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TIME PATTERNS OF FEEDING AND RUMINATION IN DOMESTIC CATTLE

(with a summary in Dutch)

J. H. M. METZ

*Department of Animal Husbandry, Agricultural University,
Wageningen, The Netherlands*

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CONTENTS

1. GENERAL INTRODUCTION

Feeding behaviour in vertebrates has been subject of many investigations. On the one hand, the strategies of food searching, selection and capture have been studied (De Ruiter, 1967; Hinde, 1970). On the other hand, much interest has arisen in the way the animal adjusts feeding behaviour to its caloric and nutritional requirements (see various chapters in Code and Heidel, 1967). The latter problem underlies the present study.

Of course, food intake depends on the factors that govern onset and cessation of the successive feeding spells. These factors may be studied either at a purely behavioural level, or at the level of the underlying physiological mechanisms. However, in both cases detailed specification of the overt behaviour is a necessary prerequisite (De Ruiter et al., 1974). The present study attempts to present such a specification for domestic cattle.

Various studies of feeding behaviour in cattle have already been made, particularly in grazing animals (McClymont, 1967; Hafez et al., 1969; Porzig, 1969). However, so far as I know the temporal pattern of feeding in this species has not yet been analyzed in detail, in contrast to some other vertebrate species, e.g., the rat (le Magnen and Tallon, 1966; Thomas and Mayer, 1968; Levitsky, 1970; Panksepp, 1973), mouse (Wiepkema, 1968), guinea pig (Hirsch, 1971), domestic fowl (Duncan et al., 1970), pigeon (Zeigler et al., 1971), and zebra finch (Slater, 1974). Cattle differ from any of these species in that they have developed rumination, a special behaviour for remastication and reinsalivation of the ingesta. Obviously, for explaining the feeding pattern in cattle the time pattern of rumination must be investigated too.

The aim of this paper is to present a model of feeding and rumination in cattle which describes:

(1) the autonomous components in the rhythms of these behaviours;
(2) their facilitatory and inhibitory relationships.

Chapters 2, 3 and 4 consider the feeding and rumination patterns under ad lib. food conditions. Chapter 2 gives definitions of the behaviour units, and discusses the durations of these units and the order in which they occur. Chapter 3 surveys the total amount of feeding and rumination performed per day and the diurnal rhythmicity of these behaviours. Chapter 4 describes to what extent duration of a unit is dependent upon type and duration of the preceding units. From the results reported in these chapters a preliminary model emerges that may account for the interrelation between feeding and rumination. This model is further specified in Chapters 5 and 6 on the basis of three experiments, each involving one or another restriction of the opportunity to ruminate and/or to feed. As the various points leading to the model in its final form are scattered over several chapters, they are put together in Chapter 7. This will lead to a brief discussion of one or two implications. Finally, there is the question of the validity of the model. The obvious test of this is the reliability of its predictions. Some suggestions for such tests are made.

2. UNITS OF FEEDING AND RUMINATION BEHAVIOUR, AND THEIR DURATION

2.1. INTRODUCTION

This chapter gives the definitions of the various behaviour units used in the present study, and discusses the following aspects of their temporal organization:

(1) the duration of uninterrupted performances (*bouts*) of feeding and rumination;
(2) the duration of intervals between bouts;
(3) the order in which feeding and rumination bouts occur.

All three aspects are fundamental to a model of the autonomous and interactive components of the feeding and rumination rhythms.

2.2. MATERIAL AND METHOD

2.2.1. *Basic experiment*

Seven adult, non-pregnant and non-lactating cows were used, five of the Meuse-Rhine-Ysel (MRY) breed (nos. I, II, III, VI and VII) and two of the Dutch Friesian (FH) breed (nos. IV and V). Body weight ranged between 560 and 650 kg.

The animals were used two at a time. They were housed in an experimental room with two cowstands, each equipped for automatic recording of feeding and rumination (Fig. 2.1.). For recording rumination the animals had to be tied up. In the room a 16-8 light-dark cycle was maintained (lights on at 08.45 h). The ambient temperature fluctuated with the season, but it was never lower than 8.5°C or higher than 23.5°C.

