studies for grazing activity in sheep are very limited. Tribe (85) considered the behaviour of one sheep was representative of a group. From a series of 24 hour observations over a year it was found that less time in the summer was spent in grazing in the 7.00 -- 19.00 hour period than during the winter months. For the 19.00--7.00 hour period the opposite was the case. The reason was considered due to the longer daylight period and excessive summer heat.

It is interesting to note that the findings of widely dispersed workers place the duration of grazing activity in cattle between $6\frac{1}{2}$ - $7\frac{1}{2}$ hours. It has been suggested that there is experimental basis for expecting a strong relationship to exist between the time an animal spends grazing and intake of herbage dry matter under constant pasture conditions, Hancock 1948 (109). There is no published evidence to support this suggestion, and the experimental application of this concept would require control of the ingestion rate as well as quantitative and qualitative control of pasture.

Nevertheless, it can readily be conceived that reduction in grazing time of sufficient proportion, under the same conditions of pasture, would lower the quantitative level of total herbage intake. This would be expected to apply even where the quantity of herbage available was at an optimum level compatible with maximum efficiency of ingestion in terms of quantitative consumption. Similarly an increase in grazing time under the same conditions would be expected to raise the quantitative level of total herbage intake provided the efficiency of ingestion remained constant.

The cyclic nature of grazing activity is a striking characteristic of ruminant behaviour at pasture.

Atkeson et al. (104), noted that the grazing habits of cattle from day to day were quite uniform, there being 4 primary grazing periods during the day, and two during the night, the latter periods being less pronounced. This cyclic grazing pattern is reported in beef cattle (58), and sheep (85). For dairy cows Hancock (108), recorded 6 cycles of grazing, 4 between morning and afternoon milkings, 1 immediately after 5 p.m. pasturing, and 1 (sometimes 2) during the night. During an observation period when all the cows were dry, it was found that this cycle was still maintained. A finding of particular interest is that the two periods of grazing following the enforced periods of loafing during milking were generally the longest.

By experiment it has been shown that a time factor operates for the consumption of a given weight of a given food, Schalk and Amadon (61), Harshbarger 1949 (110).

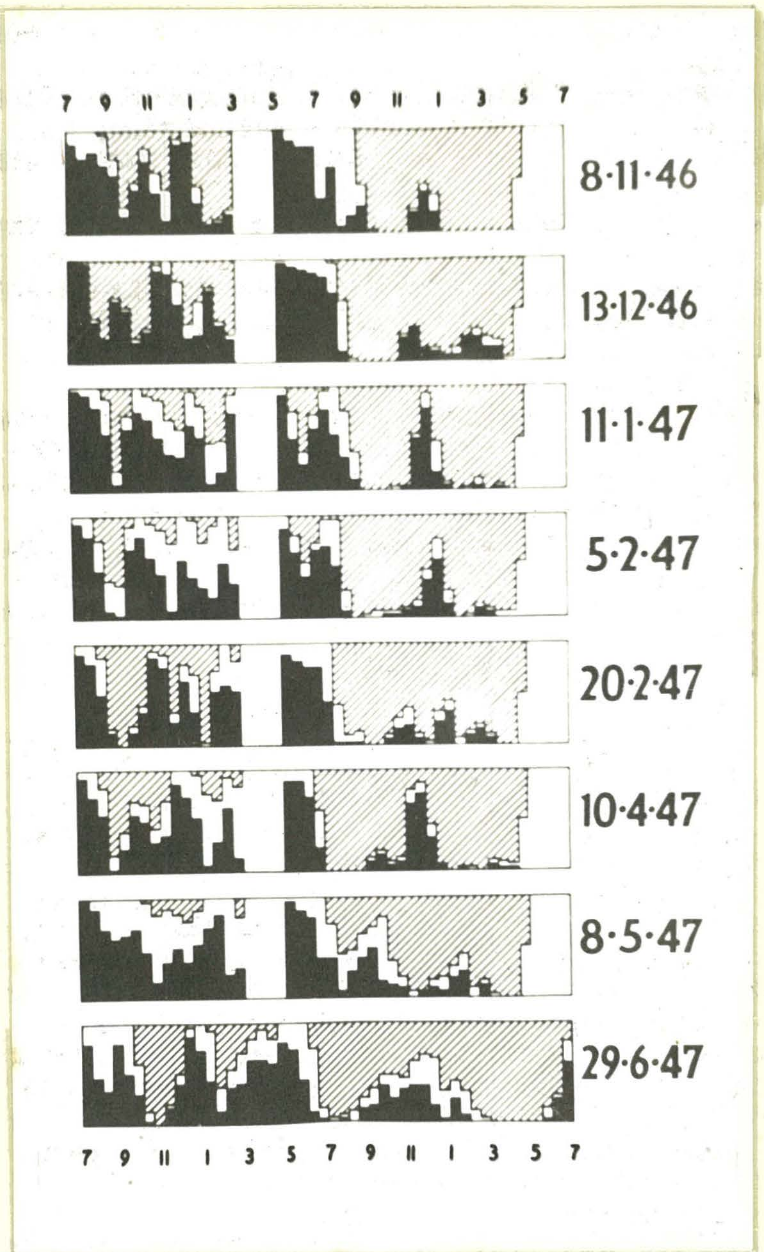


Fig. 3. Distribution of Dairy cow grazing behaviour.
Grazing (black), loafing (white), lying (diagonal lines).
Note cyclic nature of grazing and longest periods after a.m. and p.m. milking.
Cows were dry during the period 29/6/47.
After Hancock (IO9).

The foregoing discussion on grazing time would therefore suggest that the longest grazing periods after milking would be those in which a relatively higher herbage intake would obtain on the same day of grazing the same pasture.

The duration and distribution of grazing activity is illustrated in FIG: 3.

Before any value can be attached to conclusions based on studies of grazing activity, the range of variations between cows on the same days should be known. Among those studies quoted no data of that nature is presented except by Hancock (108). This worker showed that the differences within 6 sets of monozygotic cattle twins for the time spent in grazing averaged only 4 minutes over seven 24-hour observation periods at monthly intervals.

The difference between sets of twins for grazing time was very great, amounting to a range of 138 minutes. An analysis of variance for grazing time showed the differences between twin sets to be significant at the 1% level, and of the total variances for grazing time, nearly 90% were due to between-set differences.

It was considered that as far as the cow's behaviour pattern on pasture depends on her individuality, this is mainly reflected in the time she requires to spend grazing.

A further measure of ruminant grazing activity is to be found in the number of bites per time unit. Johnstone-Wallace (58), reports that nursing beef cows were observed to take on an average from 50--70 bites per minute but occasionally under very favourable conditions as many as 90 bites per minute were recorded.

Cochrane 1948 (111) questions the possibility of variation in grazing rates between cattle, and reports an observation of one cow grazing at 80 bites per minute whilst others grazed at half that rate.

Hancock (60), gives a caution for quoting grazing rates if they have not been made over long periods in the day, as great variations occur throughout the 24 hours, the grazing rate being highest at the beginning of a grazing cycle followed by a continuous steep drop towards the end.

Data obtained for the speed of grazing is given by Hancock (108) for two sets of Monozygotic twins observed over a 24-hour period. The total bites averaged 23,966, and the average bites per minute 51, for the 24 hours.

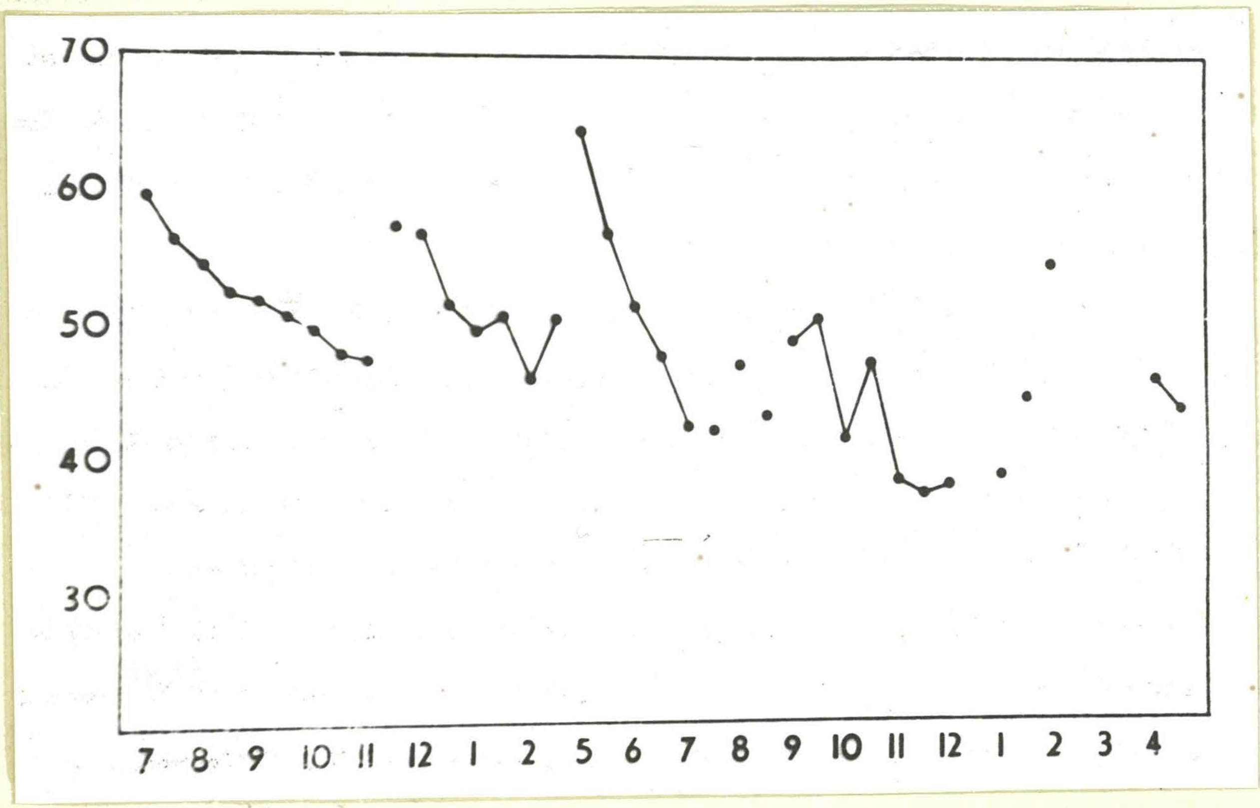


Fig.4. Shows the distribution of the rate at which dairy cows graze(bites per minute).Note that the rate was highest immediately after the morning and evening milking.i.e.7a.m. and 5p.m. respectively.
After Hancock(I09).

A cow grazing at this rate obtained only 3 grams per bite assuming a daily intake of 70 kgm of grass, which figure accords with findings at Ruakura, New Zealand. On this assumption it was suggested that a cow can not only select a specific area for grazing, but particular pasture plants in an area. The highest grazing rate was most pronounced at the beginning of those grazing cycles immediately following milking. Fig. 4.

There was a large difference between twin sets for total bites per day, but this was due to the time spent grazing, and not in rate of grazing which was similar for all cows.

It has been previously indicated (58) that the intake efficiency of the ingestion act may be impaired by long pasture of low density, resulting in fewer bites per minute.

The need for pasture conditions to permit full intake per bite is recognised by Stapledon 1948 (101) who states that if the animal is limited in its intake by the number of bites it is good for in 24 hours, it is obvious that the average intake per bite must not drop below a certain minimum weight or it will go short.

More recently Johnstone-Wallace 1950 (125) points out that a cow can either bite into the sward from the top to a depth of about 4 inches, in which case the lack of density at the height results in a very small intake per bite, or she may put her nose well into the bottom of the sward and with the aid of her tongue tear off a large bite of tall herbage.

Unfortunately, such large bites cannot be swallowed without considerable manipulation. The head is raised and a period of about 30 seconds may be taken to complete the manipulating and swallowing processes.

In the meantime, a cow on a 4-inch sward may gather 30 bites containing more herbage than one large bite, and this usually consists of herbage of a higher feeding value. Hancock (60) has also indicated that grazing efficiency may be lowered by a smaller intake per bite on pasture of low quantity and quality. This worker points out that a variety of anatomical features such as narrowness and shortness of the lower jaw may result in a low grazing efficiency.

An example of this may be evidenced in those observations made by the writer in the spring of 1950 referred to on page 28.

A group of lactating monozygotic twin cows were under observation for bloat incidence at the New Zealand Dairy Research Institute farm. The grazing activity of each cow was measured by the number of bites per half minute at 6 minute intervals over a one hour period. The average number of bites per half minute recorded for each cow during the period was as follows :--

Cow number	T90	T26	T54	T72	T25	T53
Average bites	29	36	34	17	34	33

The grazing activity of cow T72, although steady, appeared to be less than the other cows in the group, marked selective preference being shown for the longer herbage. An examination of the cow's mouth at the end of the period revealed two deformed first incisors and a severely abscessed gum; the twin to T72 was found to be similarly deformed.

There would be every reason to believe that under quantitatively poor pasture conditions the grazing efficiency of T72 in terms of herbage consumption would be seriously impaired, although to outward appearances the grazing activity did not appear abnormal.

Although the probability that variations in grazing duration and rate influence total intake levels is generally acknowledged, there is no supporting experimental evidence. The probability is strengthened however by the findings of Schalk and Amadon (61), with stall fed fistulated cattle. These workers removed food boli at the cardia as they were projected into the stomach, and weights were recorded. It was reported that a rapid ingestion rate resulted in a greater weight of food entering the rumen in a given time than with a slow ingestion rate.

After a 24-hour fast one cow was evidenced as ingesting 30 boli of lucerne in the first 5 minutes, and 19 boli in the succeeding 5 minutes of feeding. The rate of ingestion was depressed by increasing satiety, unpalatable food, and an increase in rumen volume; the latter factor also reduced the time period of ingestion.

To epitomise then, the grazing activity of ruminants as an animal-conditioned interaction which may influence the level of feed consumption.

a) Ruminant grazing studies contribute to a fuller understanding of in situ animal-pasture interactions, of which grazing activity is the primary interaction conditioned by the animal.

b) There is general agreement that $6\frac{1}{2}$ - $7\frac{1}{2}$ hours daily is the average duration of grazing activity of free grazing cattle. Individual animal and herd variation occurs.

c) There is strong evidence which indicates that as far as the behaviour pattern of a cow at pasture depends on her individuality, this is reflected in the time she spends grazing.

d) There is evidence that grazing is primarily a diurnal activity in cattle.

e) Grazing activity forms a cyclic pattern throughout a 24 hour day in cattle and sheep.

f) Wide variation in the rate of grazing has been found to occur in dairy cattle throughout a 24-hour day.

g) Differences in grazing rate (bites / min:) occur between individual cows at pasture.

h) The rate of grazing in dairy cattle is evidenced as being highest at the beginning of a grazing cycle.

i) In dairy cows there is evidence that the rate of grazing is highest at the beginning of the grazing cycles following milking.

j) There is no absolute evidence that the rate and duration of ingestion in ruminants at pasture influence the quantitative level of herbage intake.

k) There is evidence in stall fed cattle that the time period of ingestion varies with the same weight of different foods. Further, that a high rate and low rate of ingestion results in the intake of greater and lesser weights respectively of the same food.

b). SELECTIVE GRAZING HABITS.

The extent to which selective habits enter into grazing activity is necessarily a conjectural aspect of ruminant behaviour at pasture. It is none the less one which is important, as it may readily be conceived that variations occur between and within ruminant species in the degree of selectivity and preference for plants selected which variations would be expected to influence both the quantity and quality of herbage intake.

According to Stapledon 1948 (101) the sheep is more refined in its ability to select than the bovine; the sheep selects both individual plants and patches of pasture whilst the bovine selects in patches. Assuming an intake of 3 gms. per bite Hancock (108) suggests that the cow can be highly selective both in respect of a specific grazing area and particular plants.

Tribe 1949 (112), investigated the influence of the sense of smell on food selection by sheep using Cheviot lambs deprived of the sense of smell by removal of the olfactory lobes. It was found that when different herbage species or mixtures of species were fed to normal and smell-deficient lambs in the absence of accompanying smells, no difference between their selection of different species was recorded, but the normal sheep ate greater quantities of each species. The normal group showed greater initial discrimination in selection for fresh cut as against 2 day old herbage samples. This reaction was shown when a standard herbage sample was fed in the presence of a variety of very characteristic smells. It was concluded that sense of smell was only of supplementary importance in food selection by grazing sheep.

Davies (67), reports that sheep prefer to eat plants in a young stage of growth and suggests that it was merely coincidence that the young herbage was more nutritious. The succulence of a plant was considered important for its selection which accords with the opinion of other workers (58), (25).

It has been intimated that herbage selection habits of sheep (85) and cattle (58), may be conditioned in large part by the mechanical functioning of the ingestion act.

The fact that some Monozygotic cattle twins select the grass they eat to a greater degree than others is considered by Hancock (60) to contribute to low grazing efficiency causing a lower intake per grazing time unit. Supporting evidence is based on subjective observation and the fact that a) differences in speed of grazing (bites / min:) have been demonstrated to occur between sets of twins and b) the ruminating grazing time value is a characteristic specific to each set of twins.

The latter piece of evidence is open to question as it is probable that other factors such as differences in digestion can cause differences in the ruminating grazing time values even if the twin sets have consumed grass of similar quantity and quality. This worker discusses the conjectural consequences of selective grazing and considers that under mixed pasture conditions the unselective grazer will obtain a full food intake in a shorter time than the selective grazer.

Arising from this supposition the writer would suggest that the intervention of selective habits in grazing activity may be contributory to a longer time onset to acute bloat. The unselective grazer on a bloat provoking pasture would be expected to consume a greater amount of herbage in a shorter time as well as to display a rapid grazing activity, which latter factor is often reported as associated with acute bloat incidence. (44). (51). (15). (27).

In this connection, Gould 1948 (113), cites an interesting case of the onset of bloat in a dairy herd in England. He formed the view that a psychological factor had arisen in consequence of gradually reduced grazing time, which management had dictated as essential to control bloat and states :--- " Starting with an hour and a half,---clovers preponderating in the sward --- by the time opportunity of selective grazing had passed cows were becoming blown in 20 minutes of grazing. Removal to another pasture containing somewhat less clover of the same type- S 100 - did not succeed for more than a few days. The time for which the stock could safely graze, rapidly came down to 20 minutes, and even then some cows became blown. Observation of behaviour showed that directly the cows entered the ley they grazed as hard as they could moving the shortest possible distance and never lifting their heads to swallow or belch". Changes in herd management resulting in a return to selective grazing behaviour, prevented further bloat incidence although the same pastures were grazed day and night."

The implication is then that selective behaviour was inhibited by restrictive pasturing practices resulting in a more rapid unselective grazing activity and reduced time onset to bloat; this is in accord with a similar observation by Bathe 1948 (24). It would appear that any account of selective grazing behaviour in dairy cattle needs to be related to the management practices imposed.

Ferguson 1948 (114) in England, implicates a high degree of qualitative herbage selection as ultimately contributing to bloat causing death in 2 Jersey cows grazing a new spring pasture.
The herbage consisted almost entirely of S 100 white clover " the grasses having been eaten out". Ferguson suspected that the cows grazed little clover until the grass was finished and the clover ingestion brought on bloat. It is difficult to conceive such a high degree of selection by

cows between grasses and clovers at the dense stage of pasture growth usually associated with the spring months in England.

Johnson (94), reports that dairy cows break-fed pasture highly conducive to bloat never at any time grazed clover in preference to grass. In contrast Cole et al, (25), attribute a reduction in bloat incidence to the tendency of cattle to select considerable amounts of a coarse seemingly unpalatable weed (Polygonum aviculare)on first grazing an abundant pasture of succulent lucerne. Bloat incidence followed upon a reduction of the weed by grazing. No indication was given of the cows' grazing activity or the extent to which lucerne was consumed during the grazing period.

In the absence of specific work dealing with the selective habits of grazing ruminants, the writer submits the following tentative suggestions assuming such habits exist.

a) Selective grazing habits in so far as they influence the quantity and quality of herbage intake will probably be subject to wide variation depending on pasture conditions.

b) The unselective grazer would be expected to obtain a full herbage intake in a shorter time than the selective grazer.

c) The degree of selection exercised will probably be conditioned by animal management practices. Where they restrict or delay grazing, selective behaviour would probably be inhibited.

d) Bloat is most often associated with rapid ingestion or unselective grazing activity.

e) Under pasture and management conditions conducive to bloat it would not be improbable for the time onset to bloat to be shortest for the unselective grazer, accentuated where conditions in c) obtain.

c). GRAZING ACTIVITY AND THE ONSET OF ACUTE BLOAT, WITH AN EXAMPLE.

The writer submits that the onset of acute bloat is manifest in ruminants immediately following a certain grazing time and is a direct outcome of a certain quantitative intake of that herbage conducive to bloat.

As both duration and rate of the ingestion act are known to determine the quantitative intake of the same food in cattle (61), it is necessary to examine the time and rate of grazing as those aspects of behaviour most closely associated with acute bloat.

That the behaviour of the animal may constitute a determining factor is suggested by Quin (27), who refers to the fact that certain individuals are more subject to bloat than are others feeding the same material. Likewise he notes that ravenous feeding in hungry animals frequently precipitates the condition.

An examination of the grazing time associated with the onset of acute bloat is of particular importance in view of that evidence which indicates a phenomenal rise in gas production in cattle (51), (53), (52), and sheep (96) in the first 30 minutes after commencing to feed grass and lucerne. (See FIGS:17^2 to 21^2 PAGES: 121 to 125.)

Cole et al. (25) studied the production and prevention of bloat in dairy cattle grazing thick stands of immature lucerne 8 to 14 inches high. They recorded bloat by visual inspection and palpation of the triangular area in the left flank. Three degrees were recorded, slight, marked, and severe. In one cow recorded as markedly bloated, the rumen pressure was determined by connecting a manometer to a cannula inserted in the rumen and found to be 20 m.m. Hg. " Slight " bloat was never recorded unless gas could be palpated. Severe bloat being marked by distress, frequent urination, defecation, and a ruminal pressure of 45 -- 70 m.m. Hg. (115).

These workers give 2 hours 28 mins as the average grazing time after first pasturing, recorded over 6 days on which severe bloat occurred in 16 cows on each day. The average grazing time was 2 hours 32 mins. for all degrees of bloat over 9 days on which bloat was recorded in 42 cows. The case is instanced in which 10 of 17 cows bloated after 2 hours 45 mins on pasture. It should be noted that these figures are for average grazing time and do not necessarily indicate the time at which bloat was first manifest.

In the experience of Cole et al. no cow bloated until having been at pasture at least 1½ hours; occasionally some did after 7 hours.

General observation in England gives some indication of the time onset to bloat. Johnstone-Wallace (6) refers to the onset of severe bloat in a dairy herd 1 hour after commencing to graze a pasture of Aberystwyth S.23. perennial ryegrass and New Zealand white clover.

Bathe (24) cites the case of a dairy herd restricted to 1 hour of grazing a pasture conducive to bloat, in which bloat occurred within the hour; the operation of a similar time factor has been observed by the same writer in a New Zealand dairy herd. (See Appendix)

Gould (113) reports only 20 minutes of grazing on S 100. white clover dominant pasture as being the safety margin in one case in which dairy cows could be permitted to graze, and even in this time bloat occurred.

One observer reports (36) 25 out of 80 heifers being blown, two of which died within half an hour of grazing on cocksfoot and S100 white clover sward. Bloat causing the death of 7 dairy animals in approximately a half an hour after pasturing is noted by Hall 1945 (116).

Mead et al. (15) in America, found that feeding grain 1 hour before pasturing lucerne induced the onset of bloat in an average of 1 hour 6 mins. for 9 cows over 2 days, as compared to an average time onset to bloat of 3 hours 12 mins. over the preceding 11 days during which bloat occurred in the same cows, without supplementary feed on the same pasture.

Evans and Evans 1948 (117) attempted to produce bloat in 3 Welsh Black cattle (2 heifers and 1 bullock) by starving for 12 hours prior to grazing a predominantly white clover pasture. They state that the animals grazed the clover avidly for the first 15 minutes ignoring all other herbage offered; the two heifers then stopped abruptly, stood listlessly for a while before searching for rough herbage which they selectively grazed. Within a period of 30 minutes (i.e. 1 hour after commencement of grazing) the bullock showed definite distress symptoms, was breathing rapidly, and was slightly bloated. The heifers were not blown and showed no such definite signs of discomfort.

In view of the preceding discussion on selective grazing it is interesting to note that the heifers continued grazing selectively, but these workers do not indicate the nature of that grazing.

Several observers report the onset of bloat in dairy cattle within a half an hour after depasturing (37) (118).

In the experience of Cole and his co-workers, (cited by Cole et al.(9)) rarely does bloat develop later than 1 hour after removal of cows from alfalfa pasture.

Cole et al. (51) give data on the time onset to bloat during gas formation studies in a ruminal fistula cow. They state that the gas meter was connected at 6 a.m. On the previous day the cow had received 71 pounds of green alfalfa. At 8 a.m. she was given 37 pounds of green alfalfa and at 8.50 a.m. had comsumed 15 pounds. Between 8.30 and 8.50 a.m. the glass tube leading to the rumen became partially plugged and at 8.50 a.m. the cow was distinctly bloated and uncomfortable.

Quin (96) reported definite evidence of increased intra-ruminal pressure in fistulated sheep immediately after a meal of lucerne, which pressure was not apparent several hours after the consumption of lucerne.

Observations were made by the writer (See Appendix) on a dairy herd in which bloat incidence was high when grazing the same mixed pasture of ryegrass, cocksfoot, red and white clover. One lactating dairy cow was selected for close study; the animal was usually the first, but not the only animal in the herd to become blown.

Over 12 days on which bloat was recorded during 12 grazing cycles, the average time onset to bloat to the 3 stages of bloat recognised (25) is summarised in TABLE. 3.

Table 3.

Average time onset to Bloat over 12 days on which bloat occurred on the same pasture, in Minutes.

DEGREE OF BLOAT.		
SLIGHT.	MARKED.	SEVERE.
48.	64.	71.

Each of the 12 grazing cycles was the first cycle to follow morning and evening milking.

It would seem that the duration of grazing those pastures conducive to bloat has some bearing on the onset of the condition. The writer submits that the most probable explanation is that the duration of grazing is associated with a certain quantitative level of herbage intake.

Cole et al. (9) draw attention to the relation between eating and gas production in the rumen which they consider of great practical importance. They suggest that it affords an explanation as to why cows usually bloat while on alfalfa pasture or shortly thereafter.

If the duration of grazing should be an important factor associated with the onset of bloat, how much more so would be the rate of grazing? This question is raised since an increase in rate of ingestion of the same food activates an increase in the quantitative level of intake in a given unit of time. (61). There are no studies known to the writer which are concerned with the rate of grazing during the onset of bloat.

Worthy of note however are the widely dispersed and numerous reports which associate rapid grazing with the incidence of bloat.

Begg (8) considers one of the etiological factors in bloat is excessive feeding following a period of starvation and suggests care in feeding clover and lucerne. Kephart (44) concluded from a bloat survey that the condition occurs most readily when the animal is hungry. Quin (14) recommends keeping hungry animals from gaining access to lucerne and suggests that lambing ewes and dairy cows may be more prone to bloat due to a higher level of appetite. The same worker (27) notes that bloat in fat lambs on lucerne was associated with ravenous consumption, being more evident in ewes showing a keen appetite than among others feeding less greedily.

Mead et al. (15) state that greedy feeders are more susceptible to bloat than less greedy, this fact doubtless explaining the greater susceptibility of lactating as compared with dry cows. All classes of cattle are susceptible to bloat however, and deaths are reported in dry as well as lactating dairy stock (24) and beef cattle. (86). (87). Support to the view that dry cows seldom bloat is given by Jacobsen, Espe, et al. (89) who consider it is really the milking cow, or growing animals with large appetites, that gorge themselves and bloat.

The reason given for using lactating cows in the gas formation studies of Cole et al. (51) was that they had greater appetites which would allow maximum food consumption, since it is under this condition that bloat is most frequently encountered.
Losses in dairy cattle from bloat and not in bulls and young stock grazing the same pasture are reported by Gandy (32). This observer associates

Such losses with the time break away from pasture during the milking period. Suggesting a possible explanation for this observation, Filmer (5) states that the cows may eat faster when they go back to pasture than they normally do. This suggestion is interesting in the light of that evidence which shows the rate of grazing as being highest at the beginning of the grazing cycles following milking. (108).

Bathe (24) records the evening period of grazing following milking as being the most dangerous for lactating cows on pastures conducive to bloat. Whilst general observation would suggest that bloat in dairy cattle occurs most frequently in the first grazing cycle following milking, on pastures conducive to bloat, it does occur frequently at other grazing periods during the day when a lower rate of grazing would be expected. This seeming distribution of incidence throughout certain times of the day however can only be established from a detailed investigation or survey. The practical implications of such information for evolving preventive management are obvious.

McIntosh (48) notes that if cows are kept too long in barns after milking they may eat much more on being returned hungry to lucerne and will be liable to bloat. Olson (31) in America reports from a wide survey that among the causes of bloat is the turning of hungry cattle on to legumes to gorge, resulting in too rapid and too large a consumption of green food. He states that bloat was most frequent in May and June, and between 4 p.m. and 7.p.m.

It is interesting to speculate on the effects on grazing activity of temperature (106) and light (108) under the observed conditions.

Ravenous grazing on first pasturing, followed by a diminishing rate, is recorded in the experiments of Evans and Evans (117). Of the three animals observed however, only that animal became blown which continued grazing at a steady rate for a short period longer than the others.

Jacobsen et al. (89) unsuccessfully attempted to induce bloat by turning dairy cows into a field of young alfalfa. They state that the cows refused to eat alfalfa for any extended time with the result that the conditions favourable for bloat could not be obtained. They noted however that the cows were eating the fresh alfalfa at the rate of one pound per minute, whilst the best rate at which they ate good bluegrass pasture was one third of a pound per minute. They explained this difference in ingestion rate as being due to the fact that fresh alfalfa is more or less pinched off by the cow in grazing while bluegrass must be gripped firmly and the grass cut off against the sharp edges of the lower teeth. Whilst these workers consider this type of behaviour underlies the cause of bloat on alfalfa pasture, no experimental data with bloat cases are presented to support this theory, nor are many of the supporting statements documented.

The need for herbage to be at that stage of development which permits optimum intake is suggested by Cole et al. (25), who recommend a thick stand of alfalfa suitable for rapid ingestion, as being among the conditions necessary for producing bloat experimentally.

Differences in the rate of grazing between animals have been shown to occur (108) but although bloat is more common among fast eaters it has been observed among slow ones. (15), (119).

Apart from the reports cited there are many others which make particular reference to rapid grazing as being the most characteristic feature of behaviour in those animals suffering from acute bloat. (16), (42), (45), (46), (90), (92), (121), (120).

So much for the evidence available giving some indication of the animals' grazing activity under conditions conducive to bloat.

To the writer who has observed the condition under widely differing systems of pasture management in England, France, Switzerland, Australia, and New Zealand, there would appear to be more than coincidence in the emergence from the reports cited of a common pattern in pasture conditions and grazing behaviour, implementary to bloat.

More than a pattern is necessary however upon which to base critical and constructive thought.

At the present stage of our knowledge conflicting opinions exist as to the precise manner in which bloat in grazing ruminants is manifest. Furhher confusion is added by the difficulties of producing the condition experimentally in grazing animals.

Doak 1950 (private communication) bears out this variance of views following recent discussion of the problem with British workers. Referring to the opinions of those workers on physiological phenomena implicated in bloat, Doak states that few workers believe the trouble to be caused by excessive gas formation, as animals should be able to get rid of gas by belching. The writer considers it pertinent to pose the question: Is it known that the eructation mechanism can act at sufficiently high frequency to efficiently remove against active oesophageal peristalsis, the excess gas formed during rapid grazing?

Dosk further states that differences of opinion exist as to when (or if) ruminal movements stop during the onset of bloat, but some workers are quite emphatic that these movements take place for some considerable time after pressure is apparent.

Now the investigation of these facts alone is vitally important, for, as will be shown later, the dysfunction of the aforementioned phenomena during the onset of bloat is implicated in certain hypotheses which form the basis of recent research projects by Ferguson (114), Evans and Evans (117) and Phillipson. (126).

That such hypotheses may be ill-conceived, assuming as they do the existence of conditions which may not obtain, is questioned by Anderson 1948 (127) from his clinical observations in the field.

The writer considers that close observation of grazing animals may assist in small part, to lend order to the confusion of thought that exists. For example, along with detailed studies of grazing activity, the existence or otherwise of rumen movements during the onset of acute bloat may be established. This can be done visually, by palpation, or by auscultation, the importance of this latter method being emphasised by Hoflund 1940 (128), as an aid to diagnosis.

The relationship between grazing activity and the onset of bloat, if any, can also be investigated, which is virtually a time study of ruminal gas formation as each degree of bloat represents certain rumen gas pressures. (25), (115).

Although of simple conception the application of grazing studies to bloated ruminants is solely dependent upon the co-existence of the almost entirely fortuitous circumstances which give rise to the condition. Studies are hindered by the variable incidence of bloat, which may be higher one day and fail to occur the next day on the same pasture.

AN EXAMPLE: OF GRAZING ACTIVITY AND THE ONSET OF ACUTE BLOAT.

As far as is known no detailed studies exist of grazing activity concomitant with the onset of acute bloat. Nevertheless the individual behaviour of the animal is considered to be important. Phillipson 1946, (121), has stated that greedy feeders eating more rapidly might well produce a more intense fermentation than animals which grazed steadily but slowly, and had a better chance of keeping pace with the products of digestion.

Cole et al. 1943 (25) state that if bloat can be prevented in susceptible animals the less susceptible may also be protected, and the former should be used as a measure in preventative studies.

Ferguson 1950 (120) supports this view and recommends using bloat-susceptible animals as a measure of the bloat propensities of a pasture, and suggests that such animals are generally greedy feeders.

Relevant to this discourse is an account of grazing activity studies and the onset of acute bloat, made by the writer using a bloat-susceptible dairy cow.

During January 1950 a report was investigated of bloat incidence in a dairy herd located in the Ruahine Street area of Palmerston North in the Manawatu County. Conditions were favourable for a detailed study to be made and the following record resulted.

<u>General Conditions.</u>

The herd comprised 17 lactating Jersey cows, which with one exception had all been subject to bloat during 1949 in the months of October, November, and very occasionally in December. Particular susceptibility of individual animals had been noted.

Free grazing management of the herd was practised in paddocks of 1 - 3 acres in area. Pasture was grazed as it became available and herd pasturing time was restricted on these pastures conducive to bloat. Approximately 4 - 6 lbs of brewers' grains were fed to each animal whilst milking.

As a rule the herd was pastured each day at approximately 7 a.m. and 6.30 p.m. following morning and evening milking.

The pastures which overlay recent alluvial river deposits varied in quantity of herbage available according to the grazing management imposed. Throughout these studies weather conditions generally were favourable for active herbage growth.

Method.

A preliminary observation was made on the 15th and 16th of January.

Commencing with pasturing after the morning milking, the herd was under general observation each of those days until it ceased grazing at nightfall.

Detailed observations were made on Cow X which by reputation had been most susceptible to bloat during the season. The cow's rate of grazing was measured in bites per minute, the condition of its flank and rumen movements being noted.

During this preliminary period marked bloat cases occurred on Pasture.No. 1. and the subject observed was the first cow to become blown, also showing the severest degree of bloat.
It was decided to use Cow X for further detailed studies.

Description of Cow X.

Age. 4 years.
Milk yield. 2½ gallons daily average.
Previous lactation. 379 lb fat.
Service date. 23/ 12/ 49.

Cow X had given considerable trouble with bloat on certain pastures during the season, and had been used as a bloat indicator in the normal course of daily herd management.

The cow was very easily handled and not readily disturbed when grazing, it being possible for the writer to kneel at the side of the animal's head for close observation without disturbing grazing activity.

From subjective observation Cow X was a comparatively greedy feeder, a wide muzzle was a distinct characteristic and the dental palate was normal.

Pastures.

The grazing activity of Cow X was recorded on 3 pastures, numbers 1, 2 and 3.

The preliminary observations indicated that conditions on Pasture 1. were highly conducive to the onset of severe bloat within 1 hour after pasturing.
Measurements of grazing activity were therefore largely confined to that pasture in order to obtain a repeated record of behaviour associated with bloat.

Conditions on Pasture 2. had not been known to give rise to bloat.

Conditions on Pasture 3. were occasionally conducive to bloat, usually after 3 hours of pasturing; severe bloat was not known to occur within the first hour of pasturing.

Pasture No: 1.

Area. 1 Acre.

Seeds mixture.	LB.
Certified Perennial Ryegrass	20.
Certified H.I.	10.
Cocksfoot	6.
Timothy.	2.
Red Clover	3.
White Clover	1.
	42 LB.

Sown. March 1949. without fertiliser after potatoes.

Management.

The pasture was moderately grazed during September, October, and November, when bloat incidence was high.

After topping the herbage with a mower during November 1949 the pasture was not grazed until 15th January, 1950, when marked bloat was recorded in a number of cows shortly after pasturing during the preliminary period of observation.

Pasture Composition.

At the commencement of these studies the sward was very dense with an average height of 4"--6" ; on the last day the average height of sward was 1 -- 2 inches.

Broad red clover in the pre-bloom stage was the dominant herbage with a strong supporting growth of white clover.

Of the grasses, perennial ryegrass at the seeding stage was interspersed among the clover, some cocksfoot and timothy being in evidence. Unless highly selective grazing for grass species was practised, clover species formed the bulk of herbage available for consumption.

Pasture No: 2.

Area. 1 acre.

Being near the milking shed this pasture was used for holding purposes and was frequently grazed.

It was not known to have been resown; the herbage was dominantly perennial ryegrass and white clover, sparse in ground cover and averaging 1 -- 2 inches high.

Pasture No: 3.

Area $3\frac{1}{2}$ acres.

Seeds mixture.	LB.
Certified Perennial Ryegrass	20
Certified H.I.	10
Cocksfoot	6
Timothy	2
Red Clover	3
White Clover	3
	44 LB.

Sown. September 1948 with 3 cwt superphosphate after being arable for 20 years.

1 Ton per acre of ground limestone sown during the spring of 1949.

Management.

This pasture was a ¼ mile distant from the milking shed and was approached by a public road. In consequence it was pastured by the dairy herd only after morning milking, to be returned for the afternoon milking: it was not pastured at night.

Pasture Composition.

During January 1950 white clover was dominant in the sward, the vegetation being uneven, coarse, and with loose thick runners comprising most of the ground cover.

Certain areas of the paddock were thickly populated with docks and most of the grass species were at a coarse stemmy stage of growth. White clover formed the bulk of herbage grazed, but tall coarse herbage necessitated selective grazing of the favoured areas.

Technique and Data recorded.

Records were made over 15 days in the period 17/1/50 to 25/2/50.

The following data were recorded:---

1). Grazing Activity.

2). Rumen Movements.

3). Degree of Bloat.

4). Incidental Data.

1). Grazing Activity.

Using stop watch and counter, grazing activity of Cow X was recorded by the number of bites taken :---

Fig. 5. Jersey Cow X, flank below rib level stage. Note depression in left lumbar triangle between hook bone and last rib.

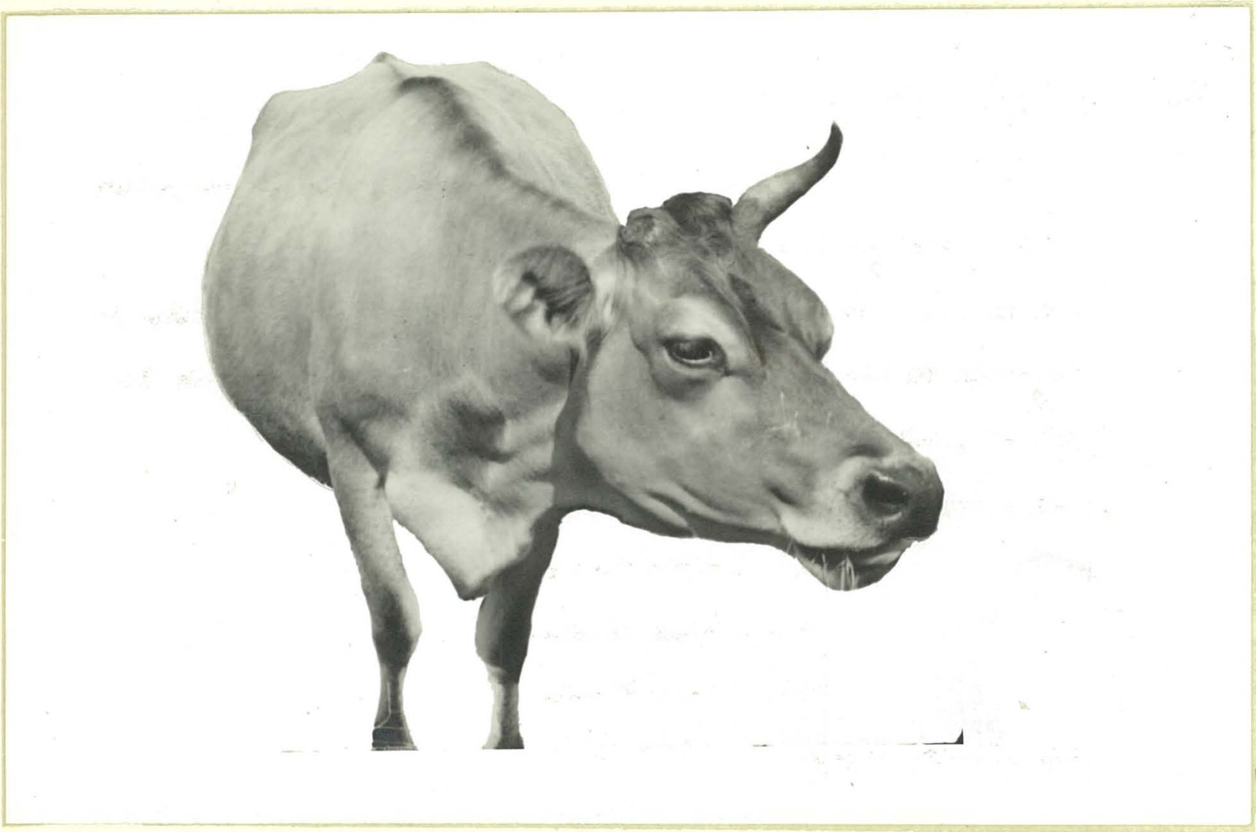


Fig. 6. Jersey Cow X, at slight bloat stage. Note distension in lateral left lumbar region and right lateral abdominal region.

Per 5 minutes on January 17 -- 18.

Per 1 minute on January 20 -- 21.

Per ½ minute on January 24 -- 27.

Per ½ minute on February 2

Per ½ minute on February 19 -- 25.

2). Rumen Movements.

The recording of grazing activity at ½ minute intervals was better for accurately locating the occurrence of rumen motility cycles relative to the time onset of bloat.
The cycles of rumen motility occur approximately at 1 minute intervals, increasing in frequency on grazing.
They were detected visually and by palpation, it being necessary to resort to auscultation when the body wall was severely distended, thus making visual detection of rumen movements difficult.
The occurrence of rumen movements during the time onset to bloat were noted.

3). Degree of Bloat.

Bloat was detected visually and by palpation of the flank in the left lumbar triangle.
Record was made according to the position of the left flank in relation to the last rib, and hook bone or tuber coxa of the pelvic girdle. FIG: 5.
Three degrees of bloat were recorded:---

a). Slight bloat.

b). Marked bloat.

c). Severe bloat.

a). Slight bloat. (FIG: 6.)

Where the flank was distended over the last rib and level with the hook bone. Slight bloat was only recorded where gas could be palpated, otherwise the flank was only considered to be full.

b). Marked bloat. (FIG: 7.)

Where the flank was well distended over the last

Fig.7. Jersey Cow X at marked bloat stage. Flank taut and strongly distended in left lumbar region.

Fig.8. Jersey Cow X, at severe bloat stage. Usually accompanied by frequent urination and rapid respiration.

rib and hook bone, marked gas pressure being evident.

c). Severe bloat. (FIG: 8.)

Where the flank and whole body wall was severely distended, the skin being tight and difficult to depress by palpation: Increased respiration, urination, defaecation, and general distress being evident.

Time onset to bloat was recorded from the commencement of a grazing cycle; Cycle 1. being the first grazing cycle after morning and evening milking.

4). Incidental Data.

Pasture conditions and behaviour of Cow X were noted in relation to the essential records, herd behaviour, and the varied grazing management.

Data obtained was subject to the effects of different grazing management imposed, which was limited by :----

a). Failure to predict bloat occurrence.

b). Risk of production and animal losses.

c). Normality being disturbed for several hours by the bloated condition.

d). Deterioration of pasture conditions conducive to bloat as the herbage was removed by grazing.

These conditions restricted the number of measurements and induced repetitions of behaviour differences.

Results.

These findings are summarised (Appendix) and presented in graphical form in Figures 9 to 15 A. Each figure will be discussed under the appropiate days and in relation to the incidental data. This discussion follows in the following pages.

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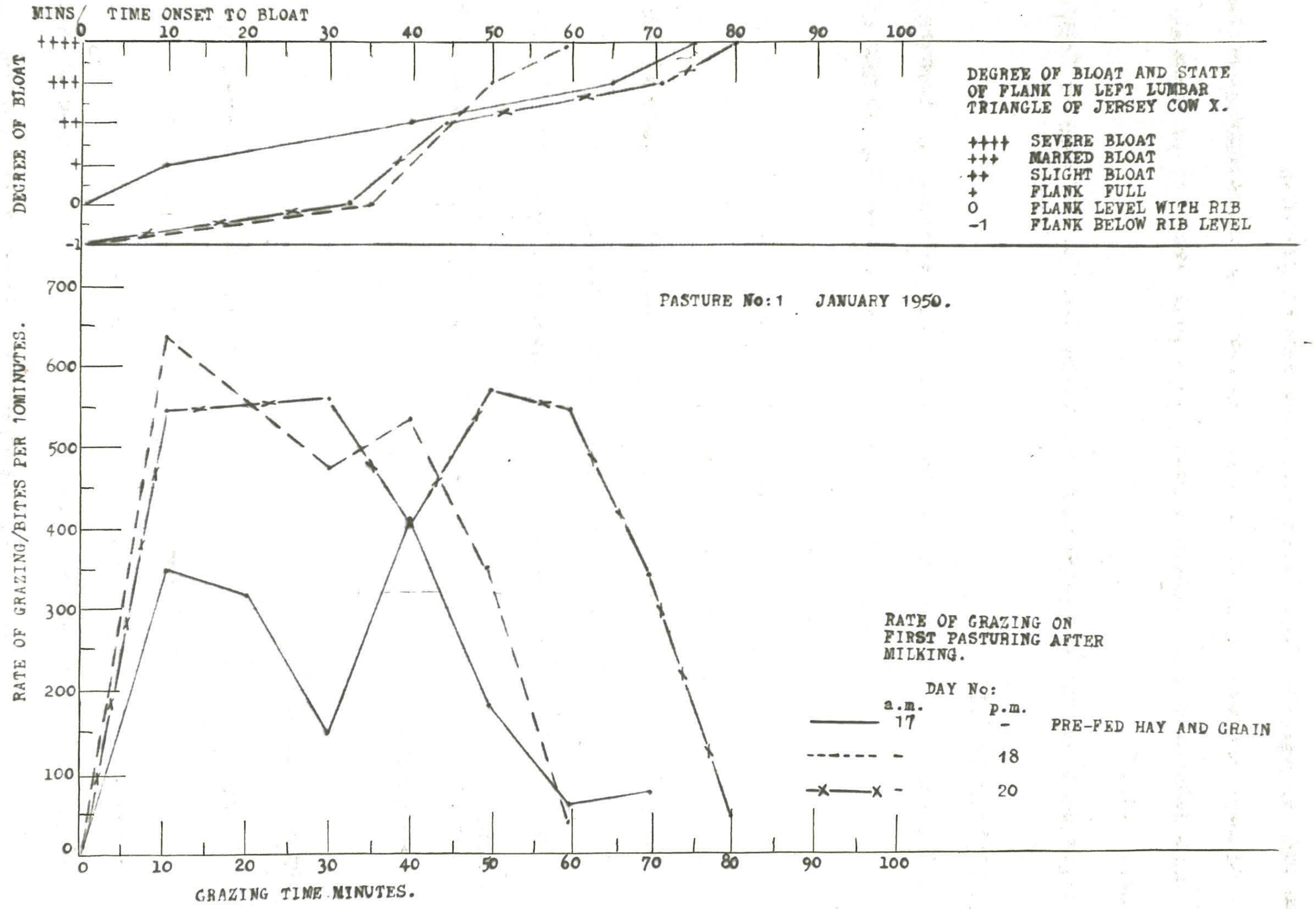

Fig.9. Grazing activity and bloat.

Figure 9. Pasture. No: 1. January.

Striking behaviour generally was shown by the herd during the first 2 weeks of grazing Pasture 1.
On being released from milking the cows would gallop towards the paddock gate and on entering immediately commence active grazing.
Even if some distance away and grazing actively in an adjoining pasture, the same behaviour was evident as soon as a move was made to open the paddock gate.
It appeared that strong preference was shown for the grazing in this pasture.

Day Number. 17. a.m.

Object.	To test the effect on grazing activity of feeding 9 lbs of brewers' grains and fresh lucerne hay ad lib prior to pasturing. Cow released from milking at 7 a.m.
Pastured.	At 8 a.m.
Grazing.	Was slow and deliberate, consisting largely of biting off red clover stem and leaf tops.
Eructation.	Occurred occasionally between slight and marked bloat.
Rumen Movements.	Were strongly evident between slight and marked bloat.
Depastured.	9.15 a.m.

Day Number. 18. p.m.

Object.	To investigate the nature of grazing activity without supplementary feeding prior to pasturing.
Pastured.	6.45 p.m. immediately after milking.
Grazing.	Rate was excessive, broken only by occasional short walking, and drinking 20 minutes after grazing commenced. No attempt was made to select herbage.
Eructation.	Was occasionally recorded after 15 minutes of grazing.
Rumen Movements.	Were strong between slight and marked bloat.
Depastured.	7.43 p.m. Cow X. ceased grazing voluntarily and walked out of paddock.

Day Number. 20. P.M.

Object.	To test bloat potency of pasture by unrestricted grazing.
Pastured.	5.48.p.m. immediately after milking.
Grazing.	Rapid and steady, broken by occasional walking.
Eructation.	Noted intermittently 14 minutes after grazing commenced.
Rumen Movements.	Detected by auscultation, were noisy, strong, and frequent 28 minutes after grazing commenced. Very strong spasmodic rumen movements detected visually 30 minutes after the onset of slight bloat during the severe bloat condition.
Depastured.	7.12.p.m. after grazing had voluntarily ceased.

Discussion.

It will be noted that the shortest time onset to slight bloat and lowest grazing rate occurred Day No: 17 where supplementary feed was received prior to grazing.

The shortest time onset to marked and severe bloat occurred on Day No: 18 where grazing rate was highest in the first 20 minutes of grazing.

The severest case of bloat occurred on Day No: 20 when the duration of grazing was longest, severe distress symptoms, high respiration rate, groaning, urinating, and defaecating were evident. It is to be noted that grazing continued even when strong distension was evident.

Rumen movements were in evidence well after the onset of bloat.

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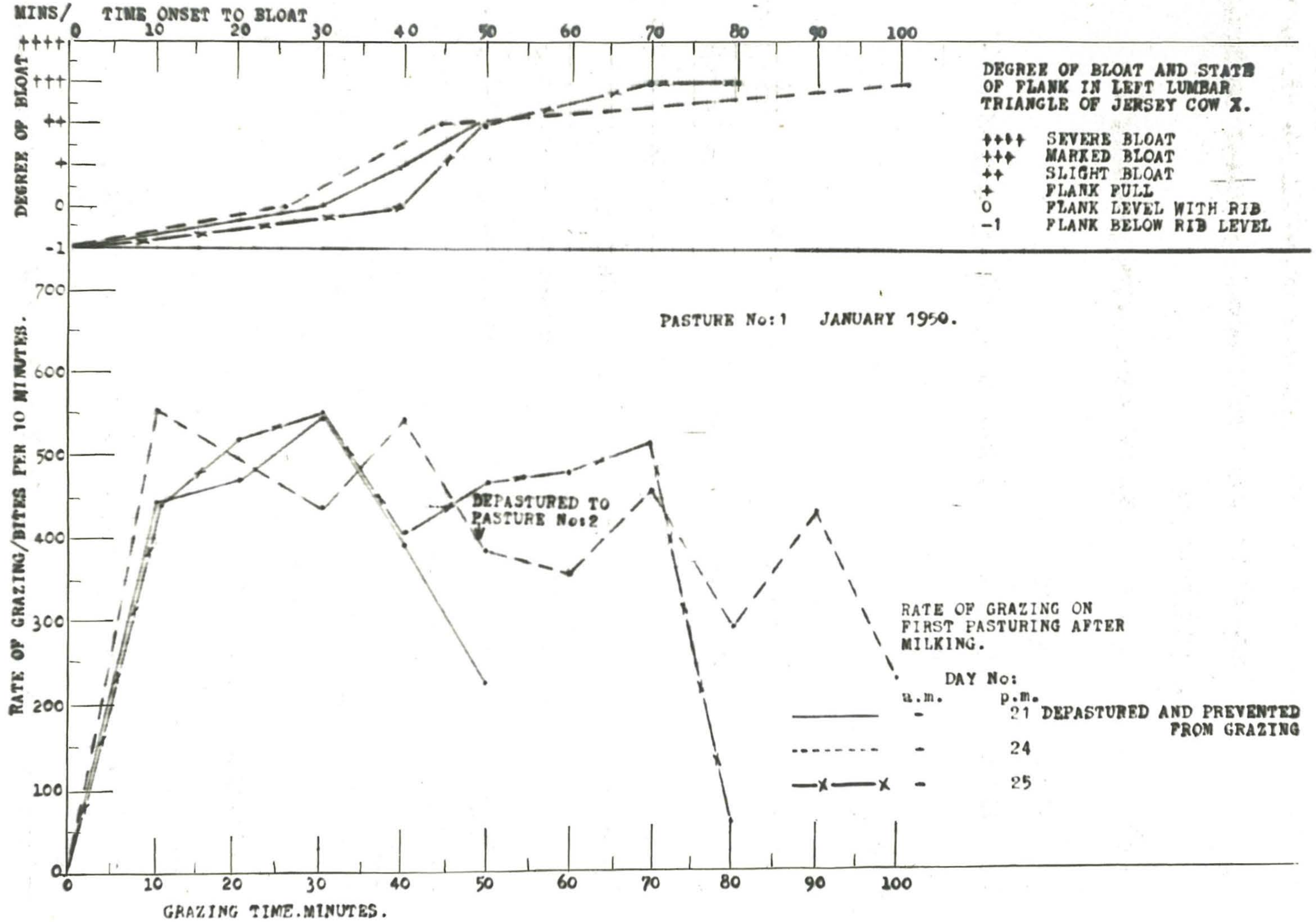

Fig.10. Grazing activity and bloat.

Figure 10. Pasture No: 1 January.

Day Number. 21. p.m.

Object. To test the effect of reduced grazing time on the degree of bloat.

Pastured. 5.39 p.m. immediately after milking.

Grazing. Was steady and some apparent selection for the tops of red clover stems and leaves, apparently conditioned by tall herbage.

Eructation. was noted 16 minutes after grazing commenced.

Rumen Movements. were regular.

Depastured. 6.27 p.m. and no further grazing permitted on Pasture 1.

Day Number. 24 P.M.

Object. To test the effect on the degree of bloat and grazing time, of reducing grazing time on Pasture 1. and continuing grazing on a non-bloat-provoking Pasture No:2.

Pastured. 6.18 P.M. immediately after milking.

Grazing. Steady, broken by walking, selective grazing for red clover being evident where herbage was tall.

Eructation. occurred intermittently.

Rumen Movements. Were regular and strong when slightly blown 44 minutes after grazing commenced.

Depastured. 7.6 P.M.

Pastured. No: 2. at 7.8 P.M.

Grazing. Following a drink was slower and broken.

Rumen Movements. Very strong and regular during the slow steady onset to marked bloat.

Grazing. Ceased voluntarily at 8 P.M.

Day Number. 25 P.M.

Object. To test the effect of unrestricted pasturing on grazing activity, degree and time onset to bloat compared with Day 24, and to confirm the bloat potency of the pasture.

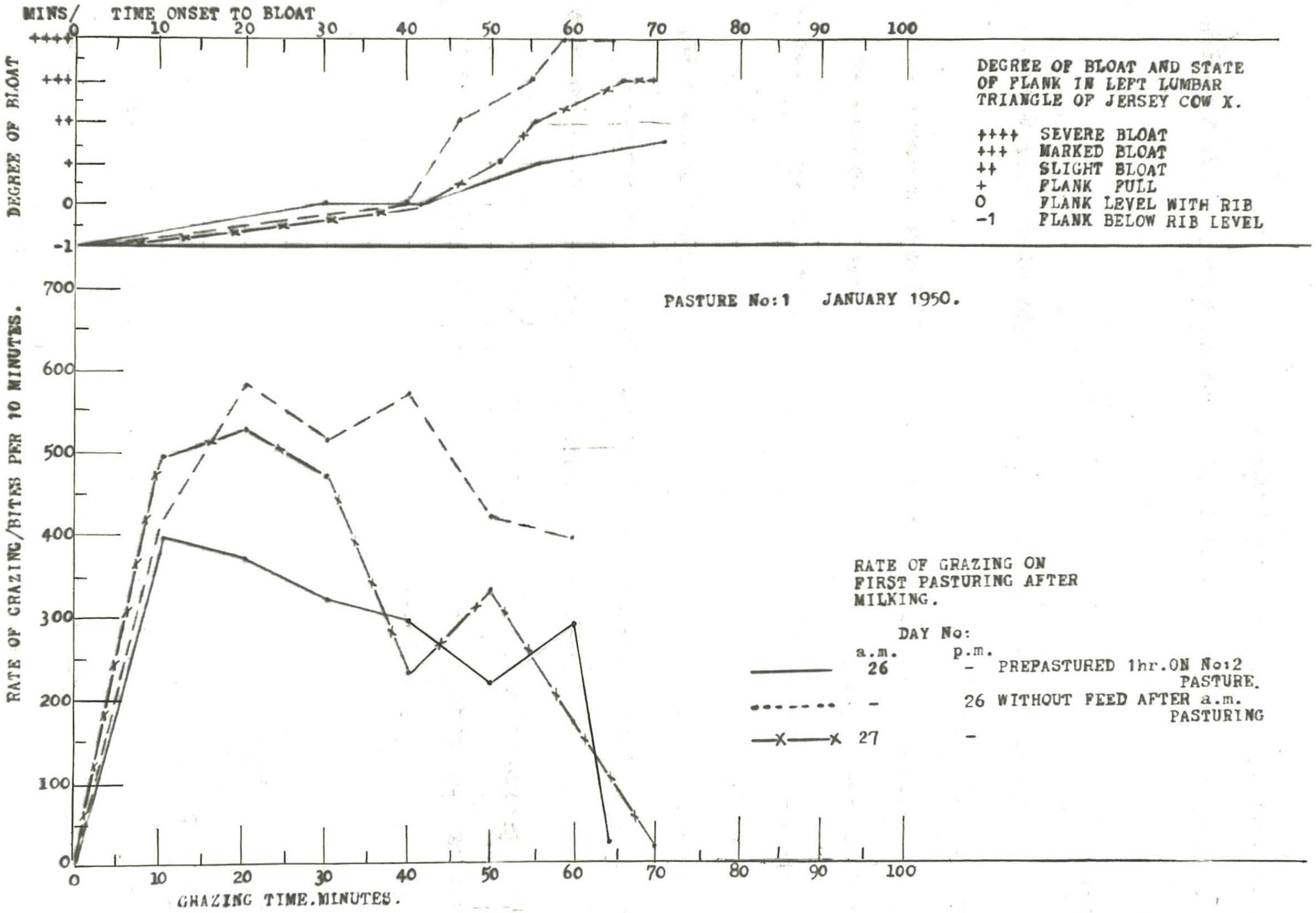

Fig. II. Grazing activity and bloat.

Pastured. 5.44 P.M. immediately after milking.

Grazing. was broken by walking; selective behaviour and browsing of grass seed heads apparent, including some browsing of the boundary hedge.
Rate of grazing fairly regular throughout.

Eructation. Noted occasionally when browsing.

Rumen Movements. Regular and vigorous.

Depastured. 6.53 P.M. although browsing slowly when removed.

Discussion.

Grazing rate and time onset to slight bloat were similar for Days 21, 24, and 25.

Where grazing time was restricted on Day 21 bloat occurred but marked bloat was not recorded; this degree was reached however at 6.57 P.M. after depasturing, approximately 10 minutes later than marked bloat on Day 25.

Reducing the grazing time on Pasture 1. and extending the total grazing time on a non-bloat-provoking Pasture 2. delayed the time onset to marked bloat as compared to a shorter total grazing time on Pasture 1.

The grazing time was the same for Day 25 and Day 20, (FIG: 9.) A faster gr^zing rate on Day 20 was associated with a shorter time onset to bloat and a more severe condition.

Figure 11. Pasture No: 1. January.

Day Number 26 A.M.

Object. To compare the time onset and degree of bloat consequent upon a low and high grazing rate induced by pre-grazing and starving respectively.

Pastured. 7.15 a.m. immediately after milking, on Pasture 2.

Grazing. Steady between 7.30 a.m. and 8.30 a.m.

Pastured 8.43 a.m. on Pasture 1.

Grazing. Very casual, broken by walking and browsing long seed heads of grass.

Eructation. frequent.

Rumen Movements. Regular but not vigorous.

Grazing. Ceased voluntarily at 9.47.a.m. and Cow X laid down Flank was full but not blown. No furhher grazing occurred and Cow X was removed frompasture and penned at 11.15 a.m.

Day Number 26. P.M.

Pastured. 6 -- 7 p.m. immediately after milking having been without food since 9.33 a.m.

Grazing. maintained at a fast rate.

Eructation. Not noted.

Rumen Movements. Strong and rapid between slight and marked bloat.

Depastured. 7.6 p.m.

Day Number 27 a.m.

Object. To impose a control treatment of Day 26 a.m. and p.m. by unrestricted grazing.

Pastured. 7.7 a.m. immediately after milking.

Grazing. Steady at first, later broken by apparent selection and browsing of tall grass.

Eructation. Not recorded.

Rumen Movements. Deep and vigorous when markedly blown noted 20 and 26 minutes after recording slight bloat.

Depastured. 9.20 a.m. after grazing had ceased voluntarily.

Discussion.

It will be noted that the highest rate of grazing was concomitant with the shortest time onset to bloat and the severest degree of bloat. Bloat did not occur in the same time where the grazing rate was low.

Rumen movements occurred well after the onset of bloat and tended to increase in vigour.

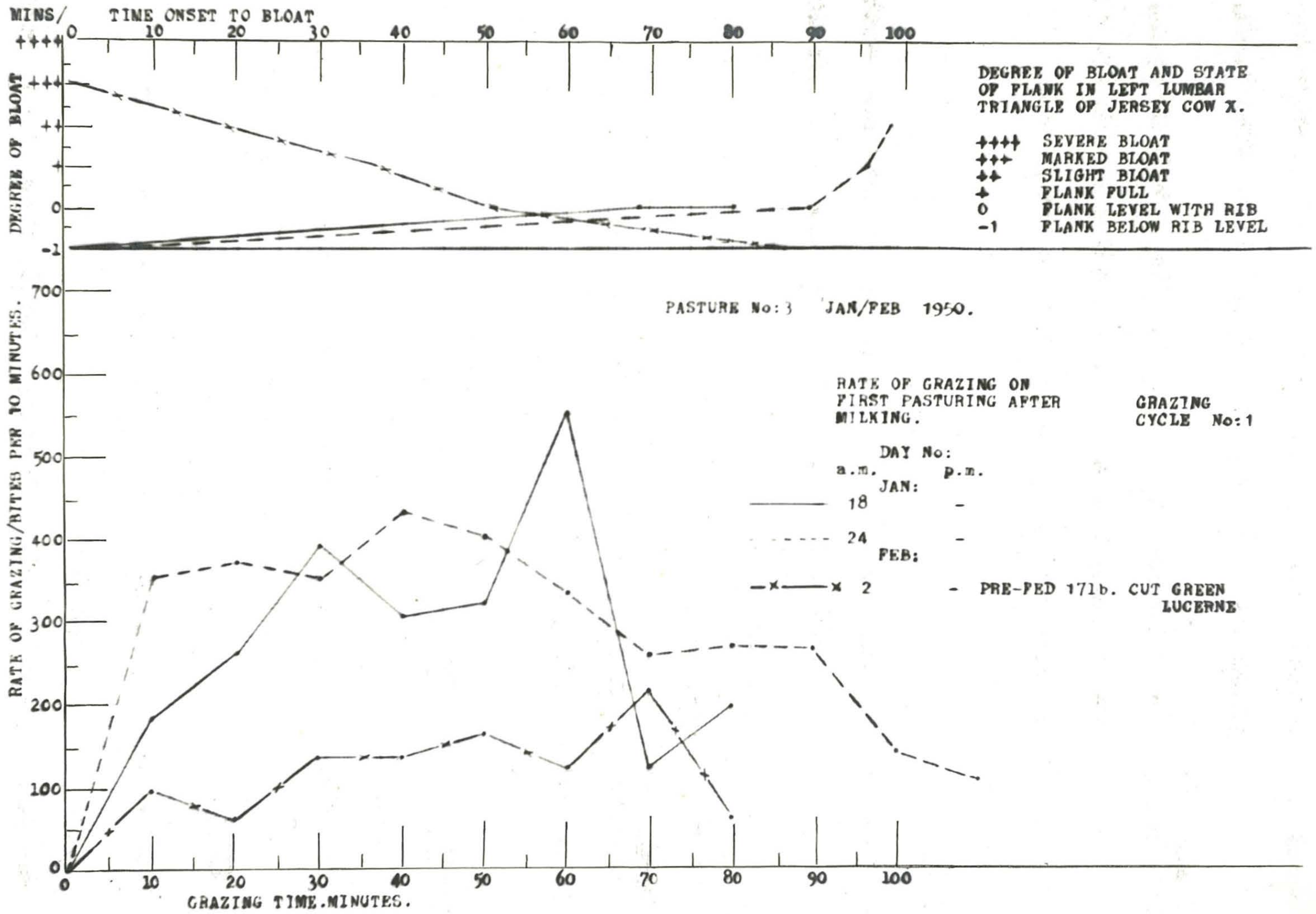

Fig.I2. Grazing activity and bloat.

FIGURES 12 and 12A. PASTURE No. 3. Jan:/Feb:

Day Number 18. a.m. January.

Object. To find if differences in grazing activity and time onset to bloat occurred between Pastures 1 and 3.

Pastured. 7.45 a.m. immediately after milking.

Grazing. Casual, broken by considerable walking and selective grazing. Laid down at 9.10 a.m. flank being level.

Rumen Movements. Strong and regular at 9.24 when the animal was lying. The movements coincided with eructation; this was readily detected usually by palpation and auscultation.

FIGURE. 12A.

Grazing Cycle. 2. Commenced at 10.55 a.m. flank being below rib. Grazing was very casual, being broken by walking and selective grazing.

Eructation. Occurred when blown.

Rumen Movements. Were regular and increased when blown.

Depastured. 12.20 p.m.

Day Number 24. a.m. January.

Object. To repeat Day 18.

Pastured. 7. 38 a.m. immediately after milking.

Grazing. Broken by walking, clover areas being selected.

Eructation. Occurred frequently.

Rumen Movements. Steady and regular, became vigorous toward end of grazing cycle.

Grazing. Ceased 9.29 flank being slightly blown. Cow X remained standing, then lay down at 9.48. At 10.1 it rose and urinated.

Rumen Movements. --at this time were very strong, associated with eructation, and contractions followed in rapid succession.
At 11.2 the flank was reduced in distension and CowX lay to commence cudding.

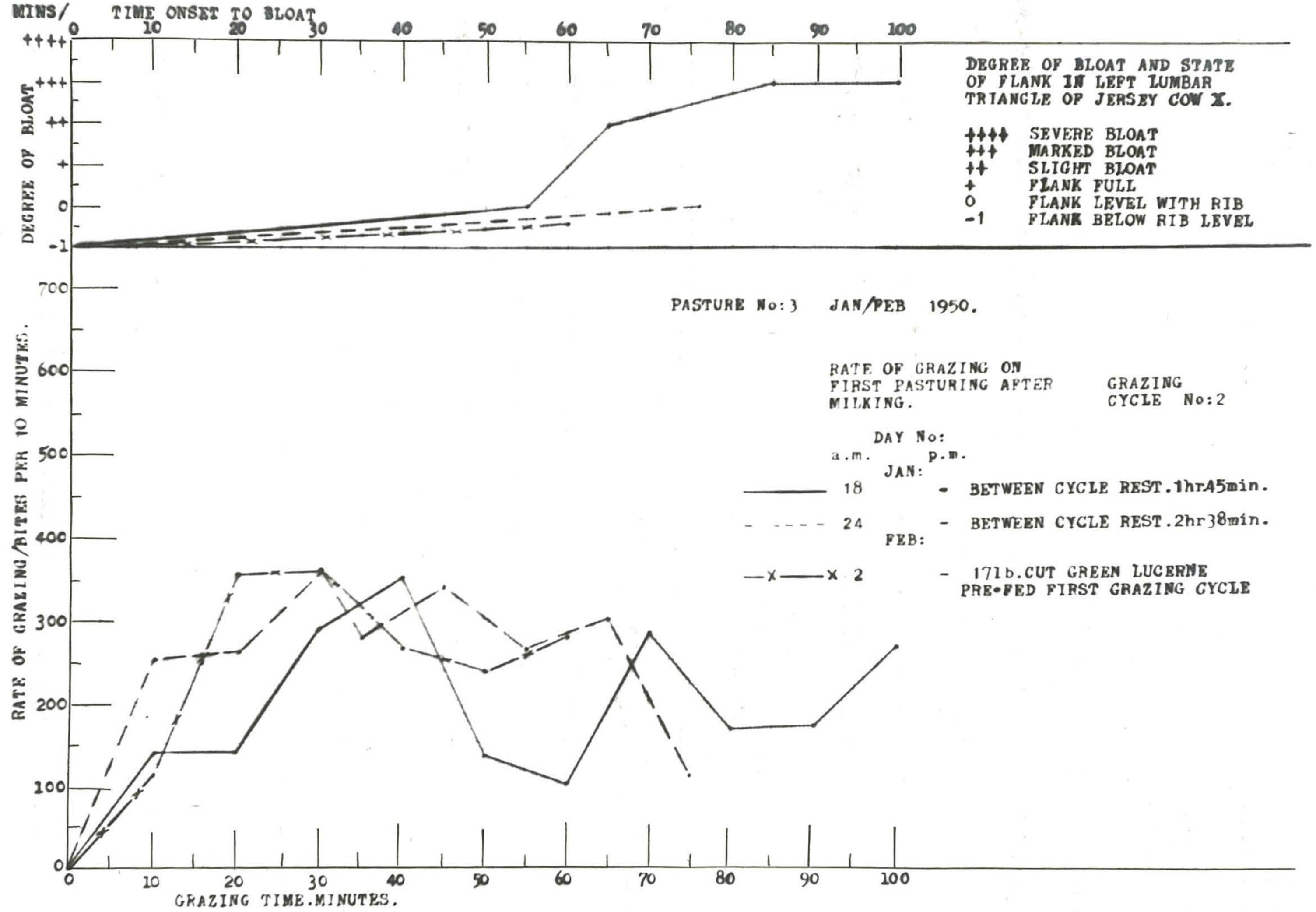

Fig. I2.A. Grazing activity and bloat.

FIGURE. 12A.

Grazing Cycle 2.	Commenced 11.36 a.m. when flank was below rib level.
Grazing.	Was slow, deliberate and broken by walking.
Eructation.	Frequent.
Rumen Movements.	Regular but not vigorous.
Depastured.	12.50 p.m.