The animals were fed ad lib. with hay wafers[1]. Fresh food was brought in and further care was taken of the animals once a day, during the first 15 min of daylight. During that time the recordings were stopped and the recorder charts were changed. The total amount of food was so adjusted that the animals left at least 10 per cent, and usually much more, of the food supplied uneaten every day. Water was freely available from a cup near the manger (Fig. 2.1.).

A detailed description of the recording equipment is given by Metz and Borel (1975). Only the main points will be repeated here. To record the feeding pattern, the manger with food was suspended from a load beam, so that its weight was continuously measured and could be recorded on a Joens six-channel point

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[1] The chemical composition and feeding value of this food were as follows: dry matter 92.2%, sand 1.5%; in dry matter: 14.3% crude protein, 29.5% crude fiber, 9.1% ash, 9.0% digestible crude protein and 430 gr starch equivalents/kg.

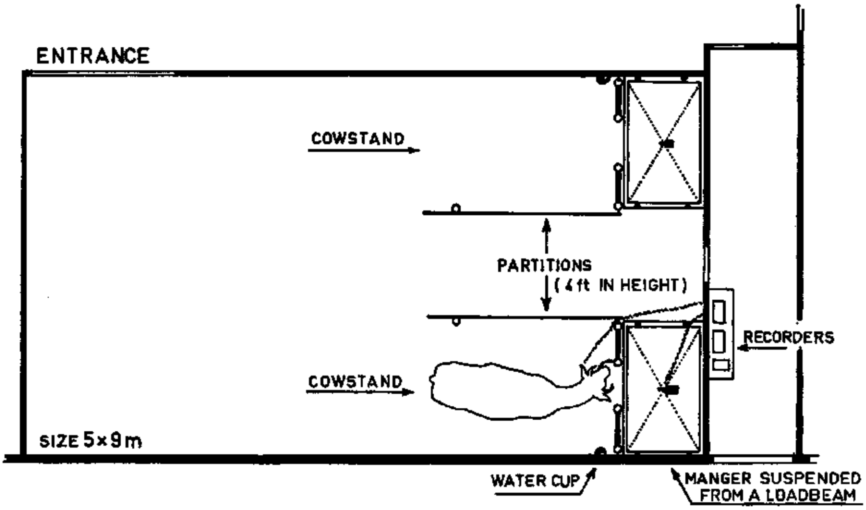

FIG. 2.1. Plan of the experimental room.

recorder. The recorder scanned each channel once a minute. Nevertheless, interruptions of feeding shorter than 4 min could not be recognized with certainty on the charts, due either to a low feeding rate or to irregularities in the records caused by the cow pushing the manger with its head while feeding (Metz and Borel, 1975).

To record rumination, a leather halter was placed on the animal's head with a microswitch between double straps under the jaw. When the animal opened its mouth the lower jaw pressed on the switch, and gave an electric signal to a ten-channel Miniscript Z event recorder. Chewing during rumination resulted in a very characteristic record which was easily distinguishable from that of jaw movements during feeding or grooming.

The recordings were made over 24-hour periods. They were stopped when the animals were in oestrus. In total between 12 and 32 daily recordings were obtained per animal.

Additional observations

In animals I and II direct visual observations of the precise time pattern of feeding and non-feeding behaviour were carried out during a total of 8 and 16 hours, respectively. These observations, lasting 4 hours at a time, were done on different days and in different periods of daylight during the basic experiment.

2.2.2. *Behaviour units*

Three categories of behaviour will be discerned: feeding, rumination, and 'other behaviour'. For describing the temporal patterns of these behaviours, units of feeding and rumination behaviour will be defined at two levels: 'bouts' and 'clusters of bouts'. The category 'other behaviour' (O) will only be considered in terms of 'intervals' between these feeding and rumination units, as bouts of this heterogeneous class would be meaningless units.

Bouts

(1) The *feeding bout* (F) is a sequence of feeding behaviour elements not interrupted by any element of non-feeding behaviour.