Day Number 2. A.M. February.

Object.	To observe the time recovery from bloat, and subsequent grazing behaviour.
7.10 A.M.	Penned. Immediately after milking.
7.30. "	Cut Green lucerne approximately 8" high at the pre-bloom stage.
7.46 "	Fed green lucerne.
8.45 "	Feeding ceased. 17 lbs lucerne consumed.
8.50 "	Slight bloat.
9.0 "	Marked bloat associated with very strong vigorous ruminal contractions and eructation.
9 30 "	Bloat still marked, but distension slightly relieved.
10.5 "	Pastured.
Grazing.	very light browsing of tall herbage.
Eructation.	very frequent.
Rumen Movements.	very frequent, and strong.
11.43 A.M.	Lay down. Strong ruminal movements and eructation whilst lying.
12.7 P.M.	Standing, flank below rib level.
Grazing Cycle 2. (FIG: 12A.)	Commenced.
Grazing.	Improved over cycle, but slow and deliberate.
Eructation.	Not noted.
Rumen Movements.	Regular.
1.6.P.M. Depastured.	3 other cows in the herd were markedly blown, having been pastured since 7.40 a.m.

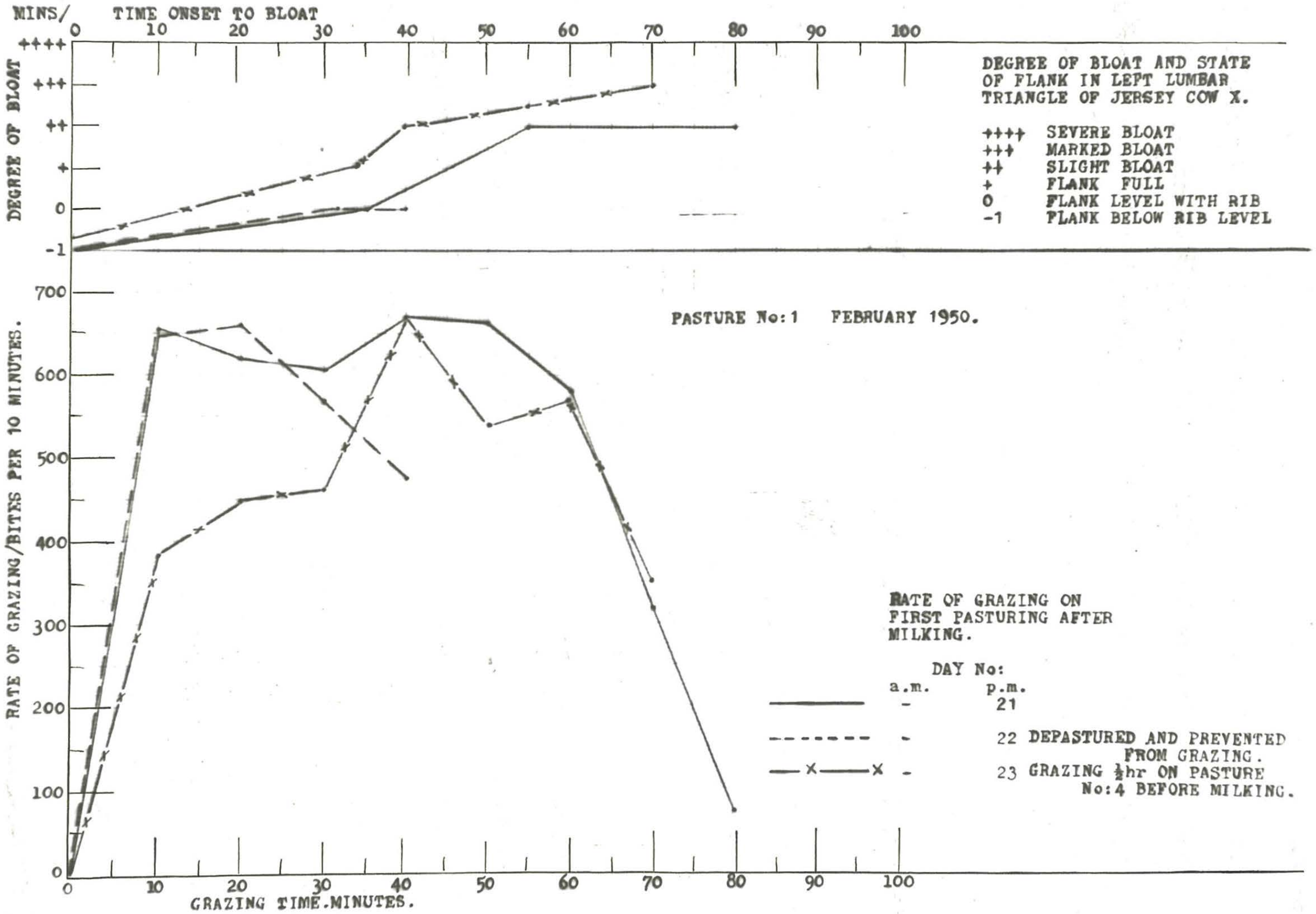

Fig. I3. Grazing activity and bloat.

Discussion.

A marked difference was apparent when comparing the grazing activity of the first grazing cycles after morning and evening milking on pastures 3 and 1 respectively. (See also FIGS: 15 and 15A.)
Grazing rate was generally highest on Pasture 1 particularly at the commencement of the cycle.
Time onset to bloat was much longer on Pasture 3 than on Pasture 1.
Time recovery from marked bloat was between 70 -- 75 minutes.
Rumen movements increased in frequency and vigour towards the markedly bloated condition.

. . . .

Figure 13. Pasture No: 1 February.

Day Number. 21 P.M.

Object.	To test bloat potency of pasture by unrestricted grazing. (Pasture had not been grazed since 25th January.)
Penned.	5.45.P.M. immediately after milking.
Pastured.	7.3.P.M. -- delayed to induce rapid grazing.
Grazed.	At an excessive rate; very little broken grazing. Pasture short 1 -- 3 inches over whole paddock, except around dung patches.
Eructation.	Not recorded.
Rumen Movements.	Increased in vigour toward end of grazing.
Depastured.	8.20 P.M. grazing ceased voluntarily.

Day Number. 22. P.M.

Object.	To test restricted grazing time on degree of bloat.
Penned.	5.50 P.M. immediately after milking.
Pastured.	7.10 P.M.
Grazed.	At excessive rate -- pasture short.
Eructation.	Not noted.
Rumen Movements.	Steady and regular.
Depastured.	7.50 P.M. and prevented from grazing.

Day Number. 23. P.M.

Object. To repeat Day 21.

Herd had been pre-pastured for 35 minutes prior to milking on hay aftermath Pasture No: 4, which they grazed actively. The herbage was fresh and 2 - 3 inches high. Stale brewers' grains were deposited on the paddock in patches.

Gas could be palpated in the flanks of Cow X and other Cows on being depastured for milking.

Cow X was milked first and pastured without the herd as declining light was limiting full observation towards the end of the grazing period.

Pastured. 5.37 P.M. immediately after milking.

Grazing. Very reluctant, disturbed by agitated manner in absence of herd. Settled to steady rapid grazing on being joined by herd.

Eructation. Not noted.

Rumen Movements. Increased in vigour towards end of grazing.

Depastured. 6.50 P.M. grazing ceased voluntarily.

The left flank was being swollen, both flanks being severely distended but no distress evident.

Discussion.

It should be noted that the quantity of herbage had been considerably reduced. Where the herbage was an average of 4 --6 inches high in FIG: 9, it was now an average of 1 -- 3 inches high and badly soiled.

The Pasture continued to be bloat-potent.

Relative to Figs: 9 and 10. a higher grazing rate was maintained for a longer time with an increased time onset in Day 21. and reduced severity of bloat. By restricting grazing time bloat did not occur. Rumen movements were in evidence during the onset of bloat.

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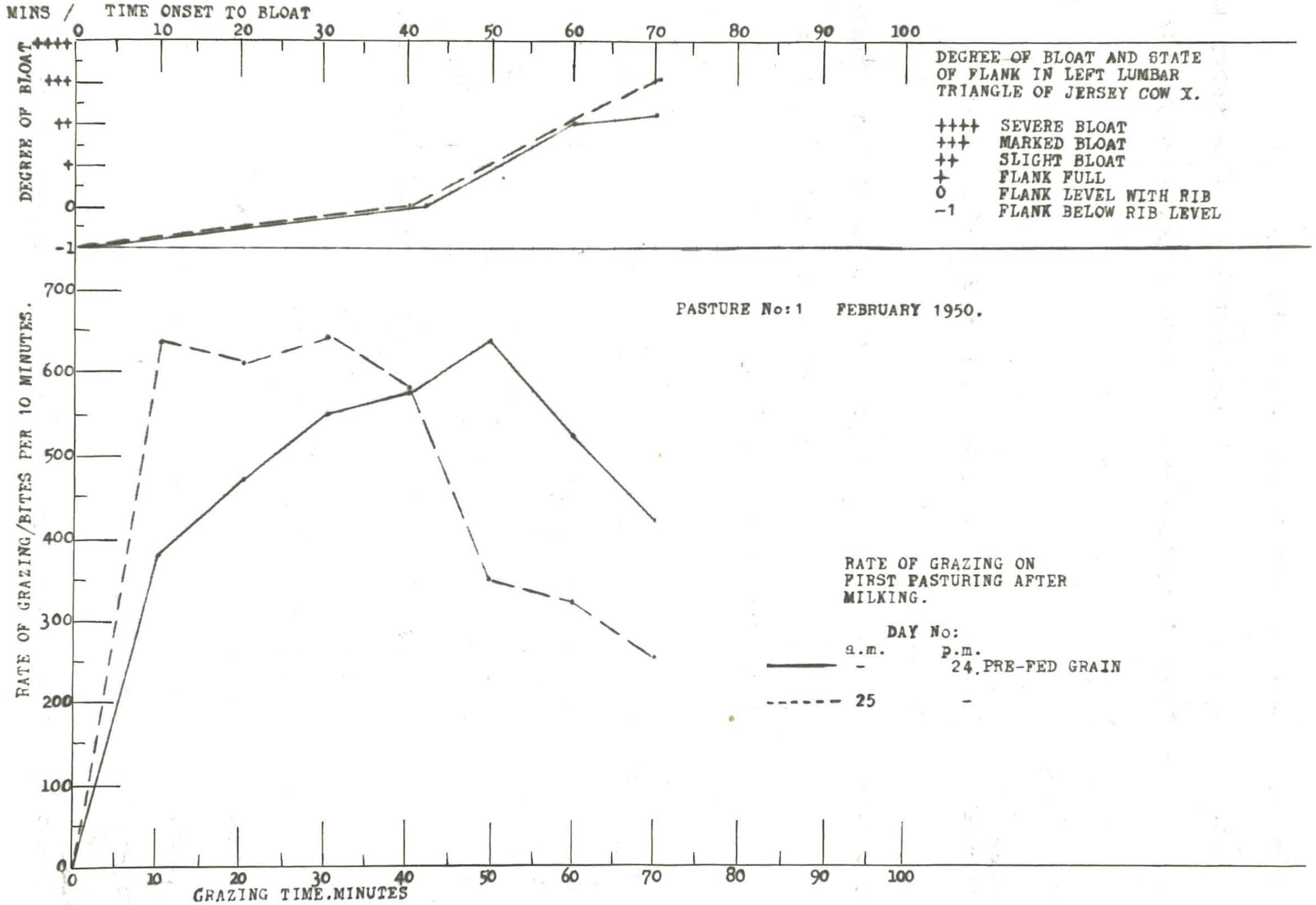


Fig. I4. Grazing activity and bloat.

Figure 14. Pasture No: 1. February.

Day Number. 24. P.M.

Object. To repeat Day 21. 6 lbs of brewers' grains fed at milking. Herbage was very short, and red clover formed the bulk of species available.

Pastured. 6.40 P.M. immediately after milking.

Grazed. In broken manner, walking, drinking, and urinating in first 10 minute period. Rate of grazing increased towards end of period.

Eructation. Not recorded.

Rumen Movements. Regular and increasing towards end of cycle but not vigorous.

Depastured. 7.47 P.M. as declining light limited further observation; Cow X slightly blown, distension increasing to the marked stage after removal.

Day Number. 25. A.M.

Object. To repeat Day 21.

Prior to milking cows were grazing Pasture 2. the herbage of which had freshened considerably. Cow X and others came in to milking showing full signs and gas could be palpated in the flank.

Released from milking 7.10. A.M.

Pastured. 8.10 A.M.

Grazed. At excessive rate -- being maintained without break.

Eructation. Not noted.

Rumen Movements. At 9.17 a.m. were very rapid and strong-- increasing in strength as distension increased.

Depastured. 9.23.a.m. having voluntarily ceased grazing.

Discussion.

The herbage was very short for grazing being composed largely of leafy red clover. The Pastured continued to be bloat-potent. Relative to Figs: 9 and 10. a higher grazing rate was maintained for a longer time, with an increased time onset to bloat and reduced severity.

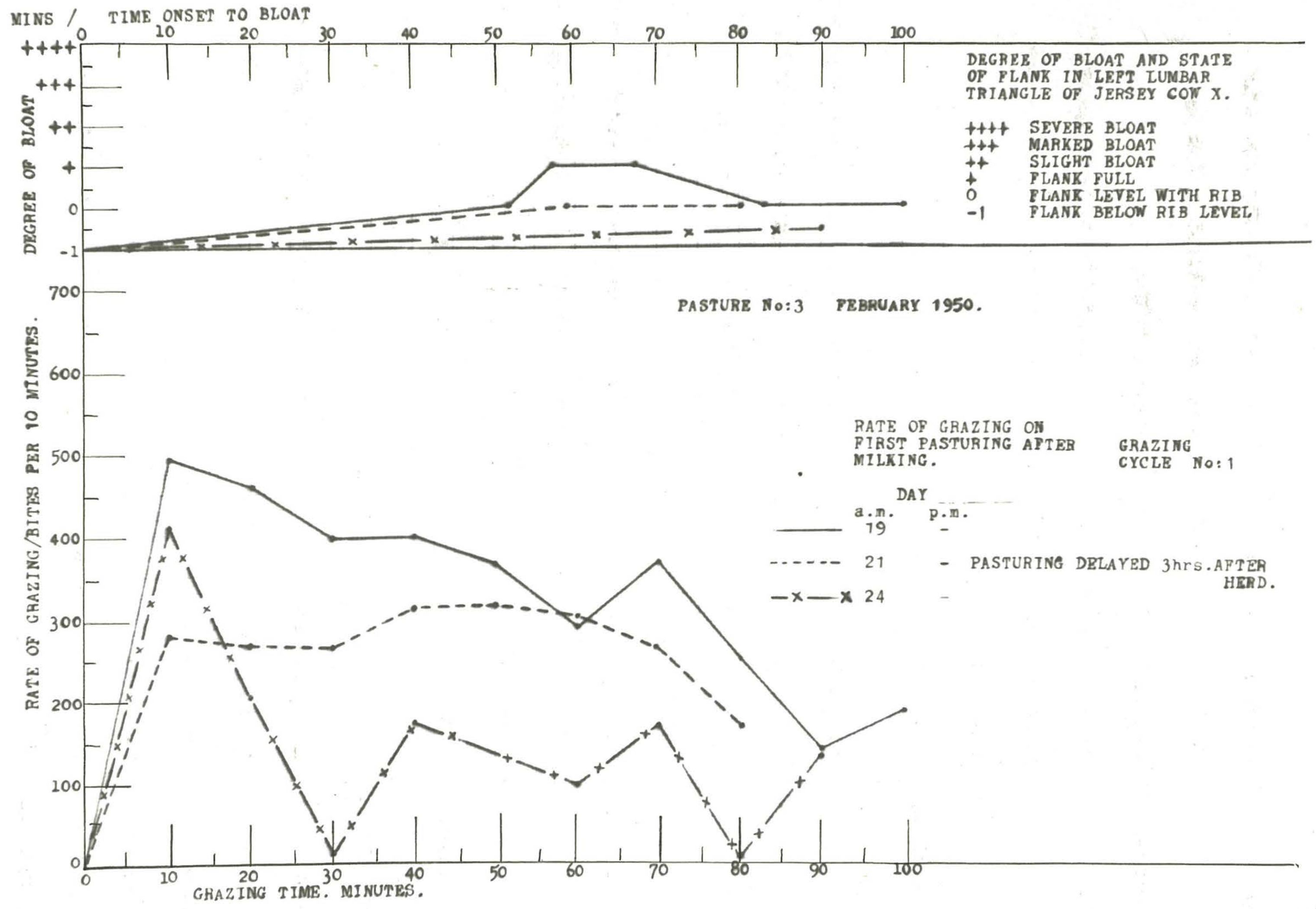


Fig. 15. Grazing activity and bloat.

Rumen movements were repeated and vigorous when marked bloat was apparent.

. . . .

Figures 15 and 15A. Pasture No: 3. February.

Day number. 19. A.M.

Object. To find if differences in grazing activity and time onset to bloat occurred between Pastures 1 and 3.

Pastured. 7.47 A.M. immediately after milking.

Grazed. Steady rate at first but progressively slower, broken by regular walking and apparent selection, herbage being coarse and patchy.

Eructation. Frequent.

Rumen Movements. Not distinct after 50 minutes of grazing, became apparent increasing in strength towards end of grazing cycle 1. At 9.29 when cow was standing gaseous sounds were detected by auscultation.

Eructation. Followed posterior wave of rumen contraction and tightening of flank. Frequent eructation whilst lying between grazing cycles.

Depastured. 3.38 P.M.

Day Number. 21 A.M.

Object. To repeat Day 19 and attempt to increase rate of grazing by delayed pasturing.

Penned. From 6 A.M.

Pastured. 10.5 A.M.

Grazing. Broken by walking and general disinterest in herbage.

Eructation. Frequent.

Rumen Movements. Faint but regular at end of cycles 1 and 2.

Day Number. 24. A.M.

Object. To repeat Day 19.

Pastured. 7.55 A.M.

Grazed. In broken manner by frequent walking and restlessness, due to a combination of very hot weather, flies, and coarse herbage.

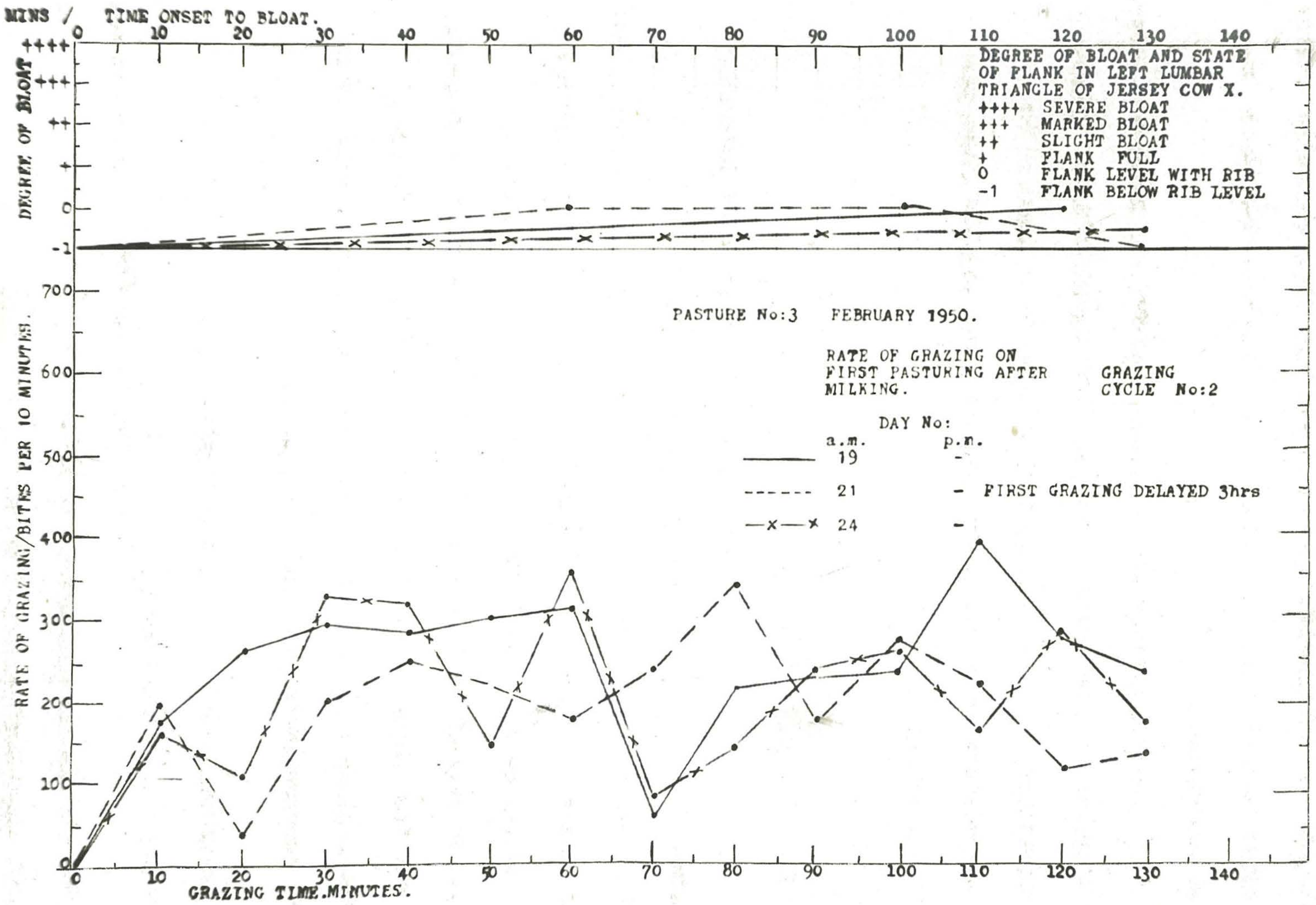


Fig. I5A. Grazing activity and Bloat.

Eructation.	Frequent.
Rumen Movements.	Very faint but regular.
Depastured.	3.15. P.M.

Discussion.

The pasture herbage in Pasture 3 had freshened in patches, but was generally very coarse. White clover was the dominant herbage available, and most frequently grazed in patches, which occurred between rank, seeded grass species and docks. No bloat was recorded in the period of observation.

A marked difference in grazing activity was apparent between the first grazing cycles after morning and evening milking on Pastures 3 and 1 respectively. The same type of difference is apparent when 3 morning grazing cycles on Pasture 3, and 1 morning grazing cycle on Pasture 1 are compared.

Figure 12. Day 2. February.

Illustrates the time recovery from marked bloat induced by feeding 17 lbs of fresh green lucerne.
It is of interest to note that at the same time together with Cow X, the same time onset (64 minutes) and degree of bloat was recorded for one other lactating animal, Cow Y, which consumed 11 lbs of lucerne.

This observation was repeated on 8/2/50 when very wet fresh green lucerne cut from the same paddock was fed to the same two animals.
Cow X became blown in 2 hours after consuming 18 lbs of lucerne, whilst 16 lbs of lucerne failed to cause bloat in Cow Y.

Similar observations were made following grazing in:-

Figure 8. Day 27. A.M. January.

After being penned for 3½ hours herbage was cut from Pasture 1. and immediately fed to Cow X which became markedly blown in 90 minutes after consuming 24 lbs of herbage.
Cow Y was fed similarly after being penned 6½ hours, and became slightly blown in 60 minutes after consuming 30 lbs of herbage.

This observation was repeated on 1/2/50 when Cows X and Y consumed 17 lbs and 18 lbs respectively of fresh green herbage from Pasture 1, but bloat was not recorded.

Discussion.

The value of these observations lies in the fact that bloat was induced by feeding herbage from pasture conducive to bloat incidence. The implications of this finding should be obvious in view of the difficulties experienced in bloat studies by failure to produce the condition experimentally.

X X X X X X X

Discussion of Results.

The operation of a herbage quantitative factor in the, onset of bloat is implied in these studies.
It is likely that a decrease in herbage available would reduce the incidence and severity of bloat.

The behaviour of the animal on pastures having a high bloat potency would also appear to be implicated.
This is most likely to be expressed in duration and rate of grazing as these factors may influence total herbage intake in a given unit of time.

There is insufficient data upon which to support the concept of a difference in the bloat potency of herbage.
It is suggested that this factor could be usefully investigated by feeding various weights of herbage against herbage from pastures conducive to bloat in conjunction with in vitro and in vivo gas production studies.

The implication of rumen inhibitory factors in bloat-provoking pasture, and their incrimination in the etiology of bloat does not find support in these studies. On the contrary, rumen movements tended to increase in vigour during the onset of bloat.

Whilst appreciating the limitations of these studies the writer would draw particular attention to the purpose of this discourse, namely, the stimulation of constructive thought as well as providing a basis for reference.

For that purpose these studies are presented, for with some knowledge of conditions pertaining in the field, then better construction is given to working hypotheses upon which to base well controlled investigations. There can be no doubt of the inadequacy of the literature for assisting the latter purpose.

SUMMARY.

A number of interesting and provocative features arise from this study, details of which are in the appendix.

a). A bloat susceptible lactating Jersey cow was used for studies relating to grazing activity, and bloat incidence.

b). Over 12 days on which bloat occurred on the same pasture, the average time onset to bloat was 48 minutes.

c). The average rate of grazing (bites/min:) was 50, in the first 40 minutes of pasturing.

d). The average grazing time was 69½ minutes.

e). Rumen movements were evident during the onset of bloat and were recorded when severely blown, 30 minutes after the onset of the condition.

f). Rumen movements tended to increase in vigour as distension increased, being rarely detected at the height of distension.

g). Generally, under similar pasture conditions and in the absence of supplementary feeding, the shortest time onset to bloat tended to be associated with the highest grazing rate.

h). Severest conditions of bloat obtained where a high grazing rate was combined with the longest grazing time.

i). A restricted grazing time was associated with a reduced severity of bloat.

j). Over all observations the average time onset to marked bloat was 64 minutes. One case is evidenced where time onset to marked bloat was approximately 70 -- 75 minutes, and recovery 70-75 minutes.

k). There was a difference in time onset and incidence of bloat between pastures concomitant with a difference in grazing activity.

SUMMARY OF SECTION (c).

To summarise then the grazing activity of ruminants and the onset of acute bloat.

a). Where herbage conditions are conducive to acute bloat its incidence is widely reported, as occurring not less than 30 minutes after commencing to graze, and most often within 1½ hours of pasturing. Bloat incidence is often associated with longer periods of pasturing.

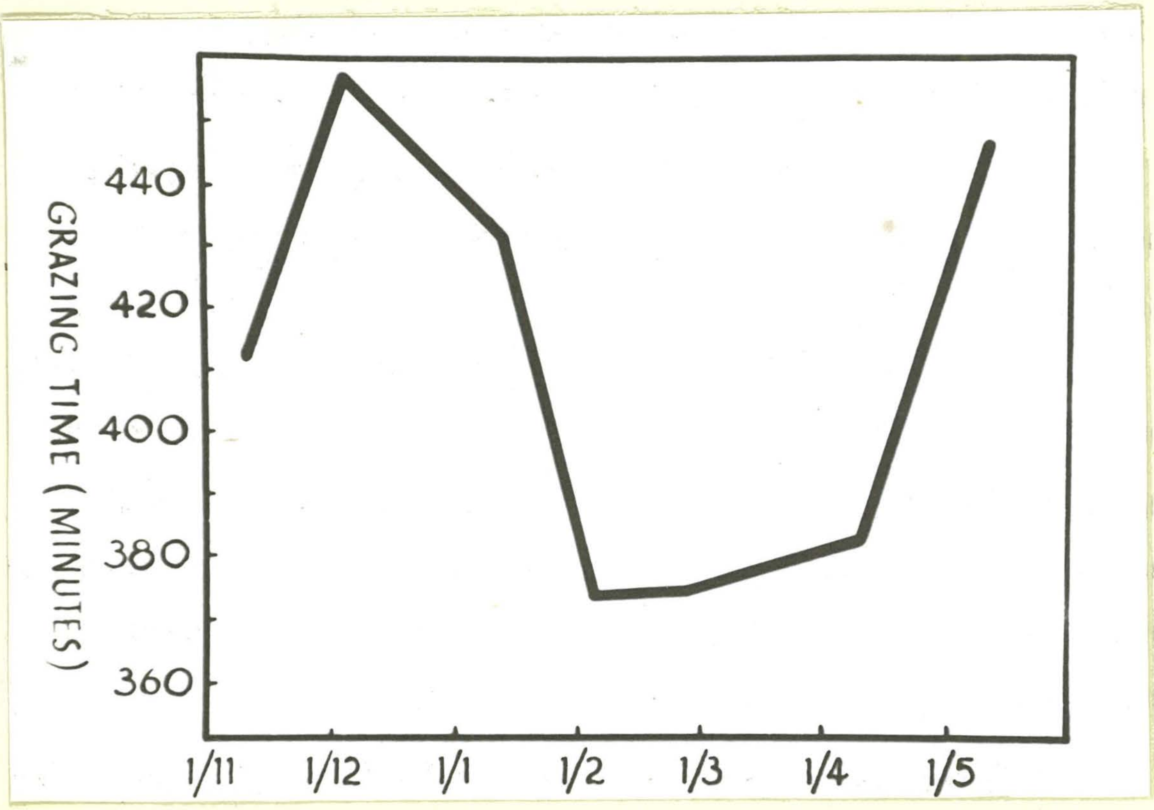


Fig.4.A. Seasonal distribution of grazing time for dairy cows.
After Hancock(IO9).

b). That the rate of grazing may be an etiological factor in the onset of acute bloat is supported by many reports, but is not known to have been investigated experimentally.

c). Evidence is presented which suggests that grazing activity as an animal-conditioned interaction with pasture may be implicated in the time onset to bloat and severity of the condition.

d). SEASONAL GRAZING ACTIVITY.

Seasonal influences are implicated in the distribution of herbage production peaks, and appear evident in the seasonal incidence of bloat.

It is as well to examine very briefly the possibility of ruminant grazing activity also being influenced by seasonal factors.

There is evidence that hot weather lowers the daily grazing time of cattle (106), (60), and it is suggested that this fact accounts for sheep (85) extending their night grazing time during summer months.

Of particular interest is the progressive decrease in afternoon grazing time conditioned by earlier nightfall due to decreasing day length. (108). Fig. 3.

Hancock (109), in New Zealand has shown that the period of longest grazing time for dairy cows occurs in December, Fig. 4A. This peak is followed by a sharp decline in the summer with a rise again in the autumn. Hancock considers that this trend shows that the time spent grazing is mainly determined by the quality of grass, which generally deteriorates during the dry spell in the summer.

Now if gas production in the rumen is proportionately related to the amount of food consumed (51), (52), it would be expected that optimum rumen gas formation would obtain where conditions provide for the optimum consumption of food. Further, where these conditions prevail it may be conceived that a lower feeding time would be necessary. The peak and total volume of gas production would therefore be reached in the minimum time interval after feeding commences.

Should the frequency of eructation be coincident with and dependent upon the minutely cycles of rumen motility, as suggested by some workers, the optimum formation of rumen gas in the minimum time interval after feeding may conceivably exceed the gas removed by eructation, and increased gas pressures in the rumen would be expected to follow. These conditions are most likely to obtain in the months of lowest grazing time which coincide with those of increasing pasture consumption (76), the peak of pasture production (55), (95), and the seasonal incidence of bloat. (19), (93), (94).

X X X X

So much then for the grazing behaviour of the ruminant as it may influence feed consumption. Those animal pasture interactions have been considered which most probably determine the quantitative level of herbage intake. The importance of this aspect cannot be doubted particularly where pasture conditions are conducive to bloat. What comprises the qualitative factors in pasture conducive to bloat remains an unyielding problem.

However, an earlier intimation was given that the grazing animal may condition the individual level of its environment by influencing the social order of the species components of a pasture.

A sufficient weight of evidence exists to give reason for believing that bloat incidence is highest on all legume or legume dominated pastures.

We know that the environment induced by the grazing animal is favourable to the growth habit of those legume species most widely used in intensive grassland practice. It is therefore necessary to very briefly examine those interactions conditioned by the animal which influence the species composition of a pasture and thereby the quality of herbage available for consumption.

C. THE GRAZING RUMINANTS' INFLUENCE ON PASTURE COMPOSITION.

Within pastures composed of more than one herbage species, a constant state of inter specific competition exists (132), with the result that a very unstable and dynamic community prevails. (54).

Of the three fundamentals, soil, climate, and animal, which constitute environment, the two latter are the most variable and would be expected to have greatest interplay upon the pasture plant community. It will follow that the pasture will become characterised by those plants best adapted to environmental conditions.

Whilst the respective environmental factors of climate and grazing animal must assume an order of influence as to be almost inseperable under intensive grassland conditions, the animal is the controllable factor and its influence capable of analysis.

The degree of influence exerted upon a pasture by the grazing animal in so far as it favours certain species to the exclusion of others, will be conditioned in large part by the complexity of the pasture composition.

Davis et al. (1946) (132), demonstrate that a greater degree of stability will be maintained in a simple mixture pasture, for example, of ryegrass, and white clover, when compared to a pasture having a complex mixture of Italian ryegrass, perennial ryegrass, Cocksfoot, Timothy, red clover, and white clover.

Having that appreciation of the factors liable to modify the influence of grazing on the pasture community we may better examine the work which illustrates those overall effects.

The classic studies of Martin Jones 1933 (129) in England, were the first to show the reaction of herbage species to different degrees of grazing intensity.

Using three widely varying species of grasses he demonstrated that in an admixture the success of a species depended largely on the aggressiveness of the other grasses and these in turn were strongly influenced by the times of stocking. Martin Jones 1933 (130), further showed that grazing management differing in time of grazing and intensity of stocking affected the botanical composition of pasture in relation both to the proportion of grasses to clovers and the inroad of pasture weeds. Martin Jones concluded that the method of stocking is the governing factor in determining the botanical nature of the sward. This work has been widely confirmed and is an accepted principle in grassland practice.

It is well demonstrated in the findings of Davis and Williams 1946 (132) in a series of trials to assess the comparative development and sward forming attributes of various grass and clover species under different grazing management over the widest possible range of country in Britain.

The principle expounded by Martin Jones is shown to apply in New Zealand where Levy and Sears 1948 (131), using a sward containing a complex mixture of herbage species sown in 1946 subjected the sward to the following systems of grazing:---

1). Close and continuous (at 1 inch continuously)

2). Sheep, rotational grazing (up to 3 -4 inches down to 1 inch).

3). Dairy, rotational grazing (up to 8 - 10 inches, down to 2 inches)

An analysis of the sward composition as at October 1st 1947 is shown in Table 4.

Table 4. October 1st 1947.

Composition. %. Dry weight.

	1. Continuous Grazing	2. Short-Spell Rotational Grazing	3. Long-Spell Rotational Grazing
Perennial ryegrass	43.3	41.6	31.1
Short rotation ryegrass	2.9	21.7	40.2
Timothy	6.8	1.2	—
Cocksfoot.	1.0	3.2	—
Other grasses	—	4.0	0.7
White clover.	42.4	24.3	23.3
Red clover	2.8	2.8	4.2
Other species.	0.8	1.2	0.5

Sears and Levy comment that the main feature of the above analysis is the failure of the short rotation ryegrass under close and continuous grazing and its dominant position in the sward (at that time of the year) when under the rotational grazing with long spells in between grazings.

It will be noted that the red clover content was low as the time of analysis corresponded to the early vegetative development of that species; red clover became dominant under the dairy cow grazing system as the season advanced as shown in Table 5.

Table 5.

December 1947 ____ March 1948.

Composition % Dry weight.

	1. Continuous Grazing	2. Short-Spell rotational grazing	3. Long-spell rotational grazing.
Ryegrass (Short rotation and perennial.)	37.3	48.8	20.4
Timothy	—	0.5	trace
Cocksfoot	0.6	1.0	0.8
Other grasses	1.6	3.5	trace
White clover	54.7	31.8	21.4
Red clover	5.1	12.1	55.3
Other species	0.7	2.3	2.1
Yield for period (in lbs dry matter per acre)	2900	3400	5100
Crude protein % dry matter	25.4	23.8	20.4
Crude Fibre % dry matter	15.5	17.3	19.9
No. of grazings.	Continuous.	5	2

The writer would draw particular attention to the fact of herbage quantity available in this case being influenced by the grazing system imposed, whilst there can be no doubt of the marked influence of grazing in conditioning the quality of herbage available, and this largely through the dominance of the clover species.

This point is further emphasised in the studies of Johnstone Wallace 1950 (125), who refers to the results of grazing treatment of pasture at Cornell. The pasture was laid down with a seeds mixture of grass species and Kent wild white clover, being uniformly treated for several years to develop a dense sward consisting of about 50% grass and 50% wild white clover. Replicated artificial grazing treatment was applied with the following results.

Artificial Grazing Treatment.		% Composition of Pasture.	
Intensity.	Interval. days.	Clover.	Grass.
Sward to within ½ inch of ground surface	7	80	20
- do -	28	50	50
- do -	56	10	90
- do -	84	1	99

Johnstone- Wallace concluded that periodical close grazing tends to increase the percentage of clover in a sward. He further reports that the experiment also showed that periodical grazing to ½ inch from the ground surface resulted in a higher yield of dry matter and protein than when artificial grazing was restricted to 2 inches from the ground surface.

From the aforementioned work it becomes apparent that this particular aspect of animal conditioned interactions may be of importance in the etiology of bloat in so far as they contribute to the qualitative factors involved. Support for this reasoning is given by the general observation and recommendations for management practice to avoid bloat described by Lyons (12) in New Zealand.

Referring to the management practices considered conducive to bloat, he states that hard winter grazing of pastures in certain localities is actually the factor most responsible for the bloating of dairy cows during the early spring. Ryegrass in particular but other grass species as well to some extent are so severely punished in the winter months that they cannot possibly afford effective competition (control) to the spring growth of white clover, and the outcome is a vitally unbalanced diet of sappy bloat-producing herbage for several weeks.

Lyons considers that in general a grazing pasture which has grown slowly without forcing over several of the winter months will be found free from any bloating tendency.

Also in New Zealand Marryat 1947 (133), gives as his opinion that close and continuous winter grazing will increase the danger of spring bloat incidence by encouraging clover dominance.

The same principle is implied by Schalk in America (cited by Cole et al. (9)) who refers to bloat becoming a serious problem in normally grass dominant pastures which have given way to clover species, to be alleviated when the balance of grass species was restored.

In England, Bathe (24), refers to the influence of climate and grazing animal as associated factors in conditioning herbage growth conducive to bloat incidence. He refers to conditions unfavourable to pasture growth, when herbage was quickly removed by grazing, grass species were grazed very close, and subsequent occurrence of climatic conditions favourable to herbage growth resulted in the dominance of rapidly growing clover, with a concomitant high bloat incidence.
Similar conditions where grazing influenced the dominance of legume species were implicated in cow fatalities from bloat reported in England by Ferguson. (114).

From the manner in which the grazing animal influences the botanical composition of the sward, there emerges good reason for considering the agronomic approach to the bloat problem. For if there is to be found valid basis for associating high bloat incidence with essentially legume dominant pasture, then both grazing management and consequent pasture composition must of necessity deserve prior consideration in evolving preventive measures.

To summarise the general effects of the grazing animal as a factor of induced pasture environment:---

a). The grazing animal strongly influences the social order of species in a pasture, the extent of that influence being subject to the degree of grazing intensity imposed and complexity of the mixture.

b). An increasing degree of grazing intensity compatible with vegetative growth generally favours the legume species in a pasture.

c). A number of reports implicate the intensity of grazing as being an accessary factor to bloat incidence in so far as the degree of grazing encourages legume dominance.

It is not unreasonable to associate specific qualitative factors with particular herbage species. In this event the above summary indicates that the grazing animal is a factor of interaction vitally affecting the quality of a pasture.

<u>COROLLARY. PART 11.</u> ------

COROLLARY. PART 11.

Once pasture has been made available for the animal an optimum consumption of herbage in a given pasturing time is primarily dependent on the efficient mechanical functioning of the ingestion act.
The manner of function and variations in performance of ingestion will doubtless influence the quantity of herbage intake in any one time.
This has necessitated a full consideration of normal grazing activity, and the variations occurring daily, seasonally, and as a result of selective grazing . With that knowledge it has been the better to examine the manner in which bloat becomes manifest in grazing ruminants.

There is evidence which affords some credence for the general statement that free pasturing cattle graze on an average 6 - 7 hours daily with a range which may extend to 10 hours.
The nature of this grazing assumes a cyclic pattern for ruminants during a 24 hour day most of the cycles being distributed throughout the daylight hours. A high rate of grazing occurs at the beginning of each cycle, being highest for dairy cattle in the cycles following milking.
It follows that where pasture, grazing management, and climate are not subject to wide variation, a certain level of herbage consumption would be expected to occur at fairly well defined periods of the day.
Now there is reliable evidence that ingestion time and rate are closely associated with food quantity consumed.
Further, that an increased intake of the same food follows an increased ingestion rate.
In the light of that experimental evidence and under the same pasturing conditions, it would reasonably be expected that the largest quantity of herbage would be consumed during these cycles when grazing time and rate are highest. The volume and rate of ruminal gas produced according to experiment (51), (52), would increase to reach a peak following each grazing cycle. (See Figs:17[2]-19[2]) and be lowered by eructation whilst resting between cycles. (51).

Volume and rate of ruminal gas production being proportional to food consumed (51), (52), (96), optimal levels would reasonably be reached when grazing time and rate were highest, which for dairy cattle would coincide with these first grazing cycles following milking.
At the same time a carry over of a certain volume of rumen gas from one

cycle to the next could well be conceived. (See Figs: 17^2-21^2) and maximal volume of rumen gas relative to the same grazing conditions may well be reached following grazing cycles subsequent to the first after milking. The maximal volume of rumen gas probably being influenced by the frequency and extent of eructation in the between cycle rest period.

Where the rate of formation and volume of rumen gas contributes to increasing ruminal pressure bloat would be expected to occur failing eructation to remove the gas formed.

The condition would most probably be first manifest during or at the end of the first grazing cycle after milking, being accentuated where pasture conditions are conducive to optimum herbage intake.

Under the same pasturing conditions differences in time and rate of grazing with subsequent differences in herbage quantity entering the rumen, would be reflected in differences of incidence, time onset, and degree of bloat.

The manifestation of such grazing activity differences may well contribute to differences in bloat incidence between pastures.

Some indication has been given of the manner in which the in situ interactions of plant and animal may influence these quantitative and qualitative factors probably implicated in the etiology of bloat.

To develop the concept of interaction, a logical pursuit of this discourse requires consideration of the internal environment of the rumen, for ultimately it is there that the normal plant and animal relationship breaks down resulting in the dysfunction manifest as bloat.

CC. RUMINANT DIGESTION AND BLOAT. THE PHYSIOLOGICAL PROCESSES INVOLVED, PARTICULARLY AS INFLUENCED BY BIOCHEMICAL AND PHYSICAL PROPERTIES OF HERBAGE PLANTS.

Each physiological stage of digestion in the ruminant progressing from the purely mechanical act of ingestion to the passage of ingesta from the rumen, will be examined with reference to current theories of bloat and relevant experimental findings. The subject matter will be treated in the following order:-----

A. The Ruminant Stomach, its anatomy and arrangement of contents.

B. Ingestion, and subsequent Alimentary function.

C. Motility of Rumen and Reticulum.

D. Eructation and Attendant Phenomena.

E. Rumen Gases, their composition and rate of formation.

A. THE RUMINANT STOMACH, ITS ANATOMY AND ARRANGEMENT OF CONTENTS.

A brief description of the anatomy of the ruminant stomach and the manner in which its contents are arranged, is a necessary introduction to an understanding of the functional phenomena to be discussed.

The four stomachs of the ruminant are the rumen, reticulum, omasum, and abomasum; it is only the first two, the rumen and reticulum which are primarily concerned in bloat, and will be considered in detail.

According to Schalk and Amadon (61), the four stomach compartments of the bovine animal hold 20 -- 40 gallons, the amount depending on the size of the animal. The rumen is the largest of the four compartments occupying 80% of the total capacity; its left side lies against the left abdominal wall in which region gas pressure first becomes apparent during the onset of bloat. The right side of the rumen is adjacent to the omasum abomasum and other abdominal viscera.

Division of the rumen into dorsal and ventral sacs, by left and right

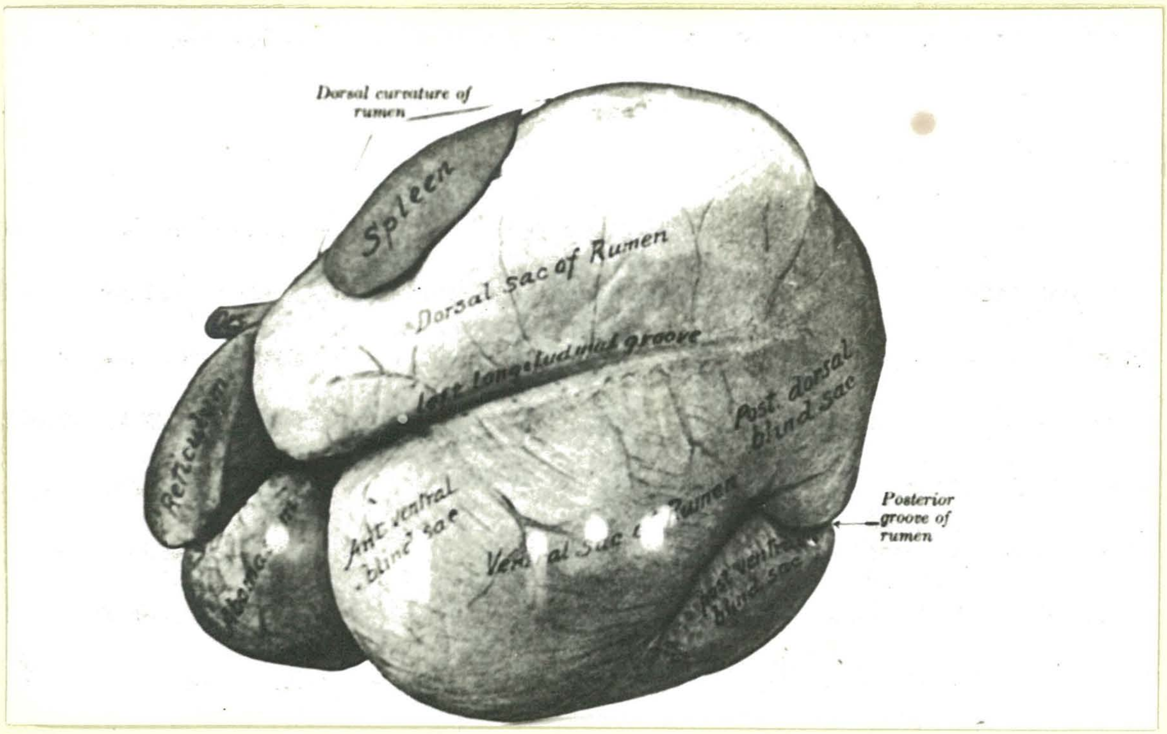


Fig.I6. Stomach of sheep. Left view.
From specimen hardened in situ.
The reticulum is somewhat contracted.
After Sisson(234).

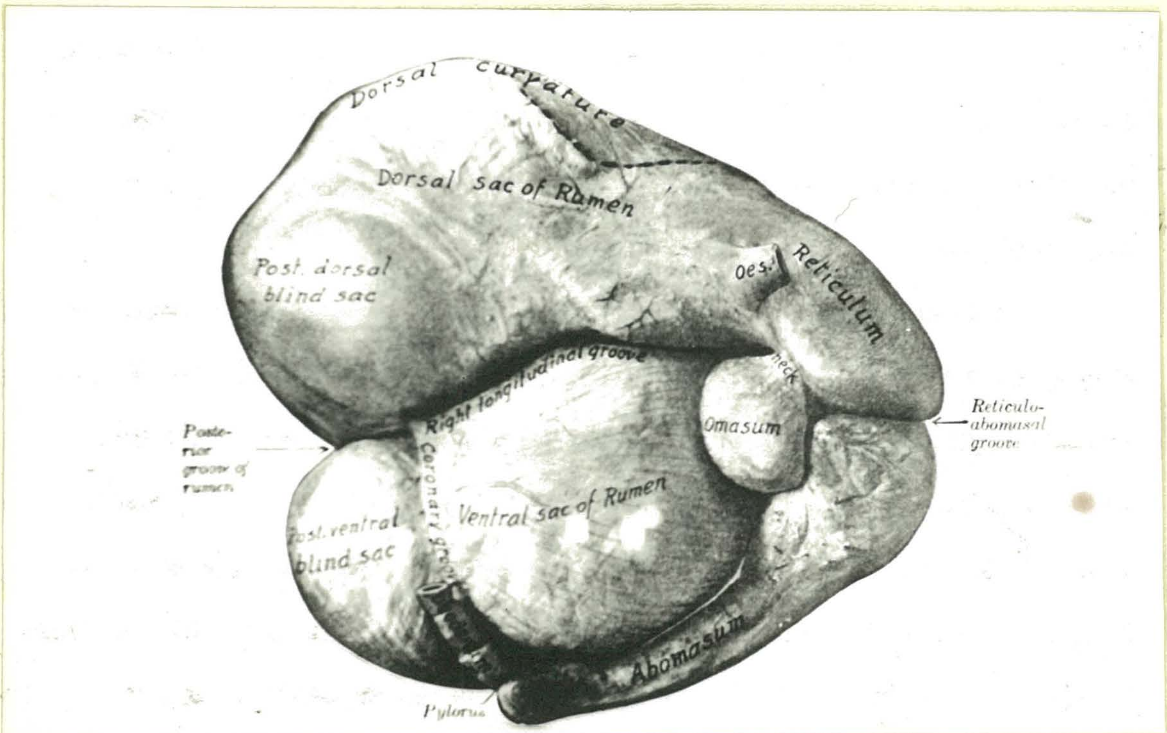


Fig.I7. Stomach of sheep.Right view.
From specimen hardened in situ.
Dotted line indicates position
of spleen. After Sisson(234)

longitudinal grooves is a marked anatomical feature, but less distinct is its division into posterior, middle, and anterior regions, by dorsal and ventral posterior coronary grooves. (See Figs. 16 and 17).

The reticulum is composed of a small blind sac anterior to the rumen, and seperated by a rumeno-reticular fold, apart from which the reticular cavity communicates freely with the rumen via the rumeno-reticular orifice. The medial wall of the reticulum designated the atrium ventriculi blends with that of the rumen, in the dorsal portion of which is located the oesophagus or cardia. Descending spirally from the cardia on the medial wall of the reticulum is the oesophageal groove terminating at the opening connecting reticular omasal cavities, which is closed by a sphincter like arrangement of muscles. (See Fig. 18).

Arrangement of Contents.

The physical nature of the rumeno-reticular contents and their arrangement are all important, in so far as they may both inhibit and stimulate rumenal motility (61).

It is in this connection that Cole et al. (51) postulate their theory that bloat is due to an absence of fibrous material, which they consider necessary for initiating the regurgitation reflex essential to the expulsion of rumen fermentation products.

According to Schalk and Amadon, the rumeno-reticular contents vary in physical nature characteristically between the ventral and dorsal regions. Liquids occupy the ventral portion of the rumeno-reticular cavities, semi-saturated food material the intermediate region of the rumen cavity, above which lies the freshly ingested forage material of low moisture content. The space between the latter material and the dorsal wall of the rumen being occupied by gas. This space varies in capacity according to the degree of filling of the rumen with liquid and solid ingesta, and according to the tone of rumenal musculature. (51).

The arrangement of liquids and solids is most clearly defined within the rumen, whilst the reticular contents under normal conditions consist of a semi liquid, uniform in consistency throughout. All the liquids are heavily loaded with completely saturated ingesta, or with concentrate food substances. (See Fig. 19)

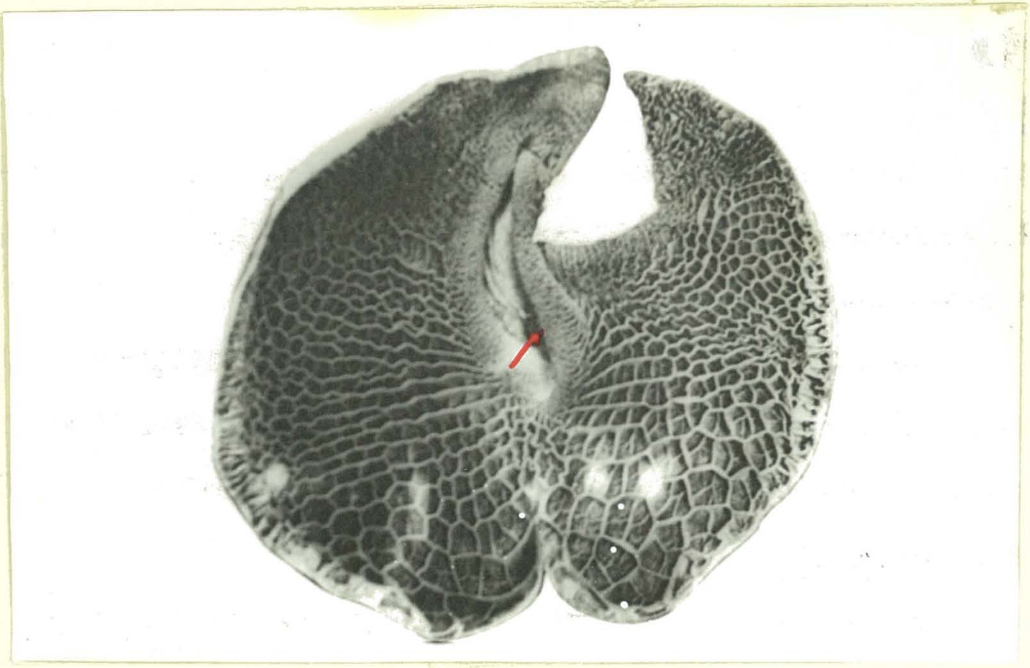
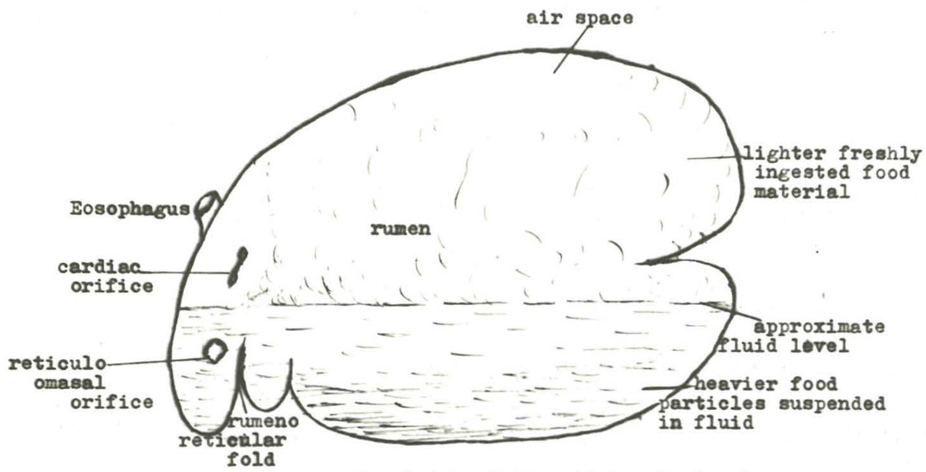


Fig.18. Reticulum of Ox.
The specimen was cut along the greatest curvature and laid open by reflecting the anterior wall.
C.is the cardia.The arrow points to the reticulo--omasal orifice.The spiral twist of the oesophageal groove was of necessity partly undone by reflecting the walls,its lips are drawn apart showing some of the peculiar birdclaw-like papillae in the ventral part.
After Sisson(234).



Diagrammatic sketch of the mid-longitudinal section of the rumen adapted from Schalk and Amadon(6I) and Cole et.al.(5I).The opening of the oesophagus into the rumen(cardiac orifice) is on the right side of the rumen,as is the opening of the reticulum into the omasum (reticulo-omasal).Note that the rumen and reticulum,are only partially seperated by the rumeno-reticular fold;also that the reticulo-omasal orifice is submerged in liquid,whereas the cardiac orifice is not. A syringe like action of the reticulum tends to force freshly swallowed food into the posterior rumen.

Fig.I9.

Balch 1950 (134), has shown that when cows eat diets containing roughages such as hay, the mean dry matter content in the dorsal and ventral regions of the rumen may vary as much as 10%, but varies much less when all the hay in the diet is ground. With such hay the proportion of dry matter in the contents of the ventral sac was often double that with diets of unground hay.

According to Nevens 1928 (135), there may be little or no free liquid in the rumen of full fed cattle, whilst much free liquids may be present in fasted animals, these findings having similar application to sheep. Ross 1934, (136), (137).

In the mature bovine animal all solids and liquids are deposited in the anterior dorsal sac of the rumen to be immediately transported anteriorly or posteriorly according to their physical nature, under the impulse of flows of liquid ingesta arising from reticulo- rumenal contractions. As these contractions increase in activity during ingestion, and may be conditioned by nervous stimuli in the oral cavity, Quin 1938, (139), it is important to first examine the physiological processes during the ingestion period.

B. INGESTION AND SUBSEQUENT ALIMENTARY FUNCTION.

Variations in the functional phenomena in this period, due both to the individuality of the animal and its reaction relative to the physical and chemical nature of the ingested food material, will determine in part the extent of the physiological activities which follow in the sequence of digestive processes.

Using stall fed fistulated cows Schalk and Amadon (61), removed food boli at the cardia as they were projected into the stomach. Considerable variation was observed in the form, weight and consistency of the bolus depending on the type of food ingested.
The following data were obtained:---

Table 6.

-----follows on next page.

Table 6.

SAMPLE WEIGHTS OF FOOD BOLI REMOVED AT CARDIA.

Weights in Grams.

Food.	Min:	Max:	Mean.
Hay.	40	140	85
Whole Oats.	70	240	140
Ground Feed.	40	191	101
Whole Corn.	27	147	81

Forage material was moulded into a firm oblong mass retaining its shape after removal. Cured hay boli had a low moisture content, floating in water, but their weight rapidly increases and identity is lost due to liquid absorption and maceration in the rumen.

Concentrate boli are much heavier than those composed of forage material due to the density of food material and more rapid moisture absorption, whilst ground feed boli are doughy and dry in the centre if rapidly ingested. Whole oats and corn were formed into loosely moulded boli.

The brief space of time devoted to the initial mastication process of the feeding period renders possible the ingestion of great quantities of food during a brief interval of time.

Furthering their investigations Schalk and Amadon observed the ingestion rate of 5 lb allowances of the aforementioned foods, their findings being summarised in Table 7.

Table 7.

INGESTION RATES.

Food.	Weight LBS.	No: of Boli.	Ingestion rate. (Minutes.)
Hay.	5	-	15
Whole Oats.	5	23	10
Ground Feed.	5	45	14
Whole Corn.	5	25	18

The figure for hay was an estimate based on the number and average weight of boli over a certain interval as the quantity of hay which can be consumed during a certain interval of steady eating is difficult of determination. This is due to the fact that hay ingestion is quite irregular under normal feeding conditions, it being impossible to feed a definite quantity and have this amount eaten in toto.

The rate of ingestion was affected most by the degree of hunger, there being a decrease in the number of boli ingested as the animal becomes partially satiated. This was clearly shown in one animal fed green lucerne after being penned 24 hours off feed, it was observed that 30 boli were ingested in the first 5 minutes and 19 in the succeeding 5 minutes.

Considering the feeding data in connection with this work as a whole Schalk and Amadon failed to note any marked difference in size between boli ingested at the beginning and end of feeding.

A combination of hunger and desirable food material resulted in the ingestion of large boli throughout the eating period, this applied particularly in the case of whole oats.

Unpalatable food exerted a pronounced depressant effect upon the ingestion act. This was evidenced by the feeding of prairie hay which was unpalatable to all animals observed. Some animals refused to eat it after a 24 hour fast; one cow ate in a very deliberate and uninterested manner and after passing 16 boli in to the rumen ingestion ceased, 15 minutes being required to prepare the boli having an average weight of 25 grams, the total weight of the meal being far below normal.

In regard to the time period required for cows to ingest a given weight of different foods, it is of interest to note the findings of Harshbarger (110). This worker fed 1 LB lots of grain, silage, and hay to five different breeds of dairy cows and obtained the following average rates of ingestion :----

Grain per LB.	2 -- 3 minutes.
Silage per LB.	1.75 -- 2.75 minutes.
Hay per LB.	7 --- 16 minutes.

For every type of feed, rate of eating was highest for the Friesian cows.

Manual removal of rumen contents by Schalk and Amadon (61) in a number of animals whilst feeding gave them cause to consider that judging by the work done on the bolus the act of ingestion appeared to contribute to satiation. In one animal ingestion ceased after the consumption of 38 lbs of lucerne, in spite of removal of rumen contents as fast as they were ingested. Likewise the ingestion period was shortened by adding ingesta to the rumen.

It was further observed in the normal subject that the desire for food always occurred a few minutes after evacuation of the rumen ingesta so that absence of volume undoubtedly created hunger.

Parallel findings of the co-operation of the ingestion act in transforming a state of hunger to one of satiety is evidenced in the simple stomach animal by the more recent work of Janowitz and Grossman 1949 (138). Using a dog with oesophageal and gastric fistulae, they concluded from their findings that oral and gastric reflexes combine to regulate food intake and the gastric reflex appears to be purely mechanical.

As the literature is singularly lacking in the field of regulation of food intake in the bovine, this aspect of Schalk and Amadon's work has been treated fully.

From the evidence presented earlier in this discourse there is every reason to believe that initially bloat in grazing ruminants is a food intake problem, whatever may be the subsequent cause.

Therefore an understanding of the functional phenomena and their variations associated with ingestion is fundamental to investigations of both cause and control of bloat.

It is often reported that only certain animals out of a herd are affected by bloat. Phillipson (121), Knapp et al. 1943 (140), Cole et al, (51), Kephart (44), Quin (96), added to this the writer has observed over a number of sets of Monozygotic twin cattle that the time onset and degree of bloat shows little variation within twin sets, but marked variation between sets.

Now this individual susceptibility has stimulated considerable speculation as to the underlying causes. Attention is drawn to the fact that the ingestion act is that expression of individuality most often commented upon during the incidence of bloat.

If the ingestion act contributes to satiation (61), variations between grazing animals in the expression of the act (108), may well account for individual susceptibility under the same pasture conditions conducive to bloat.

Further variations in this expression of individuality would be expected to occur owing to variations between animals in rumen size, should the ingestion act be an oral reflex subject to changes in rumen volume.

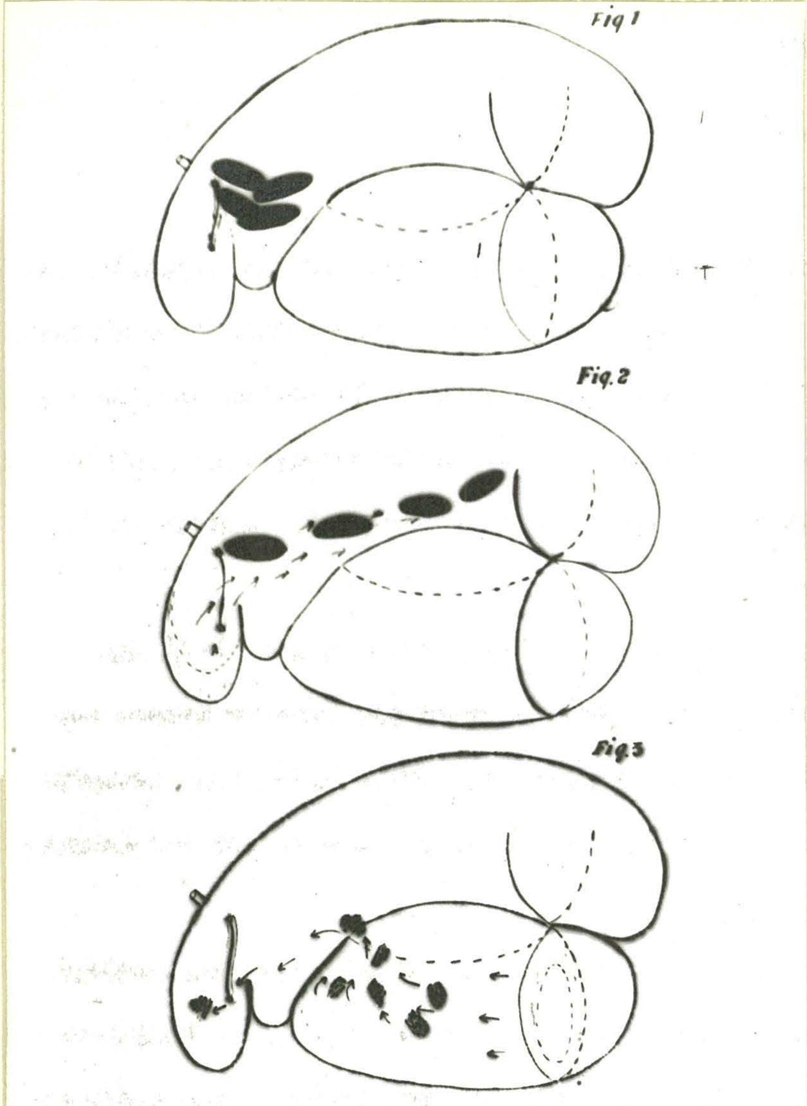


PLATE 1.—The progressive course of the lighter forage boli from the cardia into the rumen where their identity is finally lost.

Fig. 20.
After Schalk and
Amadon (6I).

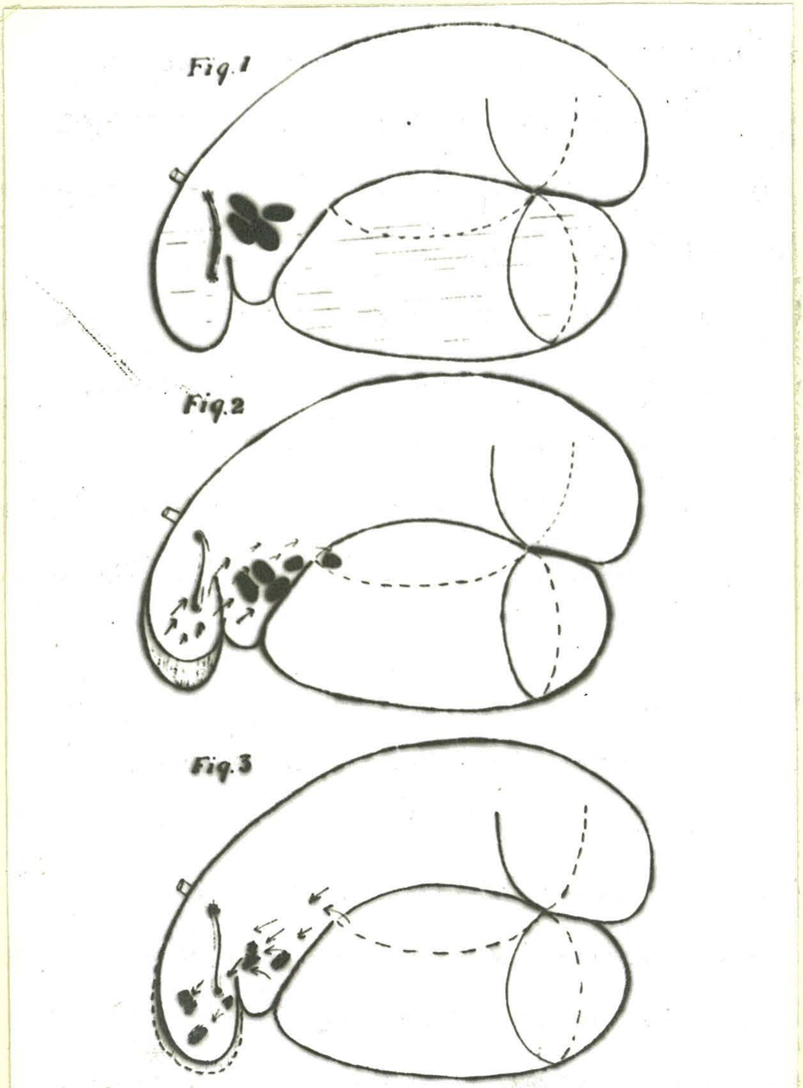


PLATE 2.—The course of the heavier concentrate boli illustrated in three figures. Note that only a minimal portion of such boli enters the rumen. The major portion remains in the reticulum.

Fig. 2I.
After Schalk and
Amadon. (6I).

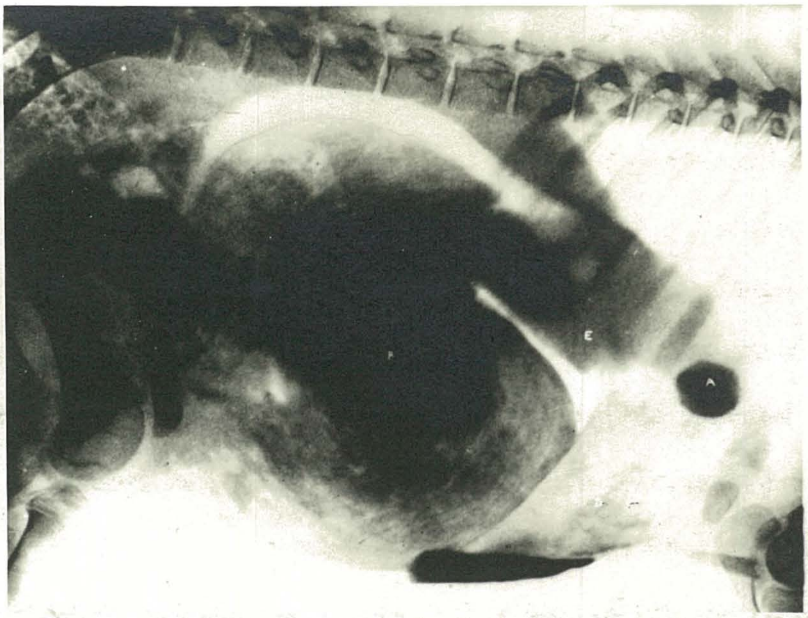
The writer submits that a closer study of food intake regulatory factors as well as ingestion rates in the bovine animal, should assist in an understanding of the physiological dysfunctions which may occur subsequent to ingestion.

Following in sequence upon the ingestion act are the physiological activities involved in the disposal of the food bolus within the stomach. These activities in cows are described as follows by Schalk and Amadon. (61). "Following ingestion and mastication the bolus is conveyed by peristaltic oesophageal contractions to be deposited just within the cardia in the anterior part of the rumen.
Immediately after the entrance of one or sometimes several boli the reticulum undergoes contraction. Two contractions closely spaced are executed by this division of the stomach, the first being less powerful than the second. Two flows of reticular ingesta are forced posteriorly into the rumen cavity.
During the feeding period, these flows of semi liquid from the reticular cavity play the important role of transporting newly arrived food material away from the cardia region into the more distant parts of the rumen or into the reticular cavity itself.

Boli consisting of light weight food material such as hay, are easily carried posteriorly and stored in the depths of the rumen cavity.

Concentrate boli follow this route in part, but their weight results in the major portion remaining in the reticulum." (See Figs. 20 and 21).
In lambs taken from grass the ingesta in the rumen are seen radiologically to be heaped up, and a fluid level appears only in the later stages of digestion. McAnally and Phillipson, 1944 (141). (See Fig. 21A).
The constant flushing of the anterior rumen region maintains a clear space for the deposit of the incoming ingesta and prevents any obstruction of the cardiac orifice.

The rumeno-reticular fold which forms the boundary line between the rumen and reticulum, aids indirectly the flows from the reticulum over the cardia region. This fold being located upon the ventral and lateral margins of the rumeno-reticular orifice diverts the posterior rush of liquids and solids in a medial direction and also serves to elevate the direction of this current thus ensuring a thorough saturation of the dorsal sac. During the period of reticular contraction, the fold is



The stomach of a lamb filled with barium by stomach-tube. The animal grazed for 5 hours between feeding with barium and exposure. The reticulum (A) is partially contracted and contains a blob of barium. The anterior blind sac of the rumen (E) is relaxing. The anterior and posterior longitudinal pillars of the rumen are contracting and can be seen as shadowless areas penetrating the shadow of the rumen. The grass in the rumen is arranged in a circular manner. The omasum is not visible. A deposit of barium is seen on the floor of the abomasum (D).