Preliminary observations showed that under the conditions of the basic experiment feeding consisted merely of short movements of approaching the food, followed by some phase of food selection (e.g. grubbing in and sniffing the food) and ingestion (biting, chewing and swallowing). A distinct selection phase was omitted in about half of the cases. A feeding bout consisted of at least one, but more usually a number of these feeding cycles (cf. De Ruiter, 1967). In the automatic records, feeding bouts could not be identified with certainty due to the limited temporal resolution of the apparatus. Therefore, the feeding 'runs' distinguishable on the charts consisted of series of an unknown number of feeding bouts not separated by interruptions $\geqslant 4$ min.

(2) The *rumination bout* (R) is defined as an uninterrupted series of rumination cycles.

A rumination cycle is one complete act of rumination, consisting of regurgitation of ingesta and the subsequent remastication and reinsalivation, and reswallowing (for a more detailed description, see Stevens and Sellers, 1968). Rumination bouts consist of a varying number of cycles, but cycle length hardly shows a trend in the course of a bout, except that the first one or two cycles may be extremely short. On the average a rumination cycle lasts about one minute. Further, cycle length and the number of chewings during the cycle highly correlate (in animals I and II: $r = +0.94$).

Occasionally short interruptions occurred within rumination bouts. These were disregarded because in the direct visual observations they were found to be very short ($\leqslant 17$ sec).

Clusters of bouts: the meal

Analysis of the duration of the intervals separating bouts of one and the same behaviour reveals to what extent this behaviour is clustered in time. In practice, such clustering proved to exist only in the case of feeding, but not in that of rumination (for obvious reasons, the analysis was not extended to the heterogeneous category of 'other behaviour'). This led to the concept of a *meal* (M) i.e. a cluster of feeding bouts. I shall specify the criterion for distinguishing meals in the following paragraphs. In fact, once the meal has been defined this will be the only unit of feeding behaviour subsequently used.

Intervals

We may distinguish different kinds of intervals, depending on the nature of the bouts they separate and that of the behaviour performed during the interval:

FoF $F^{o}_{r}F$ RoR $R^{o}_{f}R$ FoR RoF

(in this code, capitals denote the bouts bordering an interval, and small print activities during the interval, the latter irrespective of the order in which they take place).

Rumination was never seen during intervals between feeding bouts within meals. On the other hand, intervals between meals virtually always included at least one R. The final list of interval types to be discussed below therefore consists of the following classes:

(1) F/F. This class, comprising all intervals between F bouts, is subdivided into:
(1a) FF (intervals within meals, not containing an R),
(1b) MM (intervals between meals, usually containing one or more R).
(2) R/R. This class, comprising all intervals between rumination bouts, is subdivided into:
(2a) RR (not containing a meal),
(2b) RmR (containing a meal).
(3) MR
(4) RM
These intervals contain only 'other' behaviour.

2.2.3. *Concepts and analytical methods.*

What behaviour the animal is likely to perform is said to depend upon two conditions:

(1) the 'state' of the animal, which is defined by a number of 'state variables';
(2) the 'input variables', which are stimuli arising from the external environment.

State variables are conditions in the animal resulting from its entire behavioural history, including all motivational and learning processes. These variables determine, together with the input variables, both the present behaviour output and the animal's next state (cf. Geertsema and Reddingius, 1974).

Starting point of the investigation will be two working hypotheses. First, there are state variables specific to feeding behaviour, which operate in such a manner that (1) when the animal does not eat, sooner or later the responsiveness to food stimuli will increase, and (2) when the animal eats, sooner or later this responsiveness will decrease. Overt feeding behaviour is determined by the joint effect of the state variables for feeding and the food stimuli. The second working hypothesis is that there are state variables specific for rumination. As this behaviour is not dependent on specific input variables, these state variables alone will determine the likelihood of overt rumination. The present study will not consider possible changes in the state for 'other' behaviour. To refer to the specific states for feeding and rumination, the term 'motivation' will be used. Moreover, the state and (eventual) input variables together will be termed the 'causal factors'.