Fig.2IA. After McAnally and Phillipson.(I4I) also in a state of contraction.

The functional phenomena described at this stage with particular reference to the disposal of the food bolus in the cow, are essentially the same in the sheep and goat, Czepa and Stigler 1926, (142), (143), Krzywanek and Quast 1937, (144), Quin and Van der Wath, (139), Phillipson, 1939, (145) and (146).

It is suggested by the writer that any variations departing from the normal at this early stage of the digestive process which may result in reticular dysfunction and consequent obstruction of the cardia, will be contributory factors to the tympanic condition.

The food bolus may cause abnormal physiological variations in so far as it varies in respect of the factors:---

a). Density of food bolus.

b). Rate of boli ingested in a given time period.

Conjointly these factors being resolved into food mass entering the rumen in a given time.

From Schalk and Amadon's findings it would appear that light food boli are readily dispersed posteriorly on first being projected into the rumen, but heavier concentrate boli will in part remain in the reticulum or in the anterior region of the dorsal sac of the rumen for failure to be moved further by the reticular contractions.

A particular food may be conceived, for example, pasture grasses and legumes, intermediate in density, between hay and a concentrate food, which as a) and b) above remained normal, would not cause variations likely to result in reticular dysfunction. Where sub-normal conditions of these two factors prevail pathogenic variations contributing to the tympanic condition would be even less likely to occur.

With progressive variations in excess of the normal of a) and b) in the same food, conditions could be expected whereby the two consecutive reticular contractions occurring in cycles of one minute in cows (61) and sheep (145) are unable to efficiently dispose of the incoming boli, in spite of any increases occurring (139) in reticular contractions.

A piling up effect dependent on the animals degree of satiety may be conceived and the expulsion of products of fermentation prevented by obstruction of the cardiac orifice.

Furthermore, it is submitted that in pastured ruminants progressive

variations in excess of the normal variations of a) and b) are highly probable being conditioned by fluctuations in environment.
Such fluctuations as would occur between the growth and palatability of grasses and clovers, their respective dominance in a pasture, and the animals relative degree of satiety, could well cause variations in density and rate of food boli ingested.

This would reasonably accord with the postulations of Jacobsen and Espe (89), concerning the excessive consumption of dense feed resulting in bloat and would account for the incidence of bloat in those animals confined to the same pasture during the previous grazing of which no bloat occurred. (24). It may apply also to the difference in bloat incidence of the same animals on different pastures.

These studies of function in the ingestion period may be reduced to summary form.

a). Differences in weights between different foods ingested by cows in a given time are largely determined by food palatability, physical composition, and rate of ingestion.

b). All other factors being equal, an increase in the rate of ingestion of the same food will result in an increased weight of food consumed in a given time.

c). There is evidence which suggests that the ingestion act contributes to satiation, and is an oral reflex inhibited and stimulated by an increase and decrease respectively in rumen volume.

d). Depending on its density, the food bolus is disposed in the anterior or posterior region of the rumen by reticulo - rumenal contractions.

C. MOTILITY OF RUMEN AND RETICULUM.

Of the various aspects of rumenal function, that concerned with the movements of the forestomachs is of primary significance, seeing that the normal process of food fermentation, including the control of pH, and the eructation of gas is intimately associated with it.
Moreover the rumen is extremely susceptible to a wide variety of factors,

each of which may influence the motility in a specific manner, and hence also the chemical changes occurring within this organ. Quin et al. (139). Lack of rumenal and reticular motility is now authoritatively accepted as the primary etiological factor in bloat Phillipson, (40). Gas is expelled for the most part by eructation Wild, 1913 (147), which is synchronised with rumenal contraction. If the cycles of motility typical of the reticulum and rumen are disturbed Phillipson 1946 (148) states that tympanites is bound to occur, support being given to this view by Cole et al. (25).

Further emphasis is given to this point by Amadon, (cited by Cole et al (9)) who submits that rumenal contraction is essential in eructation in order to move the air pocket anteriorly to the cardiac orifice.

Such findings determine the necessity of bringing under review those relevant studies concerned with the normal movements of the reticulum and rumen, including the various conditions inhibiting and activating the tone of the reticulo-rumenal muscularis. They will be considered as follows:-

a) Reticulo-rumenal movements.

b) Factors influencing Rumenal movements

c) Rumenal movements and the onset of bloat

d) The relationship of rumenal movements to regurgitation and eructation.

a). Reticulo-Rumenal Movements.

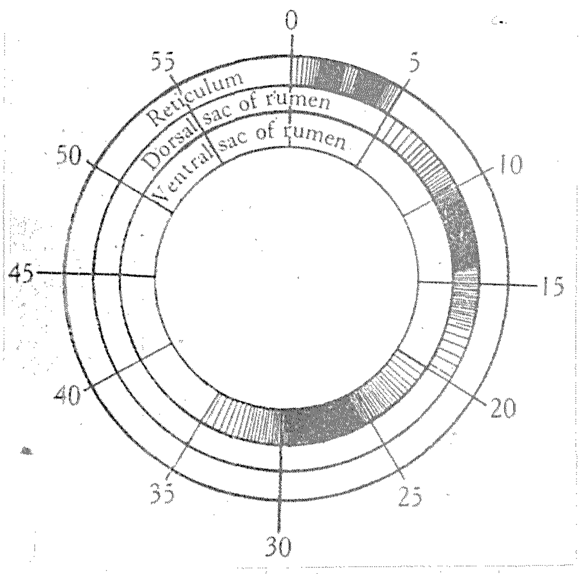
As this aspect of ruminant physiology is fundamental to the whole subject under discussion, it will be as well to quote verbatim the most recent findings of McAnnally and Phillipson (141). These workers from radiological studies and pressure tracings in sheep give a most exact account, diagrammatically illustrated, of the sequence of events in reticulo-rumenal motility which is essentially the same in all ruminants studied (142) (143) (144), although the sheep (139) (145) (146) is subject to greater normal variability than the cow (61).

"Figure 16A represents the cycle of movement found in the reticulum and rumen of sheep. The whole cycle represents 1 minute and is divided up into 5-second intervals.

The degree of contraction is shown by the depth of shading; thus the height of contraction is represented by the regions shaded black.

The outer circle illustrates the movements of the reticulum, the middle circle those of the dorsal sac of the rumen, and the inner circle those of the ventral sac of the rumen.

FIGURE 16. A.



Different sheep yield tracings sometimes more complicated, sometimes less so, but they may be reduced to a common type of which the more complicated rythms may be regarded as derivatives.

The type is illustrated in Fig. 16A it involves three principal localities:- the reticulum, the dorsal part of the rumen, and the ventral part of the rumen. The whole cycle takes about one minute. (a) We may commence with the reticulum because it is the pace maker. The contraction of the reticulum which takes about 5 seconds is a double contraction, having therefore two peaks of which the later one is the higher. (b) Before the end of the fifth second the contraction of the dorsal part of the rumen commences and lasts approximately 15 seconds, rising gradually to a maximal strength and fading at the same speed.

(c) The contraction of the ventral sac follows that of the dorsal sac immediately and gives a similar curve lasting the same time. (d) The whole organ, reticulum, and rumen, remains at rest from approximately the 35th second until the next contraction of the reticulum. Irregularities in this cycle are seen at two places: a pause may occur between the two contractions of the rumen (b) and (c), and the period of rest at the end of the cycle varies in length."

Although in the cow an appreciable time interval between the two reticular contractions is not recorded by Schalk and Amadon (61), two distinct contractions separated by complete relaxation are noted by Phillipson

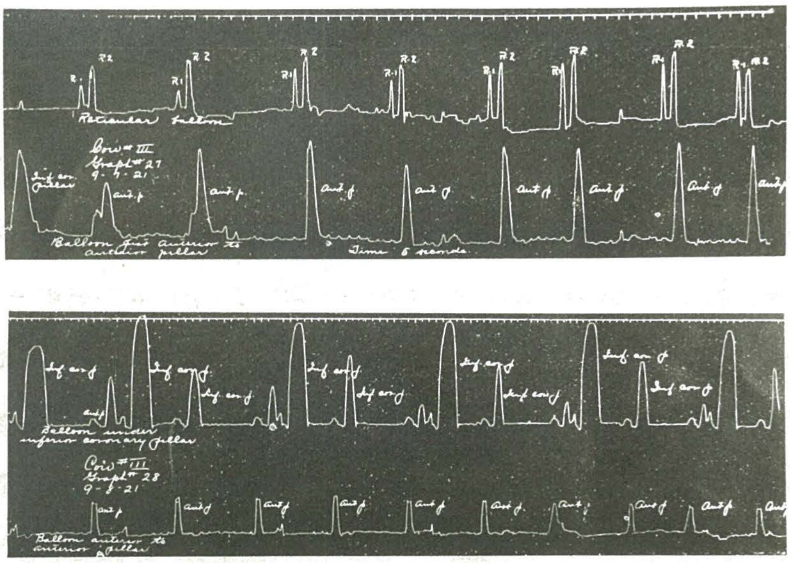
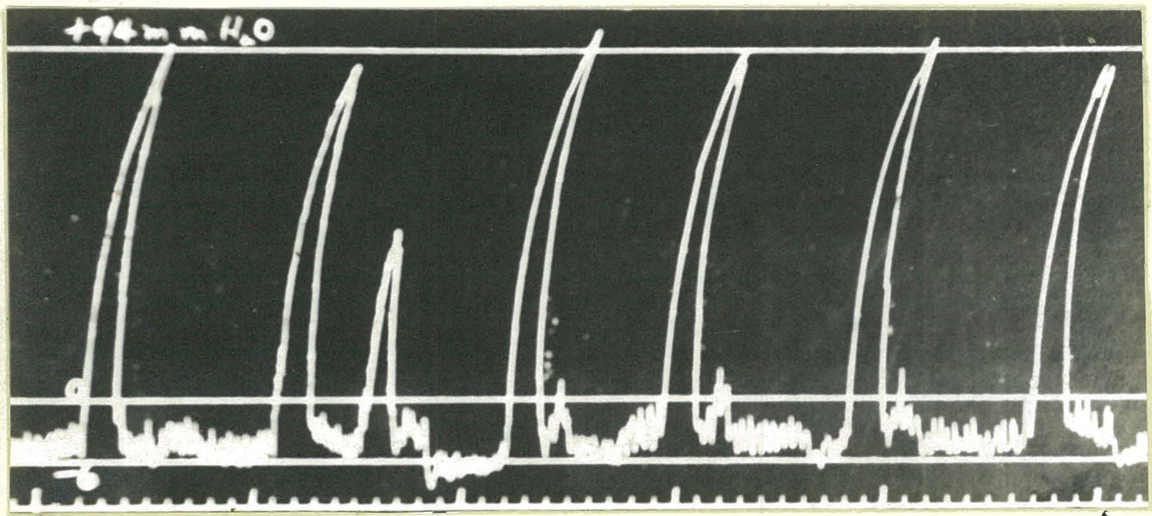


Figure 13.—Graph 27, Ox III, shows the relationship of the anterior pillar to the reticular motility. The upper tracing shows the first and second reticular contractions [redacted] and the lower tracing typical contractions of the anterior pillar of the rumen.

Graph 28, Ox III, shows the relationship of the inferior coronary pillar motility in the upper tracing to that of the motility of the anterior pillar in the lower tracing.

Fig. 22 After Schalk and Amadon (6I).



a minutes b

Fig. 22.A. (a-b) Normal rumen movements of sheep before food; 7 per 5 minutes at pressures from -6 to -94mm. water. After Quin(I39).

and McAnally (141), but in the sheep they find the second reticular contraction is superimposed upon the first and relaxation between the two stages is exceptional.

The movements of the rumen are slow and sustained compared with those of the reticulum and the pressure variations are considerable, varying in the sheep from -6 to 94 mm of water, Quin (139). In the cow a second wave of contraction involving the muscularis of the rumen only has been observed (61). It is inaugurated by the anterior pillar and completed by a ventral coronary movement, simultaneously with a forceful contraction of the ventral wall of the rumen. This wave appears at approximately 30-second intervals establishing a rather constant 1 - 2 rythm between the primary peristaltic wave over the reticulum and the rumen, and the secondary peristaltic wave which is confined to the rumen only. (See Fig. 22).

Referring to the rumino-reticular movements as a whole, Phillipson (145) asserts that they are total contractions and not peristaltic waves. The movements of the reticulo-rumen sac keep the ingesta in continual motion. The mass of ingesta of the reticulum presents radiologically a fluid level; when the organ contracts the liquid ingesta are thrown backwards from the reticulum to the anterior region of the rumen and they spread over the solid ingesta in the dorsal sac. The anterior extremity of the dorsal sac of the rumen relaxes as the reticulum contracts, and Czepa and Stigler (142) emphasize this alternate movement between the two organs resulting in an interchange of ingesta; they state that there is no correlation between these movements and those of the posterior sac of the rumen, with which observations Phillipson and McAnally (141) do not concur. These latter workers find a clear co-ordination of movements between reticulum and posterior part of the rumen in both the cow and sheep.

Using rumen fistulated sheep Quin (139) has shown that normal rumenal movement may undergo very considerable variations from any pattern temporarily established. It is essentially the strength of the individual contractions as well as the spacing of the movements which may undergo a sudden change, rather than the rate and the tonus of the rumen, both of which remain far more constant. (See Figs. 22A, 23, 24).

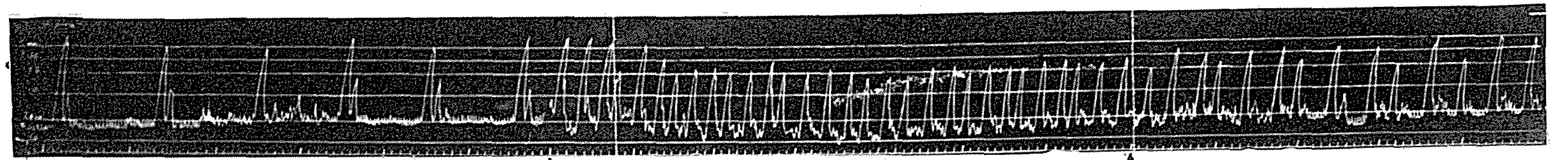
To summarise then:-

a) A number of workers implicate lack of rumen motility in the etiology of bloat.

b) Contractions of the reticulo-rumenal muscularis follow a common

Fig. 23. The Influence of Feeding on Rumenal Movements.

After Quin(139)



a) Normal rumenal movements before feeding; 8 per 5 minutes with pressures from -5 to +40mm. water.

b) At b. allowed to feed 300 grams of lucerne hay; movements accelerated to 22 per 5 minutes with pressures from -10 to +20mm. water.

c) At c. feeding stopped and movements decreased to 13 per 5 minutes with pressures between -5 and +40mm. water.

cyclic pattern in cattle, sheep, and goats.

c) The contractions are initiated in the reticulum and subsequently follow a dorso-ventral course in the rumen returning to the cardia.

d) Whether the reticulo-rumenal motility cycles are of peristaltic nature or are total contractions is controversial.

e) Reticulo-rumenal contractions serve to dispose and mix incoming ingesta.

f) The strength and spacing of rumenal contractions may vary but the rate and tonus remain steady.

b). Factors Influencing Rumenal Movements.

Further findings of Quin (139) demonstrate that feeding causes a very significant acceleration in the movement of the rumen, the opinion being ventured that this was in all probability due to vagus reflexes initiated in the pharynx and oesophagus and closely associated with mastication and deglutition. (See Fig. 23).

In some animals the sight of food may initiate weak reflex acceleration of rumenal movements.

The type of food exerts little if any effect on rumenal rythm, although contractions tend to become small on an exclusive diet of concentrates.

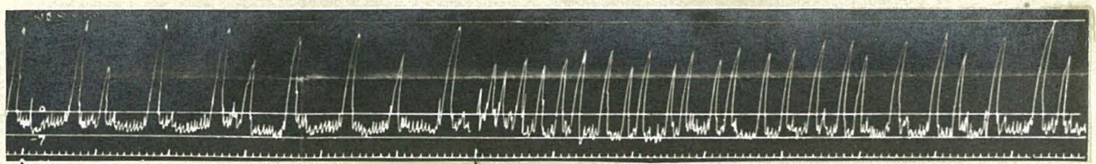
Complete starvation causes no definite change in the rate of rumenal movement up to the 3rd or 4th day, although the excursions may become progressively smaller. After this period all movements may disappear completely, there being a delay in their return on renewed feeding.

Neither the sight or actual drinking of water causes any appreciable change in rumenal motility.

Schalk and Amadon (61) demmnstrate clearly that the phases of activity of the cow influence rumenal motility which increases in frequency through the resting and rumination phases to reach a peak in the feeding period. They further emphasise the significance of complete exhaustion of the rumen muscularis and feeble motility under prolonged conditions of water deprivation.

Quin et al (139) ascertained the influence of different mineral salts on rumenal motility in sheep. It was found that copper sulphate doses on the back of the tongue accelerated rumenal motility in some animals to a rate similar to that during feeding; in others primary inhibition of rumenal

Fig. 24 The Influence of Copper Sulphate on Rumenal Movements After Quin(139)

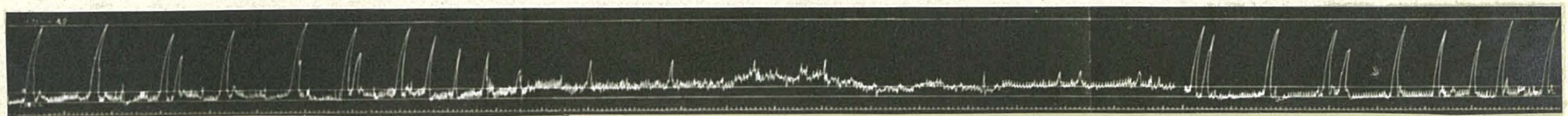


a) 10a.m. Normal rumenal movements before food, 7per 5 minutes at pressures -7 to +58mm. water.

b) 10.5a.m. Dosed 2.5cc. 10% copper sulphate on back of tongue. Note immediate acceleration to 18 movements per 5 minutes.

Fig. 24A.

The Influence of K.C.N. on Rumenal Movements. After Quin(139)



a) 9a.m. Normal rumenal movements before food at 5per 5 minutes at pressures -5 to +75mm. water.

b) 9.5a.m. Dosed into rumen 180mg. K.C.N. Note rapid decrease in movements followed by complete paralysis.

c) 2p.m. Return of normal rumenal movements 4hrs. after K.C.N. dose.

movement followed by acceleration was affected. (See Fig. 24).
Silver nitrate and nicotine sulphate solutions similarly accelerated rumenal motility. All other mineral salts tested failed to provoke this characteristic response from the rumen.
Potassium cyanide in small doses per os caused a rapid although transitory paralysis of all rumenal movements as did acetyl choline. (See Fig. 24A).
Adrenaline exerted little change in rumenal motility; other workers however have noted slowing and weakening of reticular contractions following adrenaline injection. Magee, 1932 (149), Dougherty, 1942 (150), Quin (139), further found that Lentin (Merck), Esmodil (Bayer) pilocarpine, and arecoline significantly stimulated motility.
Ictorgenin, a poisonous principle from the plant Lippia rhemanni effected complete and prolonged inhibition of rumen movements.

Clark and Quin, 1945 (151), determined the quantities of cyanide required to produce rumenal paralysis in sheep under different conditions of feed. In sheep given 300 -- 500 grams of lucerne hay, an average dose of 800 m g of K C N (340 m g H C N) was required to stop rumenal movements, whereas after 14 hours fast this effect was caused by 175 m g (70 m g H C N).

The increased tolerance after feeding was due to accelerated elimination of H.C.N. from the lungs, resulting from increased respiratory exchange, which in turn was caused by the absorption of CO_2 from the rumen during fermentation.

The writer would draw attention to the fact that the animals used were fed on hay, and it is claimed that roughage feeding is effective in facilitating eructation (25), (51).
It was further shown by these workers that sheep with paralysis of the rumen caused by K.C.N. are able to eructate gas, introduced through a rumen fistula at the rate of 2 litres per minute. There can be little doubt however that such eructation would be conditioned by the rumen volume occupied by ingesta, of which no account is given. Clark and Quin conclude that their observations afford no evidence for incriminating cyanogenetic factors in plants as being involved in the etiology of acute bloat in ruminants.
This work has since been confirmed by Phillipson (126), who fed cut grass to sheep, (instead of hay owing to its eructation stimulatory effects) with cyanide, H.C.N. poisoning symptoms and inhibition of rumenal movements

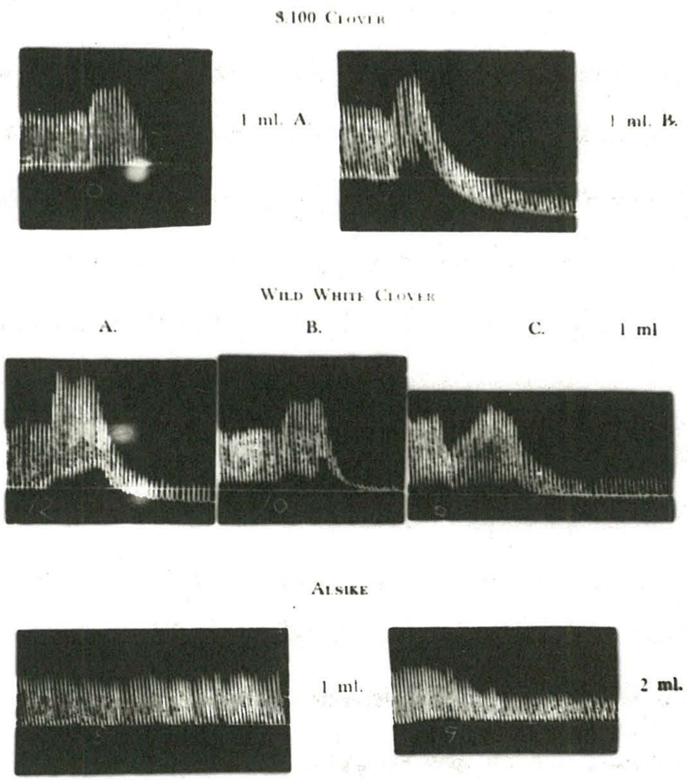


Fig. 1.
The effects of legume juices on isolated rabbit ileum.

Fig. 25. Shows that isolated rabbit ileum muscle movements are inhibited in varying degrees by different samples and dose rates of legume juices."It should be noted that only inhibitory effects were produced and no spasm or contraction of the muscle was recorded".

After Ferguson(II4). Punctuations and enclosed are the writer's.

resulted but no serious distension of the rumen was produced.

Ferguson 1948, (152), first directed attention to the muscle inhibitory power of clover juice and has since demonstrated Ferguson, 1948, (114), the influence of a factor in grasses and clovers affecting the activity of the isolated smooth muscle of the rabbit ileum.
Clover juices were found to have a stronger inhibitory effect than grasses; juices extracted from pastures upon which the incidence of bloat was high also had a very strong inhibitory action. (See Fig. 25).

Isolation of the active principle from lucerne and subsequent examination has been shown by Ferguson 1949 (153), to be a flavone which group of compounds occurs widely in plant material. More recently Ferguson 1950 (4), has identified the flavone in lucerne as TRICIN, although it cannot be assumed to be the only flavone occurring in lucerne; certain lucerne flavone preparations possess greater activity on smooth muscle movements than the purified isolated tricin.
According to Ferguson, (153), it seems that all natural flavones possess the power in varying degrees of inhibiting smooth muscle movements.
The feeding of a flavone to sheep with and without potassium cyanide has however, achieved nothing of note.

Although this work focuses attention on the pharmacological effects of certain constituents of grazing plants no evidence is provided that there is any direct connection with bloat.
Nevertheless, it is considered by Ferguson, (114), that there is a parallelism between the muscle inhibiting activity of plant juices and the expected power of the plants to produce bloat. However, this same worker has induced bloat in a bovine animal with 3 gallons of juice from spring grown lucerne, but could not do so with later cuts, Dcak, (Personal communication).
That clover juice possesses smooth muscle inhibitory properties has been confirmed by Evans and Evans, (117), (155), who have demonstrated the paralysis of rumen motility and death in sheep by the introduction of 1 litre of white clover juice directly into the rumen. (See Fig. 26).
The symptoms and P.M. findings being consistent with H.C.N. poisoning.
Crude juice from white clover had the same effect on isolated rabbit intestine as H.C.N. These workers conclude that since cyanogenetic glucosides are known to be present in certain legumes, these findings are

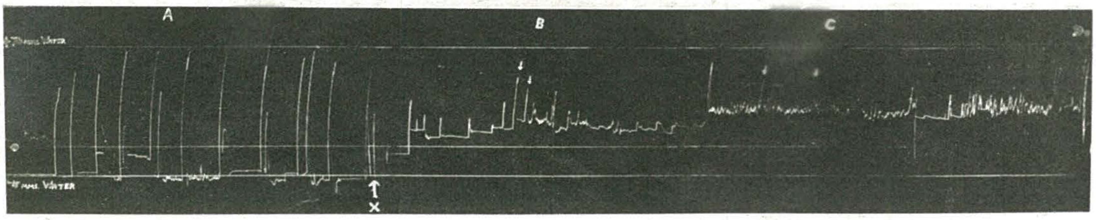


FIG. 15. A. Normal rumen activity.
X. Point of introduction of 1 litre of clover juice.
B. Arrows draw attention to the spasmodic deep respiration.
C. Tracing after one hour had elapsed since recording B. Arrows here indicate occasional rumen contractions reappearing.
D. Denotes a violent convulsive state (increase in pressure) shortly before the animal succumbed.

Fig. 26. The inhibitory effect of white clover juice on rumen motility of the sheep. After Evans and Evans(II7).

of considerable significance in elucidating the etiology of bloat. The suggestion that hydrocyanic acid as a rumen inhibitory factor present in clovers as cyanogenetic glucosides is implicated in the etiology of bloat does not accord with the findings of Clark and Quin (151). Further it is advanced without evidence of the extent of the contribution to rumenal atony, made by muscle inhibitory substances in pasture plants under normal grazing conditions.

It does not account for the reported incidence of bloat on ladino clover pastures Dougherty 1940 (156), and others (16), in which legume no hydrocyanic acid has been found, or for the high incidence generally associated with the grazing of red clover which according to Rigg et al. 1933 (157), contains a negligible percentage of H.C.N.

Rigg gives an average figure of 0.0003% H.C.N., as the average content in a number of different grasses used in improved pastures, and according to Doak (personal communication) it is questionable if even this amount exists. Nevertheless bloat occurs on ryegrass dominant pastures (93), and the writer has noted earlier in this discourse the incidence of bloat on a pasture containing 87% grass species, under which conditions it is very doubtful if sufficient H.C.N. would be ingested for toxic levels to prevail.
It must not be overlooked however that high bloat incidence is generally associated with legume dominant pasture and as Doak 1933 (158) has shown, the highest content of H.C.N. is found in the highest producing strains of white clover.

Using a rumen fistulated sheep Coop and Blakley 1949 (159), have demonstrated that the rumenal microflora can hydrolyse cyanogenetic glucosides very rapidly and the absorption of H.C.N. is equally as rapid. On an average 75% of dosed H.C.N. being absorbed within 15 minutes.

Coop and Blakley state that the peak production, concentration and absorption in the rumen of H.C.N. under most circumstances takes place within a few minutes (less than 10 minutes) of dosing free glucoside and within 10 -- 20 minutes of sheep eating cyanogenetic plant material.

It is interesting to speculate on a similar rapidity of H.C.N. production in the rumen of the cow used for bloat studies by the writer, when rumenal motility cycles were noted to increase in vigour with the onset of bloat.

If H.C.N. is a factor in herbage plants likely to inhibit rumen movements then as Coop and Blakley 1950 (160), point out rapid ingestion of cyanogenetic herbage will more probably be contributory to causing dangerous conditions in the rumen than slow ingestion as in the latter case H.C.N. formation would be balanced by absorption and detoxication.

Although Coop and Blakley (159), (160), (161), (162), used varying dose rates of both K.C.N. and Lotaustralin (the cyanogenetic glucoside of white clover) in their experiments on the metabolism and toxicity of cyanides and cyanogenetic glucosides in sheep, no reference was made of their effects being manifest in the tympanic condition.

Regarding the presence of muscle inhibitory factors other than H.C.N. in herbage plants, Ferguson (114), finds that grasses contain opposing factors, one inhibiting and another stimulating muscle action, and that usually the latter is stronger.

It remains for further work to confirm whether the inhibitory action of clover juices as demonstrated with rabbit muscle, would be effective on rumen muscle in the intact animal.

The number of factors which may influence reticulo-rumenal movements are many and varied, those of primary importance to this discussion may be summarised as follows:----

a). Under normal stall feeding conditions there is constant cyclic motility of the rumen muscularis which rises to a height of activity during feeding.

b). Rumenal rythm is not strongly influenced by different foods but excess concentrate feeding and water deprivation tend to reduce contractile strength.

c). Certain mineral salts, notably copper sulphate, and some plant extracts, accelerate rumenal motility to a degree comparable to the motility rate during feeding.

d). Potassium cyanide and certain plant extracts may effect complete inhibition of rumenal movements.

e). There is evidence that complete inhibition of rumen movements in sheep by K.C.N. dosing does not inhibit eructation of insufflated gas.

f). There is evidence that certain clover and grass principles identified as flavones inhibit isolated smooth muscle movements of rabbit ileum.

g). Evidence exists indicating that white clover juice which inhibits isolated smooth muscle movement, also inhibits rumen movements in sheep.

h). There is no known published evidence of the extent to which rumen movements vary in grazing ruminants.

i). There is no known published evidence which identifies the smooth muscle inhibitory principle in clover and grass with the tympanic condition in the rumen.

j). The implication of H.C.N. as a rumen inhibitory principle in herbage plants which may precipitate bloat is unsupported by experimental evidence.

k). Bloat is known to occur in ruminants grazing clover in which H.C.N. has not been found.

When considered in the above manner an open field of enquiry suggests itself; that is to investigate the differences which pasture plants of known mineral content may display in their respective influence upon rumen movements. Not only would this provide a logical parallel to those studies concerning muscle inhibitory factors in pasture plants, but considerable addition to our knowledge would be probable, the agronomic application of which is readily foreseen.

g). Rumenal Movements and the Onset of Bloat.

An understanding of the cyclic motility of the rumen serves to assist a more critical examination of the aforementioned postulate that the primary etiological factor in bloat is lack of reticulo-rumenal motility (40), (148).

The writer would suggest that this concept is also implied in the working hypotheses underlying the investigations of those factors in pasture plants inhibiting activity (152), (154), (148), (117), (155). There can be little doubt that the work in this field at Jealotts Hill was prompted by the association of bloat with disturbed muscle activity. (120), (114).

The incrimination of disturbed rumen motility in bloat is a controversial point concerning which Doak (personal communication) states that some workers are quite emphatic that these movements take place for some considerable time after pressure is apparent in the rumen.

Cole and Kleiber (unpublished, cited by Cole et al. (9)) have evidence that rumenal atony is not involved in the first stages of bloat on green legumes. Using a tympanometer devised by Kleiber (unpublished) for the direct determination of rumenal pressure they found periodic changes in pressure due to rumenal movements in animals mildly bloated. After bloat becomes severe however rumenal atony may develop resulting in little change in rumenal pressure.

Wester 1926 (163) states that rather than rumenal atony there is an increase in rumenal contractions in the early phases of acute bloat, whilst Gould (113), supports this by observing that marked rumenal activity occurs when bloat is arising, rumen paralysis being the end phase rather than the beginning. Further supporting evidence obtained by the writer was presented earlier in this discourse, the definite increase in rumenal contraction cycles being observed after the onset of bloat. The frequency and strength of the contractions increased with pressure and severity of the condition for periods up to 20 minutes after marked bloat was apparent and feeding had ceased.

These findings are in accord with those of Amadon and Detweiler (unpublished, cited by Cole et al (9)) - namely that increased intra-rumenal pressure causes a greater frequency of reticulo-rumenal contraction cycles and a greater strength of contraction. They conclude that this reaction to the distending effect of accumulated gas is very important, since it renders the muscular actions more effective in the process of gas removal.

Accelerated rumenal activity is undoubtedly an important factor in spontaneous recovery from mild bloat (9) as borne out also by the writer's observations. Severe cases of bloat in dairy cows closely observed from the a) commencement of ingestion during b) the onset of the condiition at c) the peak of rumenal pressure and d) on return to normal, exhibit an acceleration in rumenal movements into phase b) which were not apparent in phase c) if pressure was severe. If pressure is only marked in c) rumenal movements were characterised by very strong posterior movements in the lateral dorso lumbar region followed by anterior movements of similar strength in the lateral ventro abdominal region.
Passing into phase d) rumenal movements were again very strong and associated with frequent eructation, although the frequency of motility

cycles was lower than in phase a). A similar rythmic pattern of rumenal movements associated with apparent pressure increases and decreases in the left lumbar region has been noted in the normal grazing animal, the height of activity coinciding with each grazing cycle.

On the basis of the writer's studies earlier described, and failing evidence to the contrary, the view is supported that in the bloated animal the phases leading up to the peak of gas production in the rumen are occupied by accelerated rumenal activity which activity according to Schalk and Amadon, (61), and Quin, (139), is initiated in the feeding period. The phases returning to normal gas pressures being occupied by rumenal activity which according to Cole et al. (9), Wester (163), and Cole et al. (51) is associated with the eructation of gas.
Only during the phase of peak pressures would atony of rumenal movements appear probable.

If rumenal atony does in fact occur, whether to attribute the cause to excessive gas pressures, toxic gases, or inhibitory plant substances is a matter for some conjecture.

Whatever may be the reason, rumenal inactivity at such a late phase in the onset of bloat would be of little consequence as far as the pathogenesis of the tympanic condition is concerned.
Finally on this point Phillipson (148), confirming the work of Clark and Quin (151), states that there can be no doubt that paralysis of the rumen does not inhibit belching and does not necessarily produce bloat.
It would appear then that the primary cause of acute bloat in the grazing animal is concerned with the facility whereby rumen gases are able to gain access to the oesophagus through the cardiac sphincter, and not with rumenal atony.

To Summarise:-----

a). There is evidence which suggests that rumenal movements occur and increase in vigour during the onset of bloat in grazing ruminants, although it is the unsubstantiated opinion of some workers that rumenal atony obtains.

b). There is evidence that insufflated gas may be readily removed by eructation from the rumen of sheep in which movement is inhibited, without bloat becoming manifest.

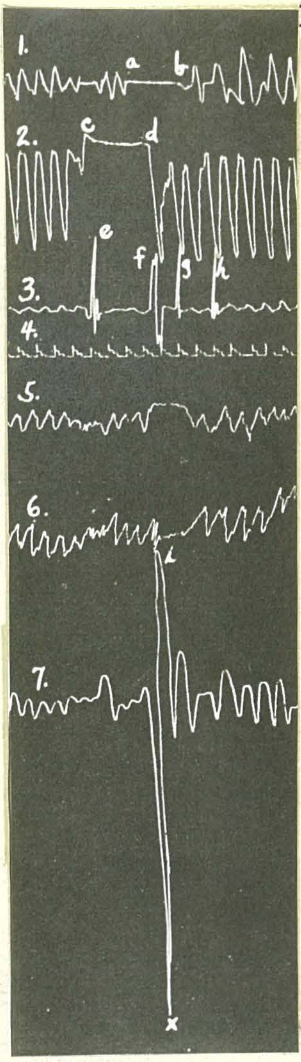


Fig. 27. Tracings to show the mechanism of regurgitation in rumination. The writing points were vertically placed. The cow regurgitated at X. (1. Movements of air in the nostrils. Note closure of the glottis from a to b. (2. Movements of the jaw in mastication. Note the pause, cd. (3. Movements of bolus in the cervical part of the oesophagus: e, the masti--cated bolus f, the regurgitated bolus; g, h, the swallowed liquid pressed out of the regurgitated bolus. (4. Time tracing showing 1 second intervals. (5. Movements of the thoracic wall. (6. Rectal pressure. Note that it is not elevated during regurgitation. (7. Pressure changes in the trachea. Note the sharp fall coincident with regurgitation. The rise in pressure at i is due in part to the momentum of the liquid (bromoform) used in the recording manometer and doubtless in part to an increase in intrapulmonic pressure due to rebound of the thoracic wall. After Dukes (165).