Of course, in the final analysis overt behaviour must form the basis of any statement about the 'state' of the animal. Two parameters of the behaviour output will be studied: duration of the units and the order in which they occur. For the analysis of duration, behaviour will be considered as a stochastic process with two possible outcomes: the behaviour in question, say A, is performed, or it is not performed. We may then ask whether during an interval of non-A the probability that A will be resumed is constant, or whether it depends on the time elapsed since the previous A bout. Similarly, we may ask whether during an A bout the probability of ending A is constant, but this question is formally identical to the former one.

If during non-A the probability that behaviour A will be resumed is constant and independent of duration of foregoing non-A, then the initiation of an A bout conforms to a first-order Markov process and the length of the intervals will be exponentially distributed (H. A. J. Metz, 1974). In this paper, distributions of unit durations will be plotted as survivorship curves (Nelson, 1965), i.e. cumulatively and backwards, so that successive points in the curve represent 'all intervals', 'all intervals greater than X min' (X is the class width), 'all intervals greater than 2X min', etc. When an exponential distribution is plotted in this way on semilogarithmic paper, it yields a straight line. This facilitates the comparison of actual data with the first-order Markov model (which will simply be termed the 'random model' in the rest of this paper). When the survivorship curve for a given unit is straight and, therefore, fits the exponential distribution (like the F curve in Fig. 2.3.), it is correct to conclude that duration of that unit is random only if also the requirement for application of the Markov model *viz.* stationarity is fulfilled. If it is not so, complications in the interpretation arise as is discussed on p. 14.

Deviations from the random model will result in convexity or concavity in the actual survivorship curve, at least when this curve is plotted semilogarithmically. Convexity is beautifully illustrated by the curves for R length in Fig. 2.5. There is a relative shortage of short units in comparison with the random model, then. This indicates that the probability of ending the unit is low at first, but it increases with the time elapsed since the beginning of the unit. On the other hand, in the case of concavity there is an excess of short units. This is illustrated, for example, by the initial parts of the survivorship curves in Fig.2.2. Concavity indicates that the probability of ending the unit is high at first, but it will decrease with the time elapsed since the beginning of unit. In one and the same survivorship curve convex and concave parts may be seen (see, e.g., the RM curve for the morning period in Fig. 6.3., p. 41), but the interpretation of each deviation remains essentially the same, of course, as indicated above for curves with either a convex or concave part. One point is especially important in the case of survivorship curves for intervals. When the curve is convex, it means that the adjoining bouts are spaced out in time. Conversely, when the interval curve is concave, it means that the bouts they separate tend to cluster.

2.3. RESULTS

In order to obtain a first global impression, the pooled data of day and night were analysed, in spite of diurnal rhythms. We shall see below (e.g. pp. 13 and 14) that conclusions reached in this way may be utilized, provided that certain precautions are taken.

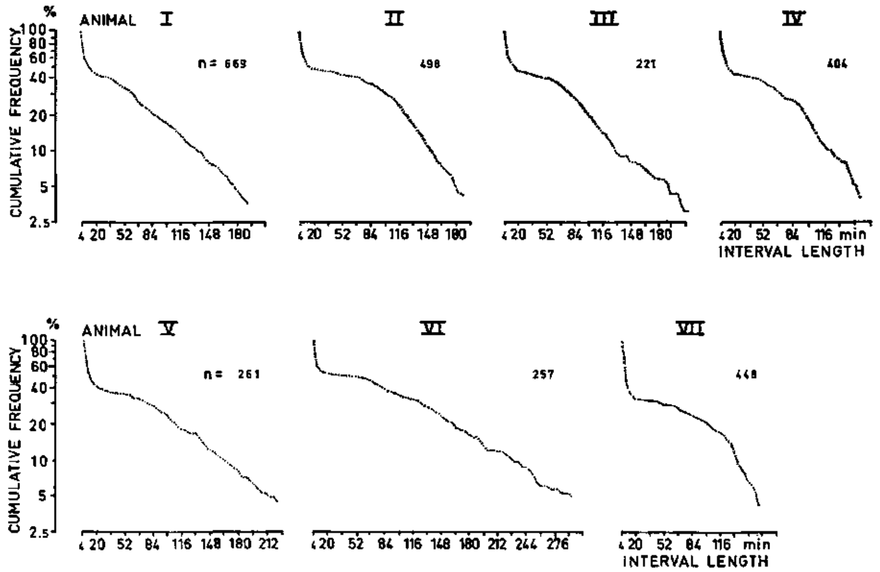

FIG. 2.2. Survivorship curves for F/F intervals of 4 min and longer.

2.3.1. *Existence of meals*

For the present purpose we must consider whether in cattle feeding bouts cluster in time. Fig. 2.2. shows the survivorship curves for the F/F intervals that could be distinguished on the recorder charts ($\geqslant$ 4 min). In each animal the curve deviates strongly from a straight line. There is a marked excess of short intervals and a shortage of intervals of medium length. These findings suggest that two types of non-feeding intervals exist (cf. Wiepkema, 1968):

(1) Intervals with a high probability of starting feeding, which for that reason will usually be short. A sequence of feeding bouts alternating with these short intervals will be called a *meal*. In this study the upper limit for the within-meal intervals will be set at 20 min. This so-called *meal criterion* fits all animals very well (see also p. 11).

(2) Intervals with a low probability of starting feeding, at least in the range of about 20 to 60 min, are those separating one meal from another (MM intervals). In some animals (nos. I and VI) the probability of starting feeding becomes more or less constant when the intervals exceed 40-60 min. In contrast, in some others (nos. II, IV, VII) the accelerated decline of the survivorship curve indicates that the probability of beginning the next meal increases gradually during the interval (Fig. 2.2.).

2.3.2. *Patterns of feeding within a meal*

Further non-randomness in the time pattern of feeding may appear from the distribution of F length as well as the within-meal interval length. These distributions were derived from data obtained by direct visual observation, as

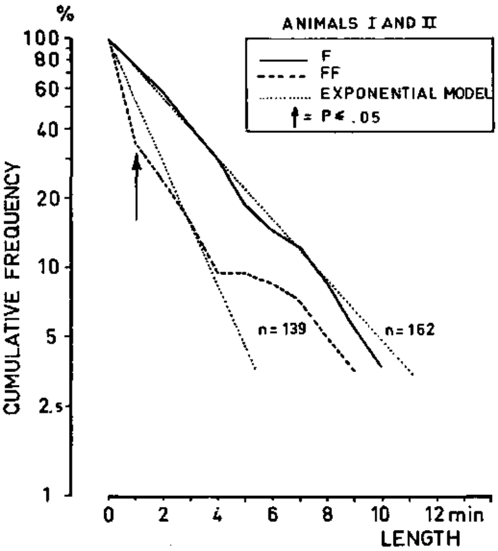

FIG. 2.3. Survivorship curves for the length of feedings bouts and FF intervals. The arrow indicates significant deviation from the exponential model.

mentioned before. The results are shown in Fig. 2.3. For each survivorship curve the best fitting exponential distribution was determined and deviations from that random model were tested with the Kolmogorov-Smirnov test (Lilliefors, 1969).

The survivorship curve for F length is close to the random model. In contrast, the curve for FF intervals deviates significantly from that model by concavity. No weight should be attached to the convexity in the range from 4 to 10 min because the material was too limited here. Fig. 2.2. reveals that concavity also appears in and beyond that range up to interval lengths of 20 min. Concavity indicates that the probability of ending the interval decreases with increasing lapse of time since its beginning.

It can be concluded that the time pattern of the various activities within a meal is non-random in that the longer an interruption has lasted, the lower the tendency of the animal to resume feeding. The explanation of this phenomenon lies outside the scope of the present paper. On the other hand, distribution of F length gives no indication of non-randomness.