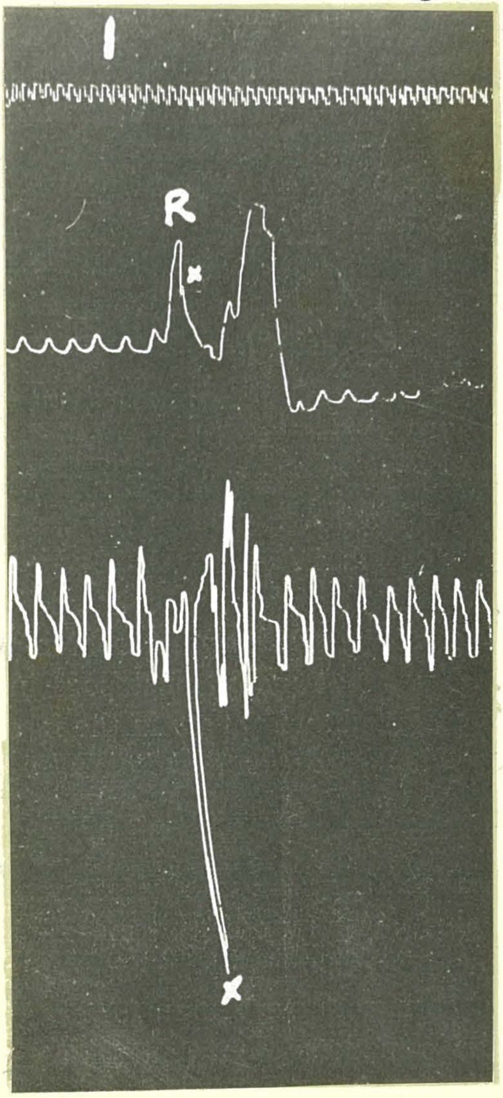


Fig. 28. Tracings from a calf to show the temporal relation of the first reticular contraction (R) to regurgitation (X). The upper curve shows contractions of the reticulum and the anterior part of the rumen; the lower curve shows intratracheal pressure. The calf regurgitated at x, but it is evident that the reticulum had already contracted. The writing points were vertically placed. After Dukes (165).

d). The Relationship of Rumenal Movements to Regurgitation and Eructation.

Regurgitation is that reticulo-rumenal function whereby ingesta is returned from the rumenthrough the cardiac orifice into the oesophagus, where it is conveyed by reverse peristalsis to the oral cavity for rumination. (See Fig. 27).

Eructation involves the removal of gas from the stomach through the cardiac orifice into the oesophagus for expulsion from the oral cavity.

According to Cole et al. (51), similar physiological phenomena underlies both these functions which are reflexly controlled by a common stimulant.

Now whilst exact knowledge exists of the functional mechanism involved in the regurgitation act according to Bourne 1950 (164), the eructation mechanism has not been critically analysed.

As it was previously inferred that the primary cause of bloat is concerned with the facility of eructation, it is therefore necessary to examine the extent to which the details of the regurgitation mechanism may be common to that of eructation.

Reticular motility studies by Schalk and Amadon (61), and Dukes 1947 (165), indicate that the regurgitation mechanism functions in the following manner:----

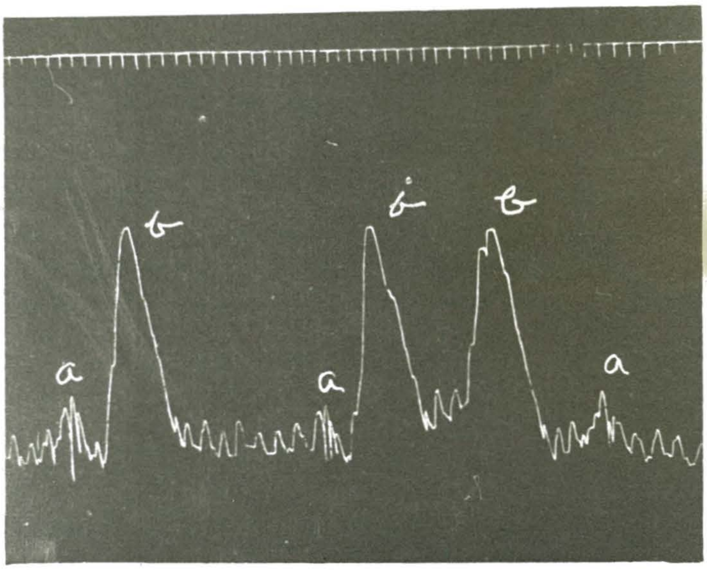
An extra reticular contraction occurs as rumination activity begins and according to Dukes (165), the reticulum contracts just before but not simultaneously with regurgitation. (See Figs. 28, 29).

An elevation of reticular liquid ingesta to the dorsally situated cardia floods the oesophageal orifice just before regurgitation.

It is at the same time that a strong inspiratory movement drawing air into the lungs reduces the pressure within the thorax and therefore within the oesophagus. This reduced pressure results in the liquid ingesta being drawn through the cardiac orifice into the oesophagus where a reverse peristaltic wave carries the food into the mouth.

Quoting these findings Cole et al. (51), conclude that regurgitation involves the co-ordinated activity of the muscles of the reticulum, diaphragm and oesophagus. They state that the muscles of the reticulum are entirely involuntary, those of the oesophagus partly so, and they infer that regurgitation represents a finely adjusted reflex act.

These conclusions are not in accord with the findings of Flourens 1844 (166), who has shown that the reticulum is probably not essential in regurgitation



Tracing from a cow to show the condition of intraruminal pressure during rumination: *a*, regurgitation; *b*, contraction of the rumen. The other waves are caused by the respiratory movements. Note that contraction of the rumen follows regurgitation but does not coincide with it. The time tracing shows intervals of 2 seconds. (Bergman and Dukes.)

Fig. 29. After Dukes(I65).

by an experiment with a sheep in which the bottom of the reticulum was cut away and the resulting rim sutured to the floor of the abdomen. The animal ruminated afterwards.

Wester 1926 (163), and 1930 (167), indicates that contractions of the diaphragm in ruminants are not absolutely necessary and states that on severance of all the phrenic roots rumination is still possible. This worker further states that the contraction of the reticulum, normally in ruminants always a preceding rejection, is not absolutely necessary for the carrying out of the rumination act; if after atropin injection the reticulum can no longer contract, rumination is still possible. This same worker considers the lowering of intra thoracic pressure is of non essential significance in ruminants, and rumination is effected by oesophageal contraction sucking ingesta from the stomach.

Dukes (165), considers the part played by the reticulum in regurgitation is not fully known and states that the entrance of food into the oesophagus from the rumen is brought about by intra oesophageal negative pressure, due to an inspiratory effort with a closed glottis, the oesophageal groove, abdominal muscles, and reticulum playing no direct part in the process. In contrast to this account Schalk and Amadon (61) have noted in rumen fistulated cattle that although diaphragmatic contraction appeared, the failure of reticular movements to coincide resulted in the non regurgitation of the bolus. They state that a perfect co-ordination of the motility is essential to a successful transfer of the gastric contents to the mouth, and the absence of any one of a number of important factors will hold the act in abeyance.

It would seem that considerable difference of opinion exists as to the precise factors involved in the regurgitation act. Whilst there is obviously place for further analysis of this function, it would appear that a co-ordination of the voluntary and involuntary muscularis is involved.

The stimulation of regurgitation may be produced by the application of friction stimuli to the anterior wall of the reticulum, such as the finger tip, (113) and hay, or straw drawn over the rumen and reticulum mucosa. (61).

A diet composed exclusively of concentrates will abolish the act of rumination although the animals will remain in a condition of health. (61).

Heifers reared from birth to 18 months by Mead and Goss (47), on a diet without roughage showed lack of regular rumination and frequent bloating.

Cole et al.(51), seek to explain the fact that the feeding of grain alone is not accompanied by a normal period of rumination, by the absence of an adequate amount of fibrous material contacting the wall of the rumen and initiating the regurgitation reflex. They make the inference that the scratching action of ingested roughage, on the anterior wall of the rumen normally initiates rumination.

On this basis these workers further state that the belching mechanism is controlled in a similar manner to that of the regurgitation mechanism. In other words gas is removed from the stomach by a reflex opening of the cardiac sphincter initiated by friction stimuli.

Cole et al. extend this inference to postulate that bloat is due to a dietary lack of sufficient fibre of proper type to initiate eructation.

The implication is, that the physiological urge to ruminate is compelled by the fibre content of the rumen ingesta, and that the same mechanism is identified with eructation and the expulsion of gas is similarly controlled.

Such reasoning does not make sufficient allowance for voluntary nervous intervention in the regurgitation act and subsequent rumination. The strength of voluntary control over regurgitation is suggested by the field studies of Hancock (108), in that the height of ruminating activity in grazing monozygotic twin dairy cattle, occurs soon after nightfall, after which a gradual continuous decline takes place until morning milking. The decline in ruminating activity is associated with shortening periods of rumination. The enforced period of loafing at morning milking is largely occupied by rumination, but if milking is delayed and the cows remain on pasture they will graze instead. If cows are disturbed during ruminating periods they may stop ruminating and revert to grazing.

It thus appears that the physiological urge to ruminate is not always compelling, and further more illustrates the animals ability to delay or promote rumination.

Thus the writer suggests that the measure of voluntary control over the regurgitation mechanism would seem to be greater than is implied by the limits imposed by the fibre content of the ingesta.

To suggest that concentrate foods inhibit rumination owing to lack of fibre is to ignore the passage of such foods through the stomach.
Owing to the density and physical state of concentrate foods, on ingestion they pass in large part directly into the reticulum and as Schalk and Amadon (61) have shown, palpation of the reticulo omasal orifice during ingestion will often reveal the passage of quantities of the dense ingesta into the omasum and abomasum. Whole corn gravitates to the floor of the reticulum, escapes the regurgitation flow of ingesta over the cardia, and passes into the third and fourth compartments of the stomach.
Balch 1950 (134), using rumen fistulated cows has shown that ground hay given as a small addition to a diet of unground hay was invariably excreted more rapidly than unground hay. Ground hay in diets in which all hay was ground was usually excreted over a longer period than hay in a similar diet in which the hay was not ground. Both of these differences were considered due to changes in the movements of the foods in the reticulo-rumen.

It will be readily conceived that the frequency of rumination and therefore regurgitation will be lower on a diet of foods which pass rapidly into the omasum. This would seemingly depend not so much on the fibrous nature of the food as upon its physical state. Therefore it does not follow that the actual regurgitation act is actively inhibited by lack of fibre only. Differences in the physical state of a diet containing similar fibre are associated with differences in bloat incidence by Mead et al. (15).
These workers report 21 cases of bloat in stall fed ground hay, as against 1 case in the same group of cattle which consumed a greater average weight of food at each meal, composed of a similar sample of unground hay and concentrates.

In addition to friction stimuli Schalk and Amadon (61), demonstrated that pressure upon the reticular mucosa is also productive of the regurgitation act, but not to the same degree as friction. This finds support in a report from Stuart and Cross (11), who note that palpation of the reticulum in a cow with chronic rumenal tympany, caused rumination which increased when the hand was withdrawn.
Anderson (127) reports that stimulation of the oesophageal groove will

cause belching and bringing up of gas in cows with complete rumenal stasis. However, regurgitation and eructation would appear to occur at different phases of rumen motility and intra-rumenal pressures, as according to Schalk and Amadon opening of the cardiac orifice and regurgitation takes place when the rumen is quiescent, and in eructation when the rumen is in an active state of contraction and intra- rumenal pressures are highest. This is in accord with the work of Wester (167), who states that eructation arises as a result of an anti peristaltic wave getting past the cardia. To accommodate this the cardia opens regularly in cattle once in a contraction period, as a result of the crossing over of the cardia by the anti peristaltic wave of the rumen. These findings would suggest that regurgitation and eructation are not dependent upon a common physiological mechanism, if it is accepted that regurgitation is a finely adjusted reflex act stimulated by fibrous ingesta.

In the light of Wester's findings, and the minutely cycles of rumenal motility reported by a number of workers (61), (141), it is interesting to note Hancock's (108) record of boluses regurgitated per minute of rumination time for 2 sets of monozygotic twin cattle over one 24 hour period. (Table 8)

TABLE. 8.

Boluses per Minute of Rumination time.

TIME PERIOD.	T1.	T2.	T17	T18	AVERAGE.
7.a.m.-5 p.m.	1.26	1.22	.97	1.09	1.17
5 p.m.- 7 a.m.	1.27	1.18	.98	.93	1.09
Average	1.27	1.19	.98	.95	1.10

Whilst there would seem to be some relationship between reticulo- rumenal motility, eructation, and regurgitation, the evidence is made the more conflicting when the findings of Quin (151) are examined. Using rumen fistulated sheep with complete rumenal paralysis effected by K.C.N. dosage 6 litres of insufflated air were readily expelled by eructation even when the rumen was flooded with water. Although this work awaits confirmation it serves to make less tenable the concept of friction stimuli being essential for eructation. Pressure would conceivably act as a stimulant in the aforementioned case, and in this connection Cole et al. (51) give evidence that eructation coincides with rumenal contraction (although not with every contraction) and resultant increased intra rumenal pressure.

The relationship of rumenal movements to regurgitation and eruct ation may be assessed in the following summary:---

a). The evidence is conflicting as to the part, if any, of reticulo-rumenal movements in regurgitation.

b). There is evidence that regurgitation and eructation may be effected during complete paralysis of reticulum and rumen.

c). The physiological urge to ruminate does not appear to be compelling.

d). Regurgitation may be effected by the application of friction and pressure stimuli.

e). Eructation may be effected by the application of pressure stimuli.

f). There is evidence that eructation and regurgitation occur during rumen contraction and relaxation respectively.

In view of this summary the writer submits that there is insufficient evidence whereby eructation and regurgitation may be identified with the same physiological mechanisms.

Thereby the postulate that bloat is due to a dietary lack of sufficient fibre to initiate eructation would seem to be untenable. Even assuming this postulate, it is necessary to concede a minor role in the initiation of eructation of insufficient consequence to alleviate excess rumen gas pressures, to factors other than fibrous ingesta, which is untenable in view of gas insufflation studies.

D. ERUCTATION AND ATTENDANT PHENOMENA.

Gas may be expelled from the rumen in the following ways: by eructation with subsequent escape through the oesophagus, by diffusion into the blood stream to be eliminated by exhalation; and it is possible for some to be removed by bacteria in their metabolic processes.

Most of the rumen gas is expelled by eructation Wild 1913 (168), through the cardiac orifice and oesophagus, and if expulsion in this manner is prevented the other means of gas removal are inadequate to prevent death from bloat. (9).

The function of eructation then and those factors contributing to its activation would seem to be of primary importance in relieving gas pressure in the rumen. Either inhibitory functional variations, or factors impedable to the onward passage of gas during the course of eructation will become pathogenic in the onset of tympanic condition.

For normal and unimpeded functioning of eructation it is necessary for the oesophagus to be clear of food obstruction, or that arising from clinical causes. The muscular tonus of the cardiac sphincter should be normal, and the cardiac orifice free from obstruction. In addition it is upheld by some workers that those rumenal movements synchronised with the eructation act should be fully co-ordinated. (61)

Ascott (10), in the course of post mortem work has shown that chronic bloat is symptomatic where dysfunction of either of the above factors occur.

It is also a point not to be overlooked that the oesophagus communicates with the rumen cavity at a much lower level than the upper limits of the dorsal sac of the rumen. This anatomical arrangement would appear to impede rather than facilitate the removal of gas particularly under conditions of rapid ingestion, although it has been indicated that eructation is unimpeded even when the cardia is submerged. (148), (139).
In the final analysis eructation is dependent on the muscular activity of the cardiac sphincter muscle controlling the entry from rumen to oesophagus.

Therefore it will be necessary to examine the role of the cardiac sphincter in eructation by considering: ----

a). Function of the Cardiac Sphincter.

b). Control of the Cardiac Sphincter.

c). Response of the Cardiac Sphincter.

a). <u>Function of the Cardiac Sphincter.</u>

The cardiac sphincter, a band of smooth muscle, encircles and controls by its action, the cardia or orifice at the juncture of oesophagus and stomach. Its function is to inhibit the passage of food from the stomach into the oesophagus.
Except during swallowing, regurgitation, and eructation, the cardiac sphincter is normally closed. Stigler 1931 (169), demonstrates this fact by palpation of the cardiac orifice through a rumen fistula. As the cardiac sphincter is composed of smooth muscle it is doubtless capable of

independent activity varying with changing conditions on the oesophageal and stomach sides.

The sphincter is however also under the control of the central nervous system being innervated by the vagus in the dog and rabbit, and in part by the splanchnic (sympathetic) in the cat, Carlson et al. (170). Spasm of the cardia in dogs has been reproduced experimentally by bi-lateral vagotomy, combined with an encircling incision through the outer coats of the oesophagus - just above the diaphragm. Since neither procedure alone is sufficient to produce the condition it may be conceived that there are fibres coursing within the wall of the oesophagus which are related in some way to relaxation of the cardiac sphincter. Grondahl and Harvey 1940 (171).

That stimulation of the cervical vagus in the dog causes relaxation of the cardia followed by contraction was demonstrated in the work of Lehmann 1945 (172). By cutting the vagus nerves in the neck he also found the lower end of the oesophagus contracted, the cardiospasm resulting was presumed to be due to the unopposed action of the sympathetic nerves, since atropine is ineffective whilst ergotamine causes a relaxation. The fibres producing contraction were found to be cholinergic and they travel in the main trunks of the vagi, the inhibitory mechanism being within the wall of the lower oesophagus.

Mann et al. 1947 (173), carried this work further by double vagotomy at different levels in trained adult dogs. Section of the nerves at or above the hilum of the lungs produced paralysis and dilatation of the distal moiety of the oesophagus. There was no impairment of appetite but the animals showed a pronounced tendency to emesis.

Swallowing thrust the meal into the dilated oesophagus but tonic contraction of the smooth muscle forced the bolus into the pharynx from which it was vomited. In half the animals used the cardia was distinctly patulous. After supra-diaphragmatic vagotomy a normal oesophageal activity to the swallowing of the bolus was observed but after a brief interval was regurgitated into the oesophagus. This was attributed to an impairment of the receptive relaxation of the stomach associated with a hypotonic cardia. It is important to note in relation to the present discussion that similar results were obtained when vagotomy was performed on sympathectomised animals.

Mann et al state that whilst the extrinsic innervation of the muscle fibres of the lower part of the oesophagus is entirely from the vagus the sympathetic supply is limited to blood vessels.

A number of workers concur that the vagal supply to the cardia is chiefly of motor function in simple stomach animals. (174), (175). Nevertheless, Hillemand et al 1943 (176), claim to have treated oesophageal dilatation and cardiospasm by injection of the splanchnic nerves and splanchnicectomy. According to Templeton, (177), weak peristalsis in the lower oesophagus fails to produce relaxation of the cardia and results in cardiospasm in human subjects.

Palpating the cardia through a rumen fistula at the moment of eructation Amadon and Detweiler 1945 (178), found it to be widely dilated which they concluded involved muscular contraction and is therefore an active rather than a passive change. They noted however that at times the cardia may not actively dilate, but relaxation occurs so that gas may escape through the orifice. In this connection it is particularly interesting to note the work of Pennington et al. 1946 (179), with dogs who examined the relation of pressure changes in a jejunal Thiry fistula to tone changes in the cardia and its relaxation following peristalsis induced by swallowing or distension. Slight increases in pressure were ineffective, but repeated moderate distension caused some relaxation without nausea or distress, there was no effect on the typical relaxation contraction pattern after peristalsis.

Reviewing this work Ingram 1947 (180), states that the paths of this reflex have not been worked out but it is not intrinsic.

The evidence then implies that the cardiac sphincter functions by active motor innervation having origin in the vagus, other movements arising from the facility of smooth muscle for spontaneous contraction.

b). Control of the Cardiac Sphincter.

To what extent the cardiac sphincter may be controlled by voluntary or reflex action in eructation, and if a reflex the identity of the stimulus, is a matter for conjecture.

Dukes 1947 (181), states that the cardiac sphincter is probably controlled reflexly, whilst Cole et al. (9), consider that the cardiac orifice is opened reflexly in eructation not simply forced open by increased rumenal

Fig. 6.—Tracing of portion of ruminal pressure curve of cow 557 on full ration of alfalfa hay and corn silage, using mercury manometer (January 29, 1937). The bottom line is the time interval in minutes. The points on the middle line indicate when audible belching occurred. The vertical scale represents pressure, 0.5 mm on the graph corresponding with 1.0 mm mercury of pressure. Note that after each belching a drop in ruminal pressure occurred and that this drop in pressure follows a ruminal contraction. The highest pressure point is due to stretching. Stretching, coughing, and so forth, cause greater changes in ruminal pressure than does the contraction of the rumen musculature itself.

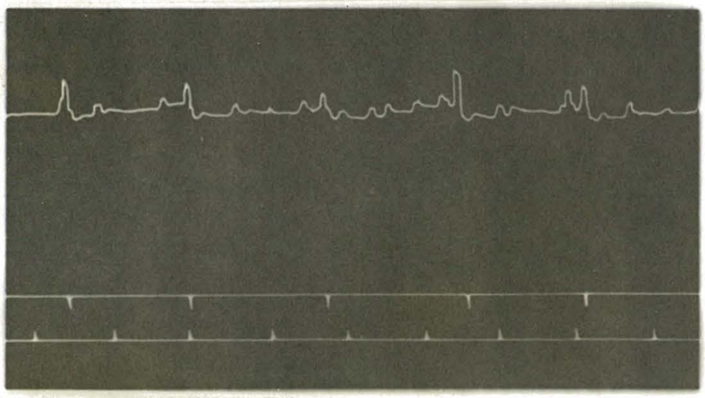


Fig. 7.—Tracing of portion of ruminal pressure curve of cow 557 while oxygen is being added at the rate of 3.6 liters per minute, using mercury manometer (April 13, 1937). As in figure 6, the bottom line is the time interval in minutes, the points on the middle line indicate when audible belching occurred, and the vertical scale represents pressure, 0.5 mm on the graph corresponding with 1.0 mm mercury of pressure. Though the ruminal pressure, during ruminal relaxation, is 8 mm mercury above the pressure before oxygen was introduced, belching still occurs only at the peak of ruminal contraction.

Fig. 30.
After Cole et.al.(5I).

pressure, and Cole, Mead, and Kleiber (51) postulate a reflex opening of the cardiac orifice stimulated by the contact of roughage with the walls of the rumen.

Wester (163) considers that the opening of the oesophagus depends on the strength of the rumenal contraction usually associated with eructation. Of particular importance is the opening of the cardiac orifice with consequent eructation and no serious distension during complete rumenal stasis and gas insufflation with hay, Quin (151), and grass, Phillipson (148) in the rumen. This suggests either stronger voluntary intervention than has been implied to date, or the implication of nervous pathways not directly terminating within the rumen walls, and of greater complexity than the simple reflex conceived by Cole, Mead, and Kleiber. (51).

As the factors postulated in opening the cardiac orifice for gas removal are not substantiated by experimental evidence they would best be examined in the light of the functional phenomena associated with eructation. Now eructation of gas from the mouth usually coincides with a strong rumenal contraction and increased rumenal pressure in sheep Quin (139), and cattle, Cole et al. (51). (See Fig. 30).

Occurring during the backward wave of contraction in the rumen, eructation was considered by Wester (167), to be of regular occurrence since contraction of the rumen and reticulum occurs approximately once a minute.

Irregularities do result according to Cole et al (51), and eructation does not occur at each rumenal contraction, with which other workers concur. (128), (163). Nevertheless, eructation of gas is considered to depend on reticulo-rumenal movements; Phillipson (40) asserts that gas will not accumulate if they are not inhibited provided the oesophagus is not obstructed.

This worker gives as evidence the development of bloat resulting from reticulo-rumenal paralysis by section of branches of the abdominal vagi demonstrated by Hoflund (128).

Earlier mention was made in those studies by the writer of strong rumenal movements being observed during the onset of bloat which questions this assertion of Phillipson (40), who has since withdrawn that view on the basis of gas insufflation studies (148).

The importance of pressure in activating the cardiac sphincter for eructation was indicated by Cole et al. (51), who prevented a pressure increase

during rumenal contraction by aspirating gas from the rumen and maintaining a slightly negative pressure, when eructation did not occur.
The influence of pressure is further illustrated by the frequency of eructation being dependent upon the fermentation activity in the rumen. Quin (151). The eructation frequency also increases soon after feeding the increased rate being maintained for 2 -- 4 hours Cole (51). These facts are in accord with the increase peak in rate of gas formation in the rumen following feeding. (51), (52). It should also be noted however that rumen motility increases after feeding commences, (61), (139), and may account for increased eructation frequency if the anterior wave of contraction in the rumen activates the opening of the cardiac orifice as conceived by Wester (167).

Pressure alone is not responsible for eructation according to Cole et al. (51), which they demonstrated by increasing the pressure through forcing gas into the rumen, when eructation occurred only during rumenal contraction, even though the pressure was greater during rumenal inactivity than the pressure associated with eructation under normal conditions. They further consider that this fact proves that the cardiac orifice is not automatically forced open whenever the pressure is increased to a certain point; therefore, in their opinion the obvious factor in eructation is the reflex opening of the cardiac orifice by fibre stimulation of the walls of the reticulum and rumen.

These conclusions fail to explain the facility with which sheep (151), and cattle (156), expel large volumes of air rushed into the rumen, even when the rumen is flooded or paralysed. Neither do they account for gas expulsion from the commonly experienced gas distended rumen of milk fed calves Corbett 1949 (181) in the diet of which roughage is usually absent. The writer has observed that certain pastures will cause acute bloat whilst others fail to do so in the same herd of cows, although the herbage in the pastures concerned were at similar stages of growth. Likewise, acute bloat can occur in animals grazing the same pasture continuously, Bathe (24), Dougherty 1941 (182), the previous grazing of which did not cause trouble.

The conclusions of Cole et al. (51) would not explain such variations in incidence without assuming a failure in attainment of the necessary threshold level for stimulating the eructation reflex. Under similar conditions of pasture growth and species composition such an assumption would be barely tenable.

Consideration needs to be given to the fact that a reflex is an involuntary act which precludes the probability of voluntary control intervening in eructation. Should the cardiac sphincter open in manner to that suggested by Dukes (165), fær regurgitation, involving solely an inspiratory act, then the involuntary muscularis of the reticulum is not involved, and the exercise of part voluntary control or a reflex having extrinsic pathways must be considered.

It has yet to be proved that lack of sufficient roughage in the rumen results in insufficient stimulus to elicit the eructation reflex. Reference to FIGURE. 12. Day.2. illustrates recovery from marked rumenal distension, which could only have been effected in the time by eructation, and this on a roughage free diet.

Whatever the factors controlling the opening of the cardiac sphincter the effects of pressure on the cardia are not to be underestimated. Pressure can stimulate the regurgitation act with consequent opening of the cardiac sphincter; in the simple stomach animal the cardia is opened for gas release under increased pressure. The frequency of eructation is coincident with pressure increases in the normal animal, whilst experimental increases in rumen pressure are met by an increased frequency of eructation. Furthermore, eructation in the normal animal is synchronised with rumenal contraction at which time rumen pressures are normally highest.

Whether the cardiac sphincter action be active or passive it is sufficient to permit of gas removal under increasing pressures in animals with complete rumenal stasis. It is of interest to note that Dukes (165), commenting on nerve impulses in the viscera, which only give rise to pain on reception of an adequate stimulus, refers to distension as being an example of such a stimulus.

c). Response of the Cardiac Sphincter.

The influence of chemical factors on the movements of the cardiac sphincter has been indicated by Lehmann (172), who induced relaxation of the sphincter in dogs by chemical stimulation with ergotamine.

It was suggested by Kerr and Lamont 1946 (183), that an allergic shock may cause spasm of the cardiac sphincter in ruminants, so preventing the expulsion of gas with resultant bloat.

Their suggestion is supported by having effected recovery in a number of bloat cases with the subcutaneous injection of adrenalin which is usually used to relieve anaphylactic conditions. Whilst protein sensitization of the cardiac sphincter is not untenable, the presence of factors in pasture plants causing contraction of the smooth muscle has yet to be proved. Muscle movement inhibitory substances have been shown to exist, (117), (153), (154), (155), but this does not support the conception of an allergic shock in which smooth muscle contraction would be expected.
Muir (3), states that it does not follow that such sensitizing protein is present in the herbage, it could well be evolved from the flora or fauna of the digestive tract. The apparent individual susceptibility of animals to bloat would need to be accounted for according to the depletion of protein reserves.

The writer submits that if by the use of adrenalin in effecting recovery from bloat, an anaphylactic shock is implied regard should be given to the nature of acute bloat incidence.
The onset of the condition within an hour of grazing pasture for the first time commonly occurs in animals not previously affected. It is difficult to account for these circumstances either in terms of the presence of a sensitizing plant protein, or as evolved from rumen microflora without first explaining the absence of a previous period of exposure for sensitizatio which is the prerequisite of an anaphylactic reaction.
The possibility of protein passing from the digestive tract into the blood circulation, although not generally subscribed to, is an open question, and the mechanism of anaphylaxis is considered by Gortner 1949 (184), to be far from being completely understood. It still remains however, to reconcile the conception of an allergic shock with the continued occurrence of bloat over long periods in animals grazing the same pasture or similar herbage, as reported by Lyons, (12), Cole, Mead, and Regan 1944(185), or with such conditions as prevail in the Argentine where animals graze permanently on alfalfa but losses from bloat occur. McMeekan (86).

Amadon and Detweiler, (178), transferred the rumen ingesta from one rumen fistula cow to another, then sealed off the fistula of the excessively filled rumen with a pneumatic plug. Belching was not prevented by this procedure. There was no indication however, of the type of food fed, the amount and rate of gas production, or whether distension of any kind was

apparent.
Nevertheless, mechanical obstruction of the oesophagus whether from clinical or physical causes is generally accepted as being contributory to the tympanic condition. Obstruction of the cardiac orifice having similar consequences is without experimental evidence but is suggested by Jacobsen et al. (89). They agree to the necessity of eructation for removal of gas which is too rapidly generated to be absorbed. Their postulate is that rapid ingestion of a dense food mass would tend to force the stomach down against the abdominal floor, depress the cardia below the level of the fluid in the forestomachs and trap the gas. The condition being aggravated by the buoying up of the freshly ingested mass by the generated gas. Interference with the reticular flow by the food mass is suggested. These workers draw attention to the fact that danger of bloat is greatest after grazing, a phenomena giving emphasis to their postulation. This hypothesis does not account for eructation from the apparently obstructed cardia in the rumen packed with ingesta, (178), or flooded with water, (126), (151).

An additional claim is made, although not substantiated, that legumes are more rapidly ingested than grasses, hence accounting for the non occurrence of bloat in grasses. This view is held to be untenable by Cole and Kleiber, (cited by Cole et al (9)), on the basis of their unpublished findings that one cow under observation to determine the relationship between feed consumption and bloat, bloated regularly upon consuming as little as 12 -- 18 pounds of alfalfa pasture. This same cow ate 47 pounds of sudan grass over a similar period without bloating. No details however, are given of the previous meal, time interval following, or rate of gas formation; All of these factors being important in determining the volume of gas present in the rumen in a given time.

Evidence of actual inhibition of eructation comes from Dougherty (182), who effected cessation of rumenal movements and inhibited eructation by insufflations of carbon-mon- oxide through a rumen fistulated cow. The same worker caused complete cessation of eructation after introducing air and water into the rumen and elevating the posterior of the animal so that the water level was above the cardia.

This is not in accord with the findings of Quin, (151), and Phillipson, (126), with sheep who found that flooding of the rumen with water made no difference to the expulsion of insufflated air, although no specific reference was made to the cardia being submerged.

Although response of the cardiac sphincter is not actively involved it will be relevant to comment on the prevention of gas escape in what a number of workers refer to as "foamy" bloat. This condition arises from the intimate mixing of rumen gas with ingesta and is attributed by Quin, (96), to the high saponin content of ingested plants which according to Clark, 1948 (185), forms an intractable emulsion of the ingesta. Bubbles of gas are formed which are not sufficiently large to burst and escape by eructation. Weight is given to this theory by successful bloat treatment with turpentine and tympanol which probably breaks the emulsion by dissolving the saponins Quin et al. 1949 (186).
The cardiac sphincter fails to open for normal eructation and tympany results following section of various combinations of the branches of the abdominal vagi, Hoflund, (128), Ellenberger 1883 (187), Mangold and Klein, 1927 (188). These findings further implicate the nervous system in the activation of the cardiac sphincter, to which support is given by the work of Jefferson and Necheles 1948 (189); these workers have noted marked, gaseous, distension in the stomach and intestine of vagotomised dogs which was relieved somewhat by left phrenicotomy.

The writer would draw particular attention however to that evidence which indicates that paralysis of the rumen does not inhibit belching, (126), (151); this suggests nervous activation of the cardia in eructation having origin in those branches of the vagi more directly concerned with the lower oesophagus, which is known to contract following electrical stimulus of the vagi in the calf. Wise, Anderson and Miller 1942 (190), and chemical stimulus of the buccal mucous membrane in the calf, Wester (167) and sheep, Clunies-Ross 1936 (191).
Electrical stimulation of the vagus also causes contraction of the oesophagus in dogs, further contraction results reflexly from stimuli originating in the upper abdominal viscera, Dey et al. 1946 (192). Whilst these findings strongly suggest thatthe eructation reflex is activated from a centre of reception located in the immediate area of the cardia, it should be noted that paralysis of the rumen need not necessarily be of neurogenic origin. This is borne out by Clark 1950 (193), following the paralysis of rumen movements by histamine treatment and cure with anti histamine drugs. It was shown that the histamine paralysed rumen was still

capable of responding to FARADIC stimulation of the vagus nerve. This respons showed that the paralysis caused by the histamine was of myogenic origin.

The possibility of the cardiac sphincter responding to nervous reflex control needs to be critically examined in relation to the normal frequency of eructation, and the state of the rumen contents in the normal and experimental animal.
Reference is made to spasm of the cardia in the human subject by Weise 1944 (1 in terms of a psychosomatic disorder, a combination of physical and psychological treatment being suggested, which implicates nervous control of a more complex nature than a simple reflex.

Earlier comment was made to the effect that the primary cause of bloat in the grazing animal would appear to be concerned with the facility whereby rumen gas was able to gain access to the oesophagus through the cardiac sphincter.

Due to the absence of a critical analysis of the eructation reflex (164) an attempt has been made in this section to examine that evidence which will permit a more critical treatment of the current theories as to the cause of bloat, as well as to assemble evidence upon which to develop further thought. To better serve this twofold purpose, and as an aid to clarity, the following summary is presented.

a). Most of the rumen gas is expelled by eructation through the cardi orifice and oesophagus, obstruction of which is pathogenic to bloat

b). The cardiac sphincter is normally closed; it is opened in the deglutition, regurgitation, and eructation; dysfunction in this respect would be contributory to the pathogenesis of bloat.

c). Relaxation and contraction of the cardia normally follows the peristaltic wave of deglutition; there is evidence that weak peristalsis fails to activate the movement of the cardiac sphincter.

d). Being composed of smooth muscle, the cardiac sphincter is capabl of automatic movement.

e). It is the authoritative opinion that the vagal supply to the cardia is chiefly of motor function.

f). Ergotamine causes relaxation of the cardia.

g). An increase in eructation frequency in ruminants is normally coincident with increasing intra-rumenal pressure, and accelerated rumen motility.

h). There is evidence that eructation normally synchronises with rumenal contraction, but not each contraction.

i). Eructation can function efficiently when the rumen is paralysed.

j). There is evidence that constant experimental distension of the simple stomach causes relaxation of the cardia.

k). Eructation can be elicited by stimulation of the oesophageal groove: oral and vagus stimulation causes reflex contraction of the oesophageal groove.

l). There is evidence of normal eructation being inhibited by vagotomy with resultant tympany.

m). There is no known published evidence which indicates that lack of roughage inhibits eructation.

n). Rumen insufflated carbon monoxide has been found to inhibit eructation.

o). Experimental findings are at variance in respect of water submergence of the cardia inhibiting eructation.

p). Spasm of the cardia and subsequent inhibition of eructation may conceivably result from an anaphylactic shock. Should the sensitising agent be of plant origin, then the conception of such a shock would be incompatible with the manner in which acute bloat is commonly manifest.