2.3.3. *Temporal order of meals and rumination bouts*

The order in which different categories of behaviour follows one another is elucidated in some aspects by Fig. 2.4. This figure shows for each animal how many rumination bouts occur within the MM intervals (rumination was never observed during an interruption within a meal, see also p. 13). Nearly every MM interval contained rumination; most frequently one, or in some individuals two bouts. As Fig. 2.4. shows, higher numbers of rumination bouts per interval were increasingly rare. However, there are marked differences between the animals, e.g. in animal VI up to 10 bouts were observed within one MM

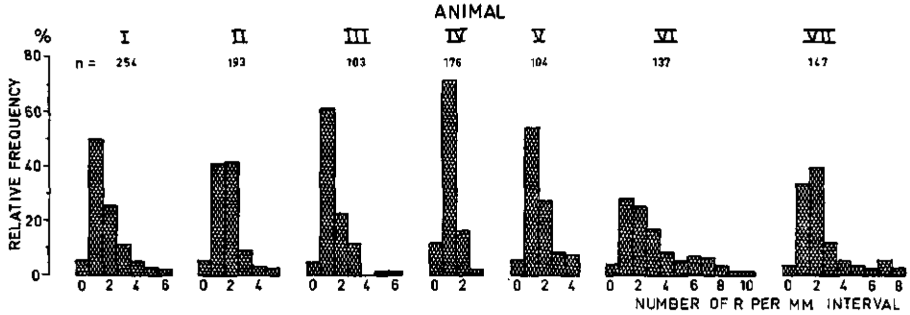

FIG. 2.4. Frequency distributions of the number of rumination bouts per MM interval.

interval, but never more than 3 in animal IV. In all, meals are usually followed by an MR interval, then by one or more rumination bouts separated by RR intervals, and finally by a RM interval and another meal.

2.3.4. *Durations of meals, rumination bouts and intervals.*

Let us now consider the duration of the units used in the subsequent analyses. For each of these units a survivorship curve was constructed (Fig. 2.5., but for MM intervals, see Fig. 2.2.). When required the Kolmogorov-Smirnov test was applied to check the significance of deviations from linearity. The following points in Fig. 2.5. deserve mention: First, the survivorship curve for M duration is rather variable between animals. In some individuals it fits the random model very well (nos. I and IV), whereas in some others it is clearly convex (nos. II, VI and VII), indicating a relative shortage of short meals. Second, the survivorship curves for MR intervals show a marked shortage of short intervals, but in their further parts these curves are more or less exponential. Third, the survivorship curves for R lenght show convexity over a wide range. Thus when an R is once started, the probability of its ending becomes gradually higher. Fourth, the R/R and RR interval curves coincide in the range of the shorter, but diverge strongly in the range of the longer intervals. Evidently, intervals between successive rumination bouts are longer when they contain a meal (RmR intervals). The R/R and RR interval curves are horizontal at first, which indicates a strong shortage of short intervals, but in their later parts they are more or less exponential. Evidently, rumination bouts are spaced out in time. Finally, the RM interval curves reveal a relative excess of short intervals ($<$ 10 min) in the majority of animals. In their later parts these curves also are more or less exponential.

2.4. DISCUSSION

Concept of a meal

In cattle, the feeding bouts are not scattered evenly over time, but tend to occur