(Section E follows overleaf -

E. RUMEN GASES: THEIR COMPOSITION AND FORMATION AS INFLUENCED BY THE INTERNAL ENVIRONMENT.

Those physiological phenomena associated with digestion of direct consequence to this exposition have been considered. In the course of treatment of the subject matter it has become increasingly evident that the many functions of the digestive tract are influenced more or less, and are inextricable from those variable factors comprising the internal environment.

Not least of these is the nature of the rumen gases, their rate of formation, volume, and composition, all of which in the grazing animal are directly consequent upon the nature of the plant material ingested.

Now the ruminant is peculiar in that fermentation is an important part of digestion; in fact the expression "gastric digestion" in either cattle, sheep or goats, and probably in all other species of ruminants, infers fermentation followed by peptic digestion. Phillipson (195) 1950.

The internal environment then, and its variations in so far as it influences fermentation, is of immediate importance to this discourse, being that physiological aspect of digestion which logically follows the more mechanical considerations.

Now the volume of all gases present in the rumen at any one time will be determined in the first instance by the metabolic activity consequent upon the type of micro-organisms present.

Gas production will be expected to proceed at a fast or slow rate according to the degree of stimulus given to the fermentative processes, provided other conditions of the nutritional medium are favourable.

Throughout a twenty-four hour period then, gas production and pressure in the rumen will fluctuate to an extent conditioned by the amount of food entering the rumen, its nutrient value, and availability for bacterial synthesis.

According to the progress of fermentation so will the peaks of gas formation be attained, their distribution throughout the day being related to the time at which the nutritional stimulus is received.

By separate examination of the influences causing fluctuation in rumenal gas formation, a more correct perspective will be given to those complexities of plant and animal inter-action as they may contribute to bloat and its incidence. The nature of the rumen gases and those factors

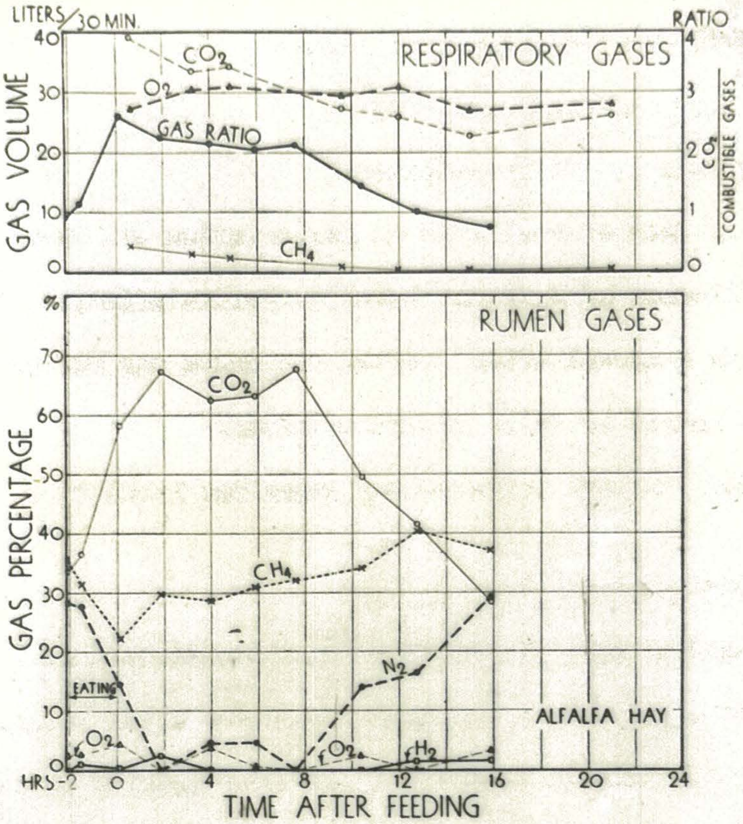


Fig. 3. Time course of the composition of rumen gas (lower quadrant); of the CO_2, O_2 and CH_4 expired and of the CO_2 to CH_4 ratio in the rumen (upper quadrant). The data were secured on a Jersey cow No. 831, fed maintenance ration of alfalfa hay.

Fig.I7[2] After Washburn and Brodie.(I97).

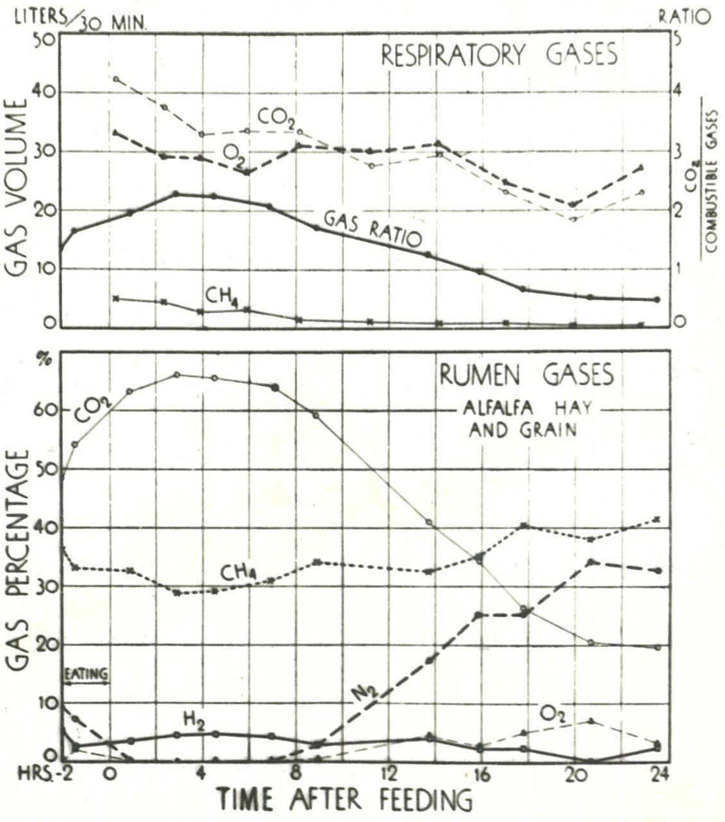


Fig. 4. Same as in Fig. 3, but on a ration of alfalfa hay and grain.

Fig.I8[2] After Washburn and Brodie.(I97).

which may influence each phase of fermentation activity will be examined under the following captions:-

a) Composition of Rumen Gases.

b) Influence of Feed Type on Fermentation and Rumen Gases.

c) Influence of Nutrient Level on Fermentation.

d) Time Interval after Feeding and Rumen Gas Formation.

e) Influence of Rumen Micro-organisms.

f) Other Factors Influenceing Rumen Gas Production.

a). Composition of Rumen Gases.

The gases present in the rumen are principally methane and carbon-dioxide, but traces of other gases are often found. Average figures given by Kleiber 1943 (196) for cows feeding on alfalfa pasture are

	%
CO_2	67
CH_4	26
N_2	7
H_2S	0·1
O_2	1

These figures agree closely with those found by earlier workers. Washburn and Brodie 1937 (152) found that as digestion proceeded the percentage of nitrogen and oxygen rose but that the ratio of these two elements was greater than that of atmospheric air, in agreement with the figures given above; the percentage of methane remained fairly constant.

The composition of rumen gases was found to be little influenced by the type of food eaten; the greatest variation occurred with the time interval after feeding, which is in accord with similar findings by Cole et al. (51). (See Figs. 17, 18, and 19)?

Olson (31) gives data on the composition of gas from the rumen of bloated cows. The average of nine samples taken from cows bloated on sweet clover was-

	%
CO_2	61·97
O_2	3·61
CH_4	18·42

Evidently these figures from bloated cows do not differ strikingly from those obtained in normal animals (196) (51); the high oxygen figure

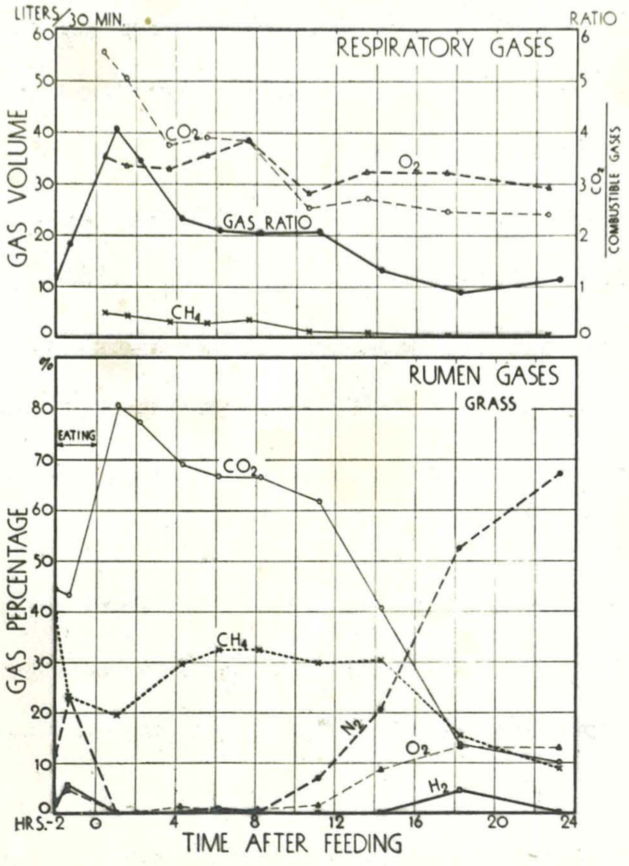


Fig. 5. Same as in Fig. 3, but on a grass diet.

Fig.I9[2] After Washburn and Brodie.(I97).

was accounted for by the sampling method used.

Dougherty (182), (197), has suggested that an increase in the amount of rumen carbon monoxide may be a contributory factor in causing death from bloat. He demonstrated that both carbon monoxide and hydrogen sulphide inhibit rumenal movements when introduced into the rumen in sufficient quantity, they are highly toxic, producing a syndrome resembling naturally occurring bloat.

Dougherty found that carbon monoxide was present in normal animals in only small amounts (not exceeding 0·17 volumes per cent) while hydrogen sulphide was present largely in solution in concentrations up to 0·309 cc in 100 cc of ingesta. He further demmnstrated that the amount of carbon monoxide and hydrogen sulphide required to produce bloat symptoms was much less when the intra-rumenal pressure was increased by insufflations of air, methane and carbon dioxide.

Critical examination of Dougherty's evidence concerning carbon monoxide is not convincing as no increase could be detected when the cow used was fed clover from a pasture known to produce bloat; in fact, no correlation between feed and the content of carbon monoxide could be detected. The concentration of gas needed to produce symptoms was in excess of that found in the rumen.

The data regarding hydrogen sulphide were more convincing; the concentration increased when clover was fed, while symptoms were produced experimentally by concentrations which did not exceed that found in a naturally occurring case.

Attempts to produce experimental bloat however by feeding cystine or sulphur failed as, although the hydrogen sulphide concentration increased, no symptoms occurred, in spite of feeding in addition cultures of H_2S-producing bacteria from the rumen.

There is further evidence that the percentage of hydrogen sulphide is high in bloated bovines. Dougherty (150) found concentrations as high as 0·7 per cent of hydrogen sulphide in rumen gas from steers that had died from bloat 3 - 12 hours before the samples were taken, whilst Olson 1942 (198) reported in bloated animals the hydrogen sulphide concentration in the rumen may be ten to twenty times that in animals on dry feed.

Olson 1944 (199) later reported that carbon monoxide and hydrogen sulphide are present in rumen gas of normal animals and that hydrogen sulphide is greatly increased in cases of bloat.

These findings are not in agreement with those of Kleiber (196) who studied the hydrogen sulphide content of rumenal gas immediately it left the rumen, from two bloated cows and three normal animals on alfalfa pasture. There was no significant difference in the hydrogen sulphide content of these samples, and no relation between the hydrogen sulphide concentration in the rumen and bloat.

To epitomize then, there is no known published experimental evidence of absolute significance, which supports the concept of an increase occurring in those gases having toxic effects, as the result of a particular feed type. On the contrary there is agreement for the most complete evidence procured in vivo (197), (51), that the composition of rumen gases is similar for different feeds and such variation in composition as occurs is largely due to time interval after feeding and bears no known relation to bloat.

b). Influence of Feed Type on Fermentation and Rumen Gases.

Whilst the incidence of bloat in grazing animals is generally associated with a legume diet, evidence exists that no more gas is produced on a bloat-provoking diet, such as green alfalfa tops, than on a non-bloat-provoking diet such as alfalfa hay and grain (51), (89), (52).

Although many analyses have been made on the principal constituents of legumes and non-legumes no essential product for bacterial metabolism has ever been isolated from legumes which are not present in non-legumes, Jacobsen (89).

There is evidence however that although the total volume of gas produced on different foods may be similar, the rate of production will vary in striking manner.

Washburn and Brodie (52) demonstrated the rapid increase of carbon dioxide percentage after feeding, the peak of which was reached more rapidly on an all grass diet than when alfalfa hay, or alfalfa hay and grain were fed. The relative amount of carbon dioxide in the rumen gas varied from 80 per cent shortly after grass was fed to 10 per cent 23 hours later. The percentages of methane for the same period were 20 and 9 respectively. Contamination with air apparently caused these marked decreases as the percentage of nitrogen and oxygen present rose from zero in both cases to 68

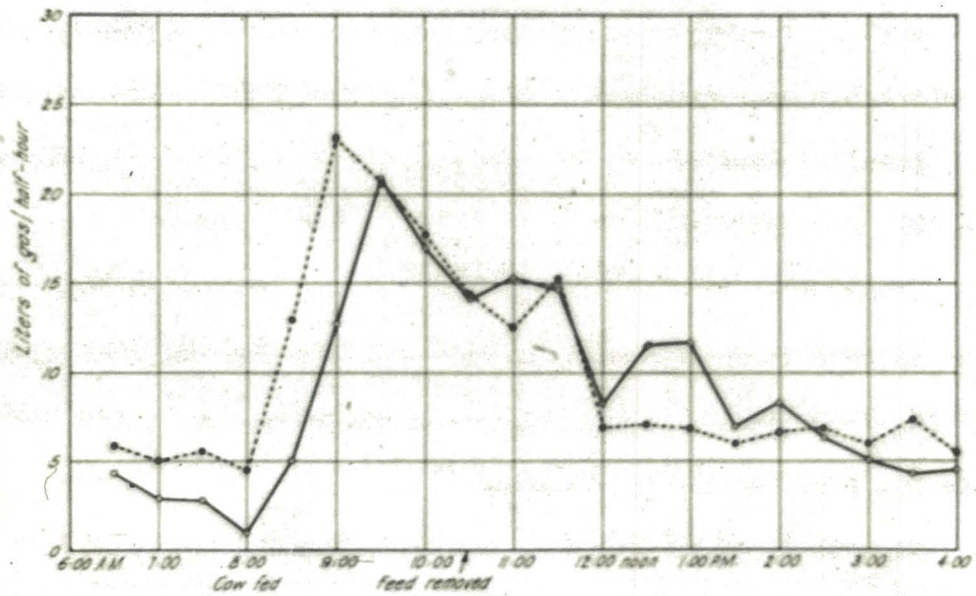


Fig. 9.—The rate of gas formation on green alfalfa alone and upon alfalfa hay alone in cow 557, expressed in liters per half-hour period. The solid line represents the average of five trials on a full feed of green alfalfa; the broken line, the average of three trials on a full feed of alfalfa hay.

Fig.20.[2] After Cole et.al.(5I)

and 13 per cent respectively. By measuring the amount of methane in the expired air and calculating from the above ratios the percentage of CO_2 due to fermentation, it was shown that a dry cow shortly after being fed 4.5 kilos DM of grass produced CO_2 and CH_4 at the rate of 32 and 10 litres respectively per hour. Five hours later the rates had dropped to 13 and 6 litres per hour, and 22 hours later the rates were 1.5 and 1.2 litres per hour.

On dry hay or on hay and grain the rate of methane production was almost the same as the figures just cited although the dry matter intake was only half as large; the rate of production of carbon dioxide was about two-thirds as large under these conditions. (See Figs. 17, 18, 19)[2]

Data on lactating cows show a maximum rate of production of methane of 16 litres per hour shortly after feeding; the feed intake was not given.

Parallel findings of the decline in the ratio of CO_2/CH_4 were obtained from the rumen of a goat.

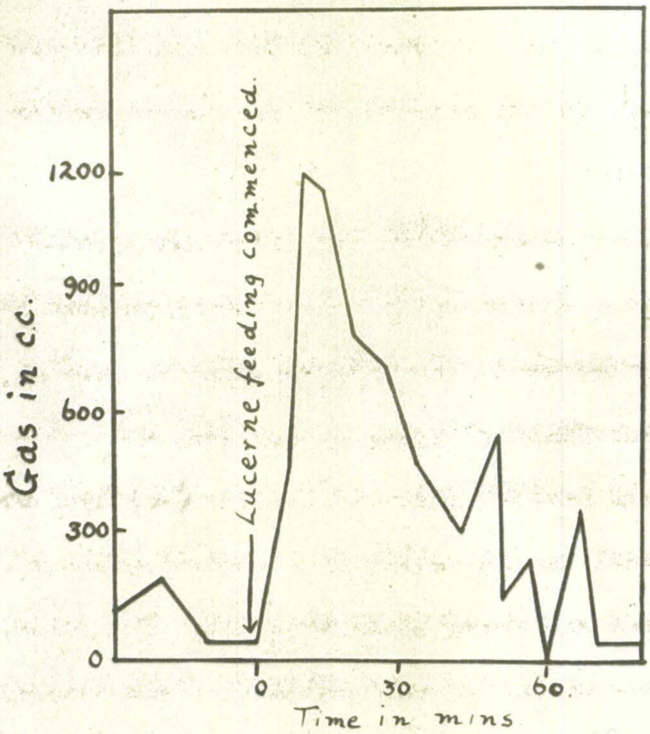
Washburn and Brodie (52) on the basis of their findings state that grass appears to be not only more rapidly digested but its digestion involves less CH_4 formation. They could not account for the unusually high level of rumen CO_2 following grass feeding.

Support is given to this work by similar findings of Cole et al. (51) who fail to find reason for attributing bloat on green alfalfa to excessive gas production. They state that the tendency is for less gas to be formed from green alfalfa than from alfalfa hay and concentrates. They demonstrated the rapid rise in gas formation after feeding which they consider shows why bloating may occur soon after animals are turned on to alfalfa pasture. (See Fig. 20)[2]

Quin (96) investigated the influence of diet on gas production in sheep with rumen fistulae.

Sheep on a basic diet of lucerne only, fed either green or as dry hay, were able to cause rapid fermentation of weighed test meals of lucerne consumed in the early morning before routine feeding took place. The amount of gas produced varied over a period of 90 minutes from more than 9 litres to approximately 4.5 litres. This difference in total gas yield when identical test meals were fed to individual animals was a feature constantly noted and was ascribed solely to the conditions present within the fore-stomachs.

This fact is of importance when considering the variable nature of bloat incidence within a group of animals. Gas production in these studies reached



CURVE No. 1.—Effect of Lucerne feeding on gas production in rumen of sheep.

Fig.2I[2] . After Quin.(96).

a peak 30 minutes after feeding commenced (See Fig. 21.)[2]

The feeding of wheat straw, or maize samp, to animals accustomed to a lucerne diet failed to provoke any gas production, within 90 minutes. Subsequent gas formation was very slow compared with that noted on lucerne. This indicates that neither cellulose (wheat straw) nor starch (maize samp) is capable of the same rapid fermentation as undergone by certain constituents present in lucerne.

The dosing of either cane sugar or glucose in amounts of 50 grams directly into the rumen of animals on a basic diet of lucerne caused prompt fermentation and gas evolution similar to that noted with lucerne itself. As according to Quin similar fermentation was obtained with juice expressed from green lucerne or with a watery extract from lucerne hay, it was evident that the sugar in the lucerne was the factor responsible for the very rapid fermentation.

It was further demonstrated that when sheep are either completely starved or kept on a ration consisting of poor quality hay or straw the power to ferment glucose in the fore-stomachs is readily suppressed in most animals, these findings being at variance with those of Cole et al. (51).

More recently however Cole and Kleiber (53) have compared the rate of formation of rumenal gas in cattle on a diet of grass with that of alfalfa, and between glucose and starch introduced into the rumen. As to date theirs would appear to be the only published data comparing in vivo the gas production rates in cattle of a specific legume and grass their figures are presented in Table 9, as it is generally held that bloat rarely occurs on grasses.

(Table 9 follows overleaf).

Table 9. Comparison of rumenal gas formation following feeding of of sudan grass and alfalfa tops. Cows fed ad libitum throughout a 4-hour experimental period.

		Cubic feet of Gas formed.		
Cow No.	lbs consumed	½-hour before feeding	½-hour after feeding	First 4 hours after feeding
SUDAN GRASS.				
760	69.7	0.08	0.28	4.02
760	50.4	0.26	0.47	5.43
757	7.5	0.32	0.47	2.77
760	63.0	0.34	0.59	6.70
Average	47.6	0.25	0.45	4.73
ALFALFA.				
760	26.9	0.06	0.48	4.17
757	3.4	0.34	0.28	3.29
760	19.7	0.30	0.78	6.82
832	12.9	0.34	0.43	3.00
Average	15.5	0.26	0.49	4.32

In addition to the tops cow 760 received 4 lbs of a concentrate mix the night before the trial. Cows 757 and 832 received 4 lbs of concentrates the night before and the morning of the trial.

The cows were prepastured for 2 days on the pasture from which the tops were taken. Gas production was measured as described by Cole et al. (51), eructation and subsequent gas loss being prevented by the use of aspirating bottles.

Cole and Kleiber summarize their work in the following manner:-

"In four 4-hour test periods there was an average consumption of 47.6 lb of Sudan grass tops fed ad libitum in the barn with an average rumenal gas production of 4.7 cubic feet for the period.

In four tests with alfalfa tops in the pre-bloom stage fed ad libitum there was an average consumption of 15.5 lb and an average of 4.3 cubic feet of rumenal gas produced over a similar period.

Gas formation during the first 4 hours after the beginning of feeding was approximately the same for three of the feeds, but the average consumption of Sudan grass was 3 times that of alfalfa. Consequently it appears that the rate of gas production would be greater with alfalfa than with Sudan grass if equal quantities were fed.

It should be noted that in the figures quoted cow 757 was distressed by discomfort from the cannula. No account is given for the discrepancy between the weights of a particular food consumed and the volumes of gas formed, when the same workers earlier indicated (51) that there is a direct relation between these factors. Measurement was not made of the food consumed 24 hours prior to the experimental period, the presence of which in the rumen could well affect the results obtained.

It is an open but none the less important question as to what may account for the degree of satiation which determines the marked differences between weights of alfalfa and Sudan grass consumed by the same animal over the same time period.

According to the gas measurement technique used, rumenal distension (which may be an important factor controlling intake) would be prevented. It is considered that alfalfa is more palatable than grass (89), hence greater intake would be expected, whilst the differences in weight of alfalfa and grass consumed indicate that satiation is not approached in the weights of alfalfa consumed in the same animal.

The writer submits that an important omission in this work concerns the lack of data relative to the quantities of grass and alfalfa consumed at specific intervals shortly after commencement of feeding, and which would embrace the peak period of gas production. This is necessary before any regard can be given to Cole and Kleiber's claim, unsupported by evidence, that increased gas production on legumes does not in itself provide an adequate explanation of bloat. Further that cows will bloat on amounts of alfalfa comparable to those consumed in the experiment described, but bloat did not occur when normal animals were given an amount of Sudan grass producing an equivalent volume of gas.

Attention is drawn to the fact that Jacobsen et al. (89) have shown that similar amounts of bluegrass and alfalfa, when partially submerged in aliquot samples of rumen fluid, produced almost the same amount of gas. The rates of gas production tended to follow the dry matter content of the materials used even when the grass was dried before immersion in the rumen fluid. It will be recalled that earlier in this discourse differences in dry matter intake in a given time due to variations in ingestion rate, accessability, and availability of herbage were considered likely to obtain. Where the approach to the optimal levels for these conditions varies, intra-rumenal gas pressures would also be expected to vary, reaching the highest peaks in a given time where the optimal levels were attained. This would be accentuated by differences in the rumen gas production potential of herbage as demonstrated by Cole and Kleiber (53).

It is pertinent to note that the appetite and coincident dry matter intake of sheep on a hay diet is increased by the addition of sugar Quin 1948 (201) which stimulates rumen gas production (96), the accumulation of which is manifest as bloat in sheep grazing lucerne having a sugar content increasing from 2.5% to 6% (dry weight basis) on the day of bloat incidence (27).

The rate of gas formation following the introduction of glucose into the rumen compared with that of starch was also measured by Cole and Kleiber (53).

When the cow used was fed 9 lb of alfalfa hay and 6 lb of barley 20 hours before the experimental period, glucose caused a more rapid increase in gas formation than did starch, although the total gas produced within 4.5 hours after the introduction of either of the 2 substances was approximately the same, that is 3.4 and 3.1 cubic feet respectively.

In vitro studies by McAnnaly 1943 (200) have also shown that sugar stimulates gas production when added to rumen ingesta. Similar studies by Jacobsen (89) indicated that molasses and sugars tended to temporarily inhibit gas production although rumen contents became more frothy when molasses was fed regularly; no data were given as to the weights used. These same workers found that ingesta after silage was added to a hay and grain ration produced less gas per gram of dry matter than ingesta from a hay and grain diet alone. It was not clear however as to the precise effect silage produced as it was not clearly differentiated from the effect of total food consumed.

Carbon monoxide was found on a hay diet to the extent of 0.02 per cent in rumenal gas, and 0.02 to 0.03 per cent on a fresh cut clover diet (197), although the amounts produced on dry and green feed appear to be comparable (182).

A number of workers report high concentrations of hydrogen sulphide in rumen gas on all legume diets (197), (198), (199), which has not been confirmed by analyses of rumenal gas immediately on withdrawal from bloated and normal cows on alfalfa pasture.

It is of interest to note the early work of Lungwitz 1892 (202), who analysed ox rumen gas secured through a permanent cannula. He found the CO_2 to CH_4 ratios varied from 2.1 to 3.5; O_2 content, 0 - 3 %; N_2 2 - 19 %, CO_2 40 - 50 % from cabbage leaf feeding, and CO_2 70 - 80 % for alfalfa clover and grass; CH_4 16 % after buckwheat, and 34 % after vetch feeding.

The following summary gives very good reason for believing that different foods have separate and marked effects in their influence on the rate of rumenal gas formation.

a) Although there is evidence which suggests that the rate of rumenal gas formation is similar for bloat and non-bloat provoking feeds, strong evidence to the contrary exists.

b) There is evidence which demonstrates that rumenal gas is formed at a greater rate on a fresh grass and lucerne diet than on hay, hay and grain, wheat straw, and maize Samp diets.

c) Variation occurs between sheep in the rate of rumenal gas formation in the same time on the same weight of lucerne feed.

d) Cane sugar dosed into the rumen of sheep induces a similar rate of rumenal gas formation to that of extracted lucerne juice.

e) Fermentation activity is inhibited in the rumen of sheep by starving or feeding on poor hay and straw diet.

f) There is evidence from in vivo studies that the same rate and volume of rumenal gas formation produced by a given quantity of Sudan grass in a given time, is produced by ½ the quantity of lucerne in the same time.

g) In vitro studies indicate that the rate of gas formation from rumenal ingesta tends to follow the dry matter content of the immersed food materials.

h) There is evidence from in vivo and in vitro studies that glucose and starch added to rumen ingesta stimulate rumenal gas formation, which proceeds at a greater rate with glucose stimulation.

c). Influence of Nutrient Level on Fermentation.

The total volume of gas evolved as a fermentation product in the rumen will be determined largely by the amount of carbohydrate available for microbial disintegration. According to the concentration of those carbohydrates which are readily decomposed, so will the rate of gas formation be determined.

The intensity of fermentation as far as can be judged by the concentration of volatile acids in the digesta was shown by Phillipson 1942 (203) to vary in direct relation to ingestion of food and to the nature of the diet. Higher values were found in sheep grazing young summer grass than in those feeding hay, or hay supplemented by bran and oats, or by mangolds and cabbage. Washburn and Brodie (52) indicate in their data that a 2 maintenance level of grass intake resulted in a rate of gas formation in the first hour after feeding greater than that on alfalfa hay, and alfalfa hay and grain diets fed at maintenance level, the increased rate of gas formation being due largely to a percentage increase in CO_2. Cole et al. (51) determined the relation between the amount of feed consumed and the amount of gas formed in the rumen. Feeding at a level of 4 lbs daily of alfalfa hay, 11.08 litres of gas were formed over the $\frac{1}{2}$ hour experimental period as compared with 77.04 litres over the same period for two previous trials on a 25 lb ration of alfalfa hay. Indicating that a reduction in hay consumed from 25 lb to 4 lbs resulted in a reduction in the amount of gas formed to one-seventh, these workers concluded that amount of feed consumed has a direct relation to gas formed.

There is evidence which questions the association of bloat with an increase in quantity ingested, of a given food. This fact was indicated by Mead et al. (15) who investigated the effects of the physical condition of feed on the incidence of bloat in stall fed cows. There were two experimental periods - In period I the cows received finely ground alfalfa hay and concentrates. In period II the same cows received unground hay and concentrates.

The average consumption in period II was 6.9 lbs per day per animal greater than in period I (which was considered due to the greater palatability of unground hay); 21 cases of slight bloat occurred during period I, one case of slight bloat in period II.

These workers refer to the fact that bloat most often occurs after eating large amounts and state that on the basis of food consumed a greater bloat incidence would have been expected in period II than in period I. They account for the lower incidence of bloat on the larger quantity of food ration on the basis that the physical state of the unground hay was sufficient to stimulate the eructation reflex.

No data were given for the rate of food consumption in the 2 periods, although these workers in the same investigation evidence rapid ingestion as being contributory to the tympanic condition. Hence it is suggested by the writer that ground hay would be ingested in less time than unground hay, and there is evidence that a given weight of hay requires greater length of time for ingestion than other foods of the same weight (61), (110). Should eructation of gas from the rumen be coordinated with rumenal motility cycles then any chemical or physical factor of the feed likely to reduce ingestion rate will a) enable eructation to keep pace with fermentation and b) reduce the rate of gas formation. These facts need to be considered before much regard is given to the findings of Mead et al. The same workers (15) report a greater bloat incidence in stall fed cattle on a ration of green alfalfa tops than on a ration of alfalfa tops cut coincidentally and dehydrated. The total dry matter consumed was the same in each case.

A point of primary interest is the amount of alfalfa consumed before bloating occurs. Mead et al. (15) state that as a rule bloat did not occur until more than 50 lbs had been consumed, but one cow bloated after consuming 8 lbs. The variable time at which bloat occurs after cows are pastured indicates that there is a considerable latitude in the amount consumed before bloating is manifest.

Quin (27) implicates ingestion of excessive amounts of lucerne in a single meal with acute bloat and consequent increased gas formation and suggests that small repeated intakes will lessen the risk of rapid gas formation. The same worker (96) associates loss of appetite and hence lowered food consumption with a decrease in the ability of ingesta to ferment glucose and stimulate consequent gas formation.

McAnally (200) demonstrates with in vitro studies that the addition of glucose to ingesta filtrate results in rapid gas formation, which after reaching a peak falls away when the sugar is exhausted. With increasing gulcose content the period of gas evolution is prolonged, there being a maximum rate of gas evolution which is not exceeded even if the original sugar content is increased in amount. There is a tendency for the rate of gas evolution to be diminished if the ratio of weight of glucose to ingesta volume is increased above a value which is approximately 0.2 gm/8 cc. These findings are in agreement with those of Quin (96) who has also shown that starvation causes a rapid and practically complete suppression in the fermenting power of rumen ingesta.

Cole et al. (9) refer to the unpublished work of Olson and Brezeale who found the hydrogen sulphide percentage in rumenal gas to be greatest in the animals that ate most.

To summarise the influence that the level of nutrients may have upon fermentation in the rumen:-

a) There is strong evidence which indicates that the rate of fermentation in the rumen is related to the quantity of food consumed.

b) In vitro studies indicate that maximum gas formation from rumen ingesta is induced by a certain glucose value, which if exceeded tends to inhibit rather than increase gas formation.

d). Time Interval after Feeding and Rumen Gas Formation.

By the use of a permanent rumen cannula in a non-lactating Jersey cow Washburn and Brodie (52) drew gas samples for analysis from the rumen at very short intervals and constructed accurate time curves of the composition of rumen gas and for the CO_2 and CH_4 ratios which were paralleled with similar curves for expired gas. This was the first published work of its kind.

It was shown that the CO_2 /CH_4 ratio in rumen gas is not a constant but declines with time interval after feeding. The peak in rate of gas formation was reached soon after feeding to decline gradually until little gas was being formed 24 hours later. (See Figs. 17, 18, 19).[2]

This general statement has been confirmed by other workers, Cole et al. (51), Jacobsen (91), Quin (96).

The writer submits that a point of particular significance in the time curves of Washburn and Brodie (52) is to be found in the fact that on maintenance diets of alfalfa hay and alfalfa hay and grain, over a 2-hour feeding period the peak gas formation rate was reached in 4 and 4½ hours respectively after feeding commenced. On a twice maintenance diet of grass over a 2-hour feeding period the peak was reached in 3 hours.

The precise time taken by the animal for eating in each instance was not specified; although Washburn and Brodie do not venture an explanation of that phenomenon it is not unreasonable to assume that both amount of material and availability of carbohydrate for microbial digestion contributed to a more rapid gas formation in a shorter time interval on a grass ration.

Cole et al. (51) estimated that the volume of rumen gas produced by cattle on diets of alfalfa hay and green alfalfa respectively was in the region of 5.1 and 2.1 in the half hour before feeding. The peak was reached one hour after feeding commenced for the alfalfa hay when the volume increased to over 23.1, and in 1½ hours for the green alfalfa with a 20.1 volume increase. (See Fig. 30).

The subsequent decline was rapid in the next 3 hours. The gases were aspirated through a wide bore cannula and it was claimed that no losses occurred via the oesophagus.

Quin (96) using fistulated sheep recorded a peak in rumen gas production 30 minutes after feeding commenced, followed by a rapid decline when diets of lucerne hay and green lucerne were fed. There was no gas formation in 90 minutes after commencing to feed wheat straw or maize samp diets; it should be noted that in these in vivo studies no precaution was taken to prevent gas losses by eructation. Quin (27) also reported definite evidence of an increase in intra rumen pressure immediately after a meal of green lucerne, which was not apparent some hours after, nor when animals were kept on a diet of grass hay supplemented with ground maize.

Cole and Kleiber (53) give evidence of marked differences in rates of rumenal gas formation in cattle on separate diets of grass and legume herbage; the latter feed induced the most rapid gas formation in the first ½ hour after feeding commenced. (See Table 9.)

In view of these studies it is interesting to recall earlier references in this discourse to those many reports of bloat becoming manifest in 60 - 90 minutes after the commencement of feeding.

To summarise:-

a) In vivo studies give evidence of gas formation in the rumen reaching a peak shortly after the commencement of feeding.

b) There is evidence that the time interval between the commencement of feeding and the peak of rumen gas formation varies with different foods, being shortest on diets which stimulate rapid fermentation.

e). The Influence of Rumen Micro-organisms.

Pursuing the overall concept of plant and animal interaction, a logical conclusion to this discourse rests in a consideration of the micro-flora and fauna of the rumen.

It was noted earlier that fermentation is an integral part of ruminant digestion; the gaseous products of fermentation, their volume and rate of formation are the direct result of microbiological activity. The stimulation of this activity may be conceived as a trigger process setting off the physical phenomena which when out of control give rise to acute bloat.

It is essential then that consideration be given to those factors which condition the activity of rumen micro-organisms.

Whilst rumen microbiology is an extensive field which may only be treated all too briefly here, excellent reviews are recommended concerning the role of microflora of the alimentary tract (205), and in ruminand digestion (206).

The greatest percentage of rumen gases is comprised of carbon dioxide and methane, these products of digestion deriving from the activity of micro-organisms in the rumen. It is reasonable to assume that increases in the gaseous products of fermentation will be a direct indication that active proliferation of the organisms is occurring. Further it is most probable that variations in the degree of such activity will be influenced by those factors which:-

a) cause changes in the population of the rumen micro-organisms as a whole

b) influence the metabolism of individual organisms.

Considering those factors jointly there is evidence which shows the nature of the diet conditions, the size of the rumen population and the activity of the individual species contained.

Mowry and Becker 1930 (207) found that when hay was fed alone the population of protozoa in the rumen was in the region of 200,000 per m.l. The addition of starch to the diet caused an increase to 700,000 per m.l., while the addition of protein raised the numbers to 2,000,000 per m.l.

Similar results were obtained by Van der Wath 1942 (208) (cited by Phillipson (121)) who found that sheep fed on wheat straw alone harboured 500,000 ciliates per m.l. The addition of maize meal to the straw produced a sharp increase in the numbers present which rose to the region of 500,000 m.l. Diets of maize and lucerne hay produced a population of between 1,400,000 and 2,600,000 per m.l.

Seasonal fluctuation in sheep grazing freely was also noted, and this was correlated with the amount of dry matter consumed, the percentage of nitrogen present and the digestibility of both nitrogen and dry matter. The numbers present were least in July (mid-winter) and greatest in January, being 98,000 per m.l. in winter and 455,000 per m.l. in summer. It is clear that the number of ciliates present depend on the food available for them in the rumen. Coarse fibrous food does not support a large population, but starch and also protein allow a much higher rate of multiplication.

In the light of these findings it is tempting to draw a parallel between those factors associated with the incidence of bloat in grazing ruminants and causing changes in the population of rumen micro-organisms; the influences of season and availability of herbage low in cellulose and high in available carbohydrate and protein being common to both.

That the composition of the diet influences the composition of the population of rumen micro-organisms is strongly suggested in the findings of a number of workers. Harris and Mitchell 1941 (209) showed that on a diet deficient in nitrogen 17.8 per cent of the cellulose was digested; supplementing the diet with urea increased the digestibility to 38.7 per cent, although this has not been confirmed. Lardinois et al. 1944 (210) observed that supplementing the diet with urea resulted in an increased synthesis of the B group of vitamins. Mollasses or starch added to the diet of sheep reduced the digestibility of cellulose (211), (212), (213).

Compositional changes of the rumen flora of sheep have been observed to accompany changes in diet (96), (214), (215), and these changes have been correlated with changes in the chemical activity of the population.

The rate of fermentation of glucose in the rumen of sheep fed poor quality hay was slow; when this hay was replaced by lucerne (96), or by clover hay (214), the ability to ferment glucose was markedly increased, and this was correlated with a change in population which could readily be observed microscopically.

Johnson et al. 1944 (216) evidenced a progressive decline in rumen microflora with an increase in time after feeding. At 16 hours after feeding, the rumen organisms were reduced to one thirteenth of the number found at the end of the first hour after feeding. The method of investigation used consisted of plating out on a simple medium and incubating aerobically. Commenting on this method Elsden and Phillipson (206) state that as neither the medium nor the method of incubation resembled the conditions in the rumen, no significance can be attached to these results. There is other indication that numbers of micro-organisms vary according to the time after feeding. Bortree et al. 1946 (217) by microscopic counts of ingesta direct from the rumen of dairy cows found an increase in the number of organisms within 2 hours after feeding, high counts being maintained or increased for several hours, gradually returning to the range before feeding. The quality of the roughage fed, and changes in diet from hay to pasture slightly effected an increase in numbers. Glucose added to hay produced micro-organism counts 100 per cent greater than on hay alone. Starch fed under similar conditions brought little change over a diet of hay alone. Similar findings have more recently been made by Bortree et al. 1948 (218) who report the time to reach a peak in the rumen bacterial population is decreased by the addition of readily fermentable carbohydrate to the diet. It appears then that the microflora of the rumen can assimilate a wide range of carbohydrates, Van der Wath 1948 (219). The fact that the rate and extent of assimilation is in some measure determined by the complexity of the molecule suggests that a variation in rate of rumen gas formation between different foods would be expected.

That increasing amounts of carbohydrate in a ration results in an increase in fast growing micro-organisms has been indicated by Gall et al. 1949 (220).

A yeast-like organism develops in the rumen of sheep when lucerne (96), mangolds (215) or a high quality clover hay is fed (219). Quin (96) first drew attention to these organisms and reported their abundant occurrence in the digesta of rumen of sheep particularly on a diet of lucerne, diminishing in numbers on a diet of coarse hay. He classified and named the organism "Schizosaccharomyces ovis", the essential characteristic of the organism being 1) rapid gas production in the presence of glucose, and 2) the deposition of glycogen in its cytoplasm. Quin (96) attributes the occurrence of bloat in sheep fed on green lucerne to the presence of these organisms, which by in vitro tests were found to produce a much more rapid evolution of gas in the presence of glucose than the bacteria of the rumen. This organism has not been isolated in pure culture, and some doubt as to its being a yeast is indicated in the work of Elsden (221), (222), who has not detected the formation of alcohol from its fermentation either in vitro or in vivo. The formation of alcohol is typical of fermenting yeast. Recent attempts to isolate the "Schizosaccharomyces ovis" have failed, Van der Westhuizen 1950 (223) although other yeast-like organisms have been isolated from rumen ingesta, but none of these organisms has the characteristic properties of

"Schizosaccharomyces ovis". Van der Westhuizen et al. concluded that S. ovis is misnamed and is probably not a member of the Eumycetes at all.

Other than a similarity of rumenal environment between related animals it is difficult to conceive changes in the population and activity of rumen micro-organisms as being influenced by genetic factors. In this connection it should be borne in mind that bloat incidence in cattle has been reported by Knapp et al. (140) as being greater in certain family lines on the basis of a statistical analysis of observed differences between Sire groups in the frequency of bloat.

Whilst the manner in which micro-organisms become initially established in the rumen is an open question, the unconfirmed work of Uzzell et al. 1949 (224) indicates that no protozoa are present in the stomach of new born calves, whilst Pounden et al 1949 (225) evidence their entry as being by way of the mouth.

It is recommended that the following summary of the findings pertaining to the activity of the rumen microflora and fauna should be examined in relation to the influences of feed, and time interval after feeding upon rumen gas formation.

a) There is evidence that the population of rumen micro-organisms increases with the availability of assimilable carbohydrate.

b) Seasonal fluctuations occur in the population of rumen micro-organisms, an increase in number being evidenced as coincident with the seasons of pasture growth, and correlated with the percentage of nitrogen present, its digestibility, and the dry matter digestibility.

c) Evidence exists indicating that compositional changes in the population of rumen micro-organisms is accompanied by changes in diet.

d) There is evidence (subject to confirmation) that numerically rumen micro-organisms reach a peak after feeding, the time interval being decreased by the availability of readily fermentable carbohydrate.

e) Yeast-like organisms have been observed in rumen ingesta having the facility for rapidly fermenting glucose.

f) There is unconfirmed evidence that micro-organisms are not present in the rumen of calves at birth.

f). Other Factors Influencing Gas Production in the Rumen.

In addition to providing the necessary energy for the fermentation process, the chemical composition of the diet may influence gas formation in so far as it affects the optimal pH condition for bacterial growth in the fluid media.

The physiological effects of the physical condition of the food, and the latter as it influences the rate of passage of ingesta through the rumen are further factors for consideration.

Monroe and Perkins 1939 (226) determined the pH of bovine rumen ingesta on different rations and obtained a range of pH 6.47 on blue grass pasture to pH 7.01 on a diet of hay plus grain. Myburgh and Quin 1943 (227) gave a range of pH 5.5 to pH 6.8 for the rumenal ingesta of sheep depending on the carbohydrate content of the diet. Rapid acid production with a pH range of 6.25 to 7.00 resulted from the in vitro fermentation of glucose. These writers state that normally the pH of rumen ingesta in sheep showed slight fluctuation only during the digestion of a single meal, the tendency being towards increased acidity within the first 4 - 6 hours, after which it steadily reverts to its previous level. Myburgh and Quin further found that a change in pH due to acidification of rumenal fluid reduced its fermentative activity. When sufficient acid was added to reduce the pH to 6.5, at the end of 20 minutes, there was a perceptible depressing effect on the amount of gas evolved. The addition of sufficient alkali to the rumen increasing the pH to 8.35 at the end of 20 minutes reduced the rate of fermentation to one third below the rate of untreated ingesta. Jacobsen et al. (25) concluded from in vitro studies of rumen ingesta fermentation that changes in dilution, temperature, and hydrogen ion concentration in the ranges normally occurring in the stomach had little effect on the rate of fermentation.

The composition and properties of rumen saliva are considered to exert an influence on the activity of rumen flora and fauna. Its reaction and activity as a buffer on the alkaline side of a pH of 4 are believed to be largely responsible for the maintenance of a medium which appears to be optimal for microbial activity and for the chemical changes occurring in the rumen, Reid and Huffman 1949 (228). This is explained by the secretion of 300 - 350 gm of sodium bicarbonate estimated as being contained in the total saliva secretion of a mature animal in 24 hours, Colin 1886 (229). The alkalinity of dairy cattle saliva further offers the possibility that certain amounts of CO_2 produced on fermentation in the rumen may be absorbed (6), Markoff 1911 (230). If such is the case it may be conceived that the excess saliva secreted on eating offsets rapid fermentation of CO_2 at this time.

The property of low surface tension of bacterial cultural media is known to influence the growth of certain bacteria, Larson et al. 1922 (231), and the low surface tension of dairy cattle saliva may be a contributory factor in the development of certain micro-organisms. A cow secreting 56 litres of saliva daily excretes approximately 86 mg of ascorbic acid by this route. In such manner saliva may encourage or stimulate fermentation by these micro-organisms known to use vitamin C in their metabolism, Reid and Huffman (228).

Owing to its physical state food may be delayed in its rate of passage through the rumen, and according to Schalk and Amadon (61) impaction interfering with rumenal motility may bring about bloat. The tympanic state resulting, whilst not acute bloat as defined in this discourse, is likely to be the outcome of impeded functional processes which may be common to both states. An example is given by Mead and Goss (47) in dairy cattle reared on a roughage free diet which showed no ill symptoms other than occasional bloat.

Cole and Mead (unpublished, cited by Cole et al. (9)) however using a similar diet reported only one mild case of bloat over a 7-week period even though the cows consumed 40 lbs of grain on certain days, a level of feeding exceeding that used by Mead and Goss.

The interpretation of this difference according to Cole et al. (9) is that over a long period of time atony of the rumen develops, food remains in the rumen longer and the result is greater gas formation. The implication is therefore that the formation and volume of rumenal gas increases to a level not fully removed by eructation before rumenal distension is apparent, and this due to the increased time food remains in the rumen. This interpretation is difficult to reconcile with the sharp rise and steady fall in rumen gas production following feeding generally reported, (52), (53), (9

A finely ground lucerne hay diet was reported by Mead et al. (15) to cause slight bloat over a certain period, whilst in the same time unground hay was without effect. A contrary situation would be expected in the light of Balch's (134) and 1950 (232) evidence that a diet consisting solely of ground hay increases the dry matter of the fluid contents of the rumen dorsal sac, and the breakdown of crude fibre in the reticulo-rumen is more rapid when the contents were fluid than when less fluid.

It is interesting to speculate on the extent to which the physical mass of ingesta contributes to the increase in volume of rumen gas by impeding its removal from the rumen as Balch (134) gives evidence of ground hay as a sole diet remaining much longer in the rumen than unground hay. The incrimination of digesta mass in impeding gas removal would also be expected to apply when highly palatable herbage was fed.

In this connection Balch and Kelly 1950 (233) find no marked difference between the specific gravity of particles of digesta in the dorsal and ventral sacs of the rumen of cows. On the basis of experimental findings these workers consider it likely that the position of the mass of fibrous material found in the dorsal sac during the feeding of certain diets is maintained largely by the contractions of the reticulo-rumen.

Since however this mass of digesta apparently floats, although few single particles lighter than rumen liquid were found, it is likely that a mass has a lower specific gravity than its individual particles. Balch and Kelly suggest that this could result from the entrapping of bubbles of the gases produced during microbial fermentation among the fibres of the digesta.

The writer submits that the situation may well be conceived where a gradual accumulation of finely ground slowly fermentable digesta would impede the forward movement of rumen gas to the cardia

To summarise:-

a) Changes in pH of rumen digesta are evidenced as being associated with different foods and time interval after feeding.

b) Increasing the acidity and alkalinity of rumen ingesta inhibits the rate of fermentation.

c) There is evidence from in vitro studies that the normal changes in pH which may be expected to occur in the rumen have little effect on the rate of fermentation.

d) There is evidence of a higher bloat incidence being associated with a diet of ground hay as compared with unground hay.

e) Evidence exists (subject to confirmation) that a diet of ground hay, compared with unground hay, increases the dry matter of rumenal fluids, and remains longer in the rumen.

f) There is evidence (subject to confirmation) of there being no marked difference in specific gravity between digesta in the dorsal and ventral sacs of the rumen.

COROLLARY.

Pasture and animal conditioned interactions were earlier considered particularly as they were likely to affect the quantity and quality of herbage consumed.

Following ingestion of pasture those same herbage factors have been examined in this section along with, and as they may influence the physiology of ruminant digestion.

It has become evident that plant and animal interactions contribute to the quantity of food entering the rumen in a given feeding time, examples in point being food palatability and rate of ingestion.

The disposal of the food in the rumen is accomplished by contraction cycles which occur in frequencies of approximately one minute, normal variations in excess of this frequency being characteristic of the feeding period.

Rumen motility has been inhibited experimentally with white clover juice, and cyanide compounds known to occur in certain legumes; its stimulation may also be induced with copper compounds. It should be noted that Muir 1949 (235) has reported the use of certain "weed" plants for concentrating copper in ley pastures.

Whilst rumen motility may be inhibited by cyanide compounds the implication of HCN in the etiology of bloat is difficult to reconcile with the incidence of bloat on legume pasture which has not been found to contain that toxic principle. Further, there is every reason for believing that rumen motility is not inhibited during the onset of acute bloat, whilst gas removal has been evidenced even when the rumen is paralysed.

Although the exact physiological mechanism activating eructation and rumen gas removal is not known, it is evident that most of the rumen gases are removed in this manner, and its dysfunction will probably contribute to the pathogenesis of acute bloat.

The effecting of such a dysfunction by sensitization of the cardia with a plant protein is incompatible with the common incidence of bloat if an anaphylactic reaction is implicated.

Whilst it is highly improbable that feed type influences the composition of rumen gases, there is good reason for believing that considerable variation occurs in the rumen gas producing potential of different foods, a difference in this respect being evidenced between grass and legume plant species. The differences in gas producing potential between different types of fodder are not known to have been conclusively attributed to the type of carbohydrate available; nevertheless glucose is more rapidly fermented in the rumen than starch, and lucerne juice induces a similar rate of gas formation to that of glucose.

Added to this the quantity of food in the rumen is known to influence the rate of rumen gas formation, which reaches a peak shortly after feeding, the time interval probably being influenced by both rumen gas producing potential and quantity of the feed.

This accords with the metabolic activity of the rumen micro-organisms which is known to increase with an increasing availability of assimilable carbohydrate, with some suggestion of a peak in activity being reached shortly after feeding.

It may reasonably be expected that those chemical and physical changes in the rumen fluid media which detract from the conditions favourable to optimal proliferation of micro-organisms will inhibit rumen gas formation. Further, it is pertinent to note that if the pH of the rumen exceeds approximately 7.5 as the result of administered alkali (sodium carbonate, or sodium hydroxide), rumenal paresis results. This recent finding of Clark and Lombard 1951 (236), not previously known to those authors, may have considerable significance in the etiology of rumenal stasis.

DISCUSSION.

In this discourse pasture and animal interaction is the essential theme which has been developed and illustrated by considering the complex problem of acute bloat in ruminants.

A dysfunction of plant-animal interaction is implied by the condition the cause of which is unknown, and it is with that concept in mind rather than the clinical aspects of bloat that this exposition has been attempted.

In considering the problem it should be noted that bloat is not one single entity; it may arise as the result of free gas on top of the rumen ingesta or as a frothy mixture of both.

For the purpose of discussion it is necessary to consider a specific example and this will be met by the writer's field study of the condition on pp.52-74 (and Appendix), being the only detailed study known concerned with the grazing animal.

There is every reason for believing that the concomitant occurrence of certain pasture conditions and animal behaviour will precipitate acute bloat. What are those conditions?

As acute bloat is an abnormal distension of the rumen with gas, then the first question may be posed in the following manner:-

What are those pasture, and animal behaviour conditions which contribute to rumen gas formation?

It is known by experiment that the difference between a large and small quantity of the same food consumed is expressed as the difference between a high and low rate respectively of rumen gas formation. Therefore the quantity of pasture available for consumption is important.

It is known that a difference between a high and low ingestion rate of an animal eating the same food is expressed by a corresponding difference in the quantity of food entering the rumen in a given time.

The ingestion rate may be influenced by- a) food palatability, b) physical condition of the food, c) food appetite of the animal.

Therefore the palatability of pasture, and its physical state, must determine in part the quantity of herbage consumed in a given time, being limited by variations in the degree of satiation and feeding habits of the animal.

It is known that in addition to feed quantity, certain qualitative factors are conducive to rumen gas formation.

Plant material of a low lignin content is conducive to a higher rate of fermentation in the rumen than material of a high lignin content. That difference existent between mature and immature pastures will therefore be expected to contribute to a relatively low and high rate respectively of rumen gas formation.

There is evidence from in vivo studies that a certain quantity of lucerne causes a higher rate of rumen gas formation in a given time than a larger quantity of grass, and that the juice of lucerne stimulates rumen gas formation at a similar rate to that induced by glucose.

This suggests the possibility of differences in rumen gas producing potential of herbage species, which may result in a higher rumen gas formation on those pastures in which legume species are dominant. Those conditions would be accentuated where the optimum concentration of that qualitative factor in pasture causing rapid fermentation corresponds with vegetative development conducive to optimum herbage consumption.

How may this reasoning be reconciled with the onset of bloat?

There is undisputed agreement between widely dispersed workers that the peak in rumen gas formation is reached in a certain time interval shortly after feeding commences. (See Figs. 17[2], 18[2], 19[2], 20[2], 21[2]). The time at which the peak is reached varies with differences in type and quantity of food consumed.

Assuming, (A) a pasture having a constant rumen gas producing potential it would be reasonable to expect that in a given time an increase in the quantitative intake of that pasture resulting from an increased rate of ingestion (X), would stimulate an increase in rumen gas formation.

Therefore the shortest time interval to the peak of rumen gas formation would be concomitant with the largest quantity of pasture consumed. Rate of ingestion then will be a contributing factor in determining that time interval within the limits of the assumption.

Again assume (B) differences in rumen gas producing potential between pastures, and a constant ingestion rate for a given feeding time. Then the time interval to the peak of rumen gas production would be shortest on that herbage (Y), most rapidly fermented in the rumen.

The shortest time interval to the peak of rumen gas formation would obtain where (X) and (Y) coincide under conditions conducive to optimum consumption.

Of what relevance to bloat is this time interval to the peak of rumen gas formation?

The volume of the rumen is the limiting factor to an accumulation of gas.

Failing its removal the volume of gas accumulated would reach its peak shortly after feeding; to accommodate the gas the rumen will distend.

The degree of distension and time at which it is manifest will be determined by the quantity of food consumed (being related by experiment to gas produced) and the fermentative power of the food (known to vary between foods: grass and lucerne).

The varying degrees of severity with which acute bloat is manifest is indicative of an accumulating volume of rumen gas.

Therefore the time interval to the condition in the same animal will be determined by one or both of two factors:-

a) The rate of formation of rumen gas in excess of the volume removed.

b) Direct inhibition of the mechanism for gas removal, including obstruction of the escape pathway, the degree of inhibition and time at which it is effected.

Reference to Figs. 17^2 - 20^2 gives a range of $\frac{1}{2}$ hour - $2\frac{1}{2}$ hours as the time interval from the commencement of feeding to the peak of rumen gas production.

Now there is an accumulation of empirical evidence which indicates that under pasture conditions conducive to bloat the onset of the condition may occur in 30 minutes after commencing to graze and most often within $1\frac{1}{2}$ hours of pasturing.

Bearing in mind assumption (A), reference to the Appendix, Figs. 9 - 15A, pp.52-74, and in particular Fig.11, p.63A, indicates that under similar pasture conditions conducive to bloat, and in the absence of supplementary feeding, the severest degree, and shortest time interval to bloat after feeding commenced, tended to be associated with the longest grazing time and highest grazing rate respectively. Further, a decrease in the quantity of pasture available even when associated with an increased grazing rate resulted in a longer time interval and a reduced severity of bloat. A restriction of grazing time to less than 50 minutes increased the time interval to bloat and reduced its severity (See Fig.10, p.62A) whilst bloat did not occur when grazing was restricted to less than 40 minutes (See Fig.13, p.67A).

An acceptance of those experimental findings relating rate of ingestion to quantity of food consumed will concede an increased quantity of herbage entering the rumen with an increase in ingestion rate.

Therefore pasture quantity is implicated in the above findings.

If there is a further acceptance of those in vivo experiments (51) (52) which find that an increase in rate of gas formation and products of fermentation (203) is related to an increase in the quantity of food consumed, then the writer's findings suggest that the onset of bloat is associated with a rapid rate of rumen gas formation.

It is not within the bounds of the writer's studies to suggest that differences in the fermentative potential of pastures may be expected, as marked differences in grazing activity were associated with different pastures. This point would be well worth investigation both for different pasture mixtures and herbage species with in vivo and in vitro studies.

It may be sought to dispute the implication of excessive gas formation with the onset of bloat on the grounds of those findings relating to gas insufflation studies.

The writer would submit however that rumen gas which during feeding consists largely of CO_2, must be removed against gravity.

This may be effected in the following manner:-

a) Lowered intra-oesophageal pressure as the result of an inspiratory movement.

b) A reverse peristaltic wave of the oesophagus carrying the gas to the mouth.

c) Pressure of the gas within the rumen.

Where rapid ingestion takes place and is sustained for a considerable period, the active peristaltic action of the oesophagus would be most certainly opposed to the frequency of a) and b) and would most probably impede gas removal by c). There is evidence that increasing intra-rumenal pressure is not alone responsible for gas removal.

That rapid ingestion in itself may impede gas removal would be a contributory factor to acute bloat in common with the clinical and physical obstruction of the oesophagus well known as the causes of chronic bloat.

There is no evidence known to the writer clearly indicating that gas insufflation studies have been carried out under conditions of rapid food ingestion and subsequent active peristaltic action of the oesophagus.

It may be that general failure to produce bloat by gas insufflation is due to not taking into account the aforementioned factors. Attention is also drawn to those findings (51) that distension contributes to intake regulation, and it is conceivable that during gas insufflation ingestion is inhibited; subsequent oesophageal activity and obstruction would not then be opposed to gas removal.

In view of the hypothesis submitted that bloat is a consequence of rapid gas formation in the rumen, the removal of which is impeded by active ingestion, it may well be questioned if a herbage inhibitory factor might not be involved in preventing gas removal.

To entertain this concept, the manner in which a herbage toxic factor affects the eructation mechanism needs to be explained.

Should such a factor weaken the mechanical means of gas expulsion by inhibiting rumen motility as conceived by Evans and Evans (117) account must be given for those findings of the writer that rumen contraction cycles are increased in vigour during the onset of bloat. It is possible that a herbage toxic factor may directly inhibit the cardiac sphincter without influencing rumen motility.

An explanation would then be necessary for those findings of the writer that the average time interval to slight bloat was 48 minutes over 12 periods of incidence.

In this case inhibition of the cardiac sphincter and eructation would need to be effective soon after the commencement of feeding, to permit sufficient accumulation of gas to cause distension in 48 minutes; this assumes that normal eructation is not impeded during ingestion.

To effect such inhibition of eructation rapid absorption of the toxic factor is implied.

Whilst according to the findings of Coop (159) this is possible, inhibition of eructation early in the ingestion period by a herbage toxic factor would need to account for the fact that bloat did not occur in Fig.11, Day 26, p.63A. In that example 1 hour of grazing a non-bloat-provoking pasture was immediately followed by 1 hour of grazing herbage highly conducive to bloat.

Whilst a reduced ingestion rate was effected the total grazing activity shown would most probably have resulted in a quantitative consumption comparable to the first 20-25 minutes in those cases when bloat occurred. Although normal distension was noted bloat did not occur as would have been expected after the consumption of toxic herbage at a sufficient level to inhibit eructation.

Alternately it may be suggested that the time interval is greater than 20-25 minutes for the assumed inhibitory principle to become effective. There would then be good reason for doubt as to whether sufficient gas would accumulate to cause distension in the time remaining to the 48 minutes recorded as the average time interval to slight bloat.

It should be borne in mind that during the period when toxic inhibition of the cardiac sphincter is assumed, the opening of the cardiac orifice continues to be activated from the oesophageal side to permit entry of the food bolus.

Further, the toxic effect would need to be of transitory nature, as in all cases observed by the writer bloat recovery was effected by eructation associated with vigorous rumenal contractions after grazing had ceased.

Such a transitory toxic effect would be incompatible with the quantity of herbage in the rumen at the end of grazing and toxic levels likely to exist unless detoxication was taking place.

Discarding toxic inhibition of eructation, what explanation would account for the failure of the mechanism to remove rumen gas?

As far as is known the eructation mechanism has not been analysed. The following widely divergent schools of thought are implied:-

a) Eructation is coincident with rumen contraction cycles but not every cycle.

b) Eructation is a reflex act initiated by friction stimuli.

c) Eructation proceeds under increasing intra-rumenal pressure without either a) or b) being involved.

There is no known evidence for b), and c) which results from findings with sheep, remains to be substantiated in the literature.

A number of workers subscribe to a) and there is some supporting evidence for that school of thought. (See Fig. 30, p.112A.).

Eructation frequency in cattle is evidenced (51) as increasing after feeding (in some cases to 10 eructations per hour).

From subjective evidence the writer has noted an average eructation frequency of 1 per 2 minutes in cattle after grazing, and evidence of regurgitation for rumination (See Table 8), implies that the cardiac sphincter may relax for that purpose on an average once per minute.

Now it is generally agreed that the cycles of motility in the normal rumen have a frequency of approximatdy one per minute increasing on feeding. Assuming that in the normal rumen the cycle of motility is the primary factor effecting gas removal, certain limits are then set by the frequency of contraction.

Is it not conceivable then, that in a given time, by increasing the intake of a highly fermentable herbage, the volume of rumen gas formed between motility cycles may exceed the volume removed by eructation?

It is of interest to note that instance of bloat recorded, (Fig.12, Day 2, p.65A.), in which the time interval to marked bloat was approximately 70-75 minutes, with a similar time interval for recovery.

The question of acute bloat incidence now becomes pertinent.

Certain empirical evidence exists, (requiring investigation), suggesting that the incidence of bloat in dairy cattle is highest in the feeding period after morning and evening milking. Throughout a 24-hour day dairy cows show a strong tendency to graze for the longest time, and at the highest rate, after morning and evening milking (See Fig.3, p.39A, and Fig.4, p.40A).

The greatest herbage intake would be expected during those periods; with a rise to a peak in rumen gas formation after feeding, and the rate of gas formation being proportional to feed consumed, it would be logical to assume that a failure in gas removal would most frequently be expressed by distension and bloat during those grazing cycles immediately after milking.

Acute bloat may quite well occur at other periods of the day; in that case it should be noted that grazing behaviour is of a cyclic nature, well defined periods of intake occurring throughout the day. The same principle of rumen gas production would apply however, with the difference that a lower grazing activity may give rise to the condition, owing to continued fermentation and an accumulation of gas from the previous grazing cycle.

This manifestation would accord with observations made by the writer. It has repeatedly been observed that eructation is frequent in the rest period between grazing cycles, and even normal distension is relieved before commencing to graze. (See Fig.15, p.70A, and Fig.15A, p.71A.).

Known differences between animals which may account for such differences in bloat incidence, may result from differences in grazing activity (time and rate), rumen capacity, and rate and volume of rumen gas produced.

Whilst the same pattern of grazing time and rate may be maintained for long periods it is readily conceived that when pasture attains optimum conditions of quantity, palatability, and quality in terms of readily assimilable nutrients, so also will optimum conditions obtain for rumen gas formation.

In the final analysis the products of fermentation will be related to the activity of rumen micro-organisms. Such activity is known to be stimulated after feeding, and to display seasonal peaks in accord with the nutrient stimulus received.

EPILOGUE.

By making a study of pasture and animal interaction the purpose of this dissertation, the stimulation of a growing trend of thought in general and in particular is implied.

In general the purpose has been to prompt a realisation of the need to appreciate an emergence of a certain school of thought evolving in conjunction with the expanding effort towards objective progress in the biological sciences.

The primary conception of that school of thought concerns the necessity of an integrated approach to problems in the biological field.

As applied to agricultural science this is expressed by Stapledon 1948 (237) in England who considers "that there is no greater danger to agriculture than too many bits and pieces of specialised knowledge blowing around before either science itself or the farmer knows how to fit all the pieces together in a way it can be safely used... Integration of the highest order must keep pace with specialization, for agriculture and farming are integration - facts without integration lead first to chaos and then to disaster final and irreparable."

The increasing trend towards specialization is considered by Bronk 1951 (238) in America as serving only to add unrelated incoherent data to the literature of science which already frustrates comprehension. A motive for scientists is conceived which embraces a broader function than the mere collection of facts. It is the need to bring order out of chaos multiplied in the growing literature of science, the need to interpret their discoveries according to the best traditions of literature, to synthesize and integrate a vast mass of data.

From the general to the particular: Stapledon (2) expresses a dissatisfaction with the present trend in grassland research owing to the apparent neglect of this concept of integration.

It is evident when considering the work on the problem of bloat that "specialized" thought has resulted in a confusion of findings in the literature often at variance with the principles of scientific investigation.

For example, on his own admission Phillipson (148) at the Rowett Research Institute in Scotland states that an armchair hypothesis was adopted in the physiological approach to the problem, field knowledge of which may have led more directly to findings of value not necessitating withdrawal, whilst the chemical approach of Ferguson (114) at Jealott's Hill in England would have been better founded with a knowledge of grazing behaviour and rumen motility.

The writer shares the apprehension of Stapledon (2) and is possessed of a growing conviction from impressions gained at some of the principle centres of grassland research in Britain, Australia and New Zealand, that a stage has been reached when, if new facts are to be formed into conceptual schemes (238), then studies with plant and animal must go hand in hand.

ACKNOWLEDGEMENTS.

A work of this nature must necessarily depend upon an efficient and cooperative library department. In that respect the writer is indebted to Mr H.D. Erlam and his staff.

Particular thanks are due to Mr Bennet for the unrestricted use of his dairy herd, and to the herd manager Mr B. Mitchell, who gave invaluable assistance at all times with the field work concerning the section on an example of grazing activity and acute bloat.

An appreciation is extended to Mr J. Hancock for the use of data from his MS. (part now published) on grazing behaviour.

For the careful photography and assistance in preparation of the text figures, the writer desires to express his indebtedness to Miss V. Bailey.

Advice from the staff of the Plant Husbandry, Dairy Husbandry, and Biochemistry departments of Massey Agricultural College has always been readily available.

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APPENDIX I.

GRAZING ACTIVITY AND TIME ONSET TO BLOAT FOR JERSEY COW X.

JANUARY 1950.

GRAZING CYCLE I.

Date	Field no.	Grazing commenced A.M.	P.M.	Number of bites per 10-minute period 1	2	3	4	5	6	7	8	9	10	11	Total bites	Length in Mins.	Total bites in first hour of grazing	Time onset to bloat (Minutes) Degree of bloat: Nil	Slight	Marked	Severe	Total cows: Pastured	Blown
17:1:50	1	8·0		349	318	147	409	182	55	70	-	-	-	-	1530	65	1428		40	65	75	17	6
18	3	7·45		186	261	390	305	321	551	170	195	-	-	-	2079	80	1714	+	-	-	-	17	0
18	1		6·45	635	556	474	536	346	39	-	-	-	-	-	2686	55	2686		45	55	-	17	7
20	1		5·48	548	555	562	405	570	547	339	46	-	-	-	3572	72	3187		44	72	80	17	7
21	1		5·39	443	468	548	391	224	-	-	-	-	-	-	2074	48	2040		48	88	-	4	1
24	3	7·38		353	370	353	430	402	333	258	266	265	141	106	3282	110	2241		99	-	-	17	1
24)	1		6·18	553	495	439	549																
24)	2							388	360	460	296	437	232		4209	100	2857		44	102	-	17	2
25	1		5·44	448	520	550	407	469	483	519	59	-	-	-	3443	73	2865		49	69	-	17	3
26	1	8·43		396	374	320	298	217	289	21	-	-	-	-	1915	64	1894	+	-	-	-	17	0
26	1		6·7	419	580	512	570	423	393	-	-	-	-	-	2897	58	2897		47	55	58	7	4
27	1	7·7		494	526	536	469	227	332	170	20	-	-	-	2774	71	2584		56	67	-	17	1

APPENDIX II.

GRAZING ACTIVITY AND TIME ONSET TO BLOAT FOR JERSEY COW X.

FEBRUARY 1950.

GRAZING CYCLE I.

Date	Field No.	Grazing commenced		Number of bites per 10-minute period											Total bites	Length in Mins.	Total bites in first hour of grazing	Time onset to bloat (Minutes) Degree of bloat				Total cows	
		A.M.	P.M.	1	2	3	4	5	6	7	8	9	10	11				Nil	Slight	Marked	Severe	Pastured	Blown
2:2:50	3	10·0		96	62	134	134	161	127	213	62	-	-	-	989	73	714	+				17	0
19	3	7·47		495	460	398	399	365	284	366	246	134	181	-	3328	100	2401	+				17	0
21	3	10·5		277	268	267	307	310	297	259	164	-	-	-	2149	84	1726	+				17	0
21	1		7·3	654	620	606	671	666	576	324	78	-	-	-			3793		52	-	-	17	5
22	1		7·10	646	661	567	476	-	-	-	-	-	-	-	2350	38	2350	+				17	0
23	1		5·37	381	448	460	671	542	570	352	37	-	-	-	3461	73	3072		40	70	-	17	6
24	3	7·55		411	203	9	167	96	165	-	125	-	-	-	1533	90	1051	+				17	0
24	1		6·40	379	466	549	572	637	522	419	-	-	-	-	3544	67	3125		59	-	-	17	1
25	1	8·10		635	611	642	579	348	322	251	-	-	-	-	3388	68	3137		58	71		17	3

APPENDIX II.

GRAZING ACTIVITY AND TIME ONSET TO BLOAT FOR JERSEY COW X.

JAN./FEB. 1950. GRAZING CYCLE II.

Date	Field No.	Grazing commenced		Number of bites per 10-minute period											Total bites	Length in Minutes	Total bites in first hour of grazing	Time onset to bloat (Minutes) Degree of bloat				Total cows	
		A.M.	P.M.	1	2	3	4	5	6	7	8	9	10	11				Nil	Slight	Marked	Severe	Pastured	Blown
18:1:50	3	10·50		137	138	291	350	134	100	282	167	170	257		2016	100		+	65	85		17	0
24	3	11:26		250	261	363	276	342	265	300	109				2172	76		+				17	0
2:2:50	3		12·7	112	351	356	264	238	276						1597	59		+				17	3
19	3	10·35		174	259	290	280	295	310	57	212	224	230	Continued.									
21	3	11·50		195	35	198	246	217	174	234	343	168	267										
24	3	10:21		158	104	322	315	140	353	82	164	141	236										
				PERIODS CONTINUED																			
19 Cont.				393	273	232									3229	135		+				17	0
21 Cont.				216	112	128	111	125	49	39	110	194	28	10	3199	206		+				17	0
24 "				254	156	280	167								2872	143		+				17	0