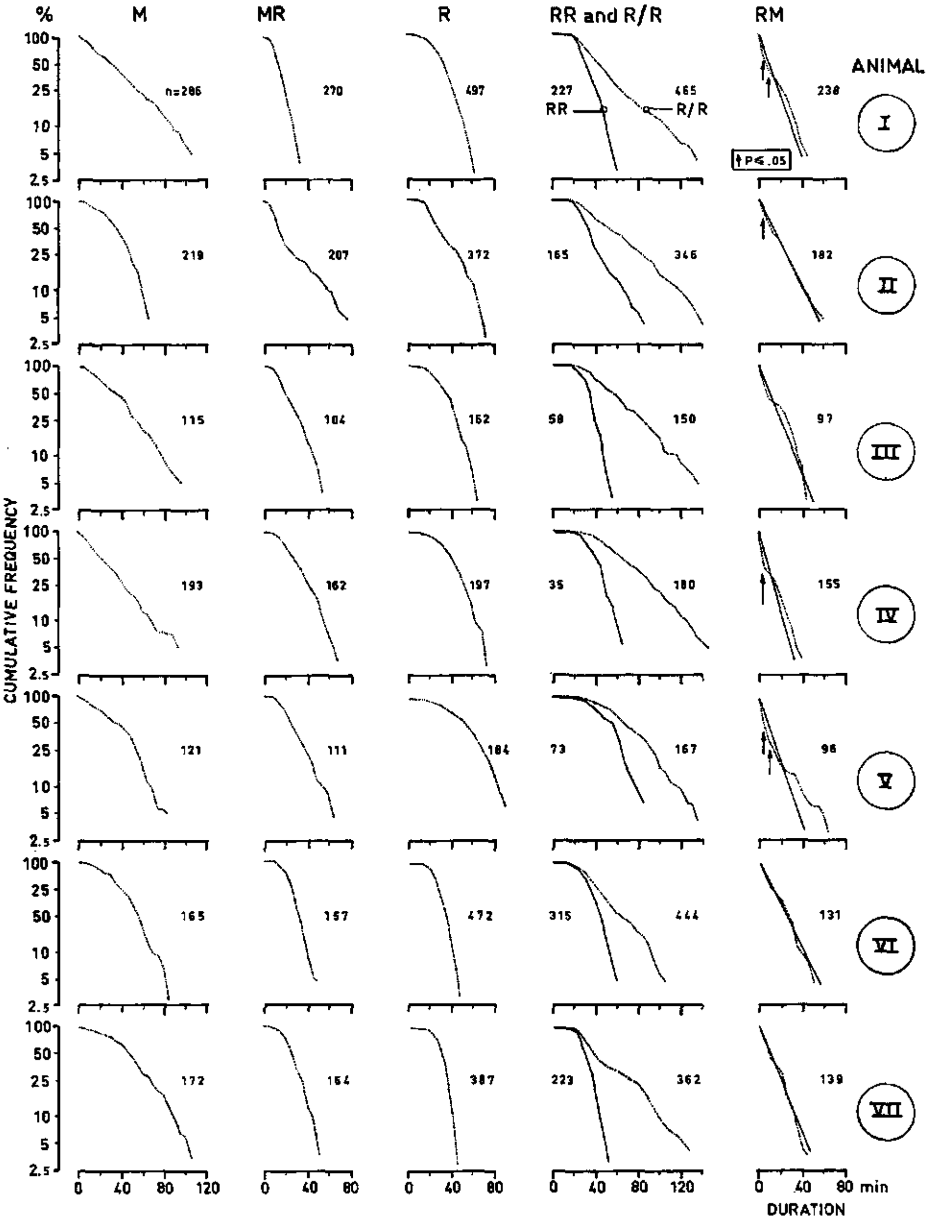

FIG. 2.5. Survivorship curves for the duration of meals, rumination bouts, and various types of intervals. Arrows in the RM graphs indicate significant deviations from the random model (straight line).

in clusters as indicated by the strong excess of short non-feeding intervals (Fig. 2.2.). Therefore, the existence of 'meals' was accepted.

The existence of meals implies, that when feeding begins, a few bites of food usually will not suffice to reduce the motivation for this behaviour far enough for it to stop again (cf. De Ruiter and Wiepkema, 1969). First a sizable meal will be taken but, because behaviour is a stochastic process, this will usually consist of feeding bouts alternating with (within-meal) non-feeding interruptions. Finally, however, satiety induced by that meal will suppress feeding for a long time, so that a (between-meal) interval results. In other words, as regards feeding behaviour, the animal switches back and forth between two clearly distinct states.

In terms of this model, occasional bites (representing extra short feeding bouts) scattered within the non-feeding intervals should not be considered as meals but as chance events during the interval (cf. De Ruiter et al., 1974). For that reason it may be necessary to put a minimum duration to 'real' meals, but the need for this in the present study did not seem urgent as the smallest meals observed in the records lasted at least 3-4 min and their frequency was not excessive when considered in relation to the overall frequency distribution of meal duration (Fig. 2.5.).

If one wants to describe feeding behaviour in terms of such a two state model, it is important to find a meal criterion that enables the observer to specify in which state his animal is at a given time with minimal risk of error. For obvious reasons, only non-feeding intervals with a high probability of resuming feeding should be attributed then to meals. On this view, a meal criterion higher than 20 min would not be valid in our cattle (Fig. 2.2.). Even though any criterion in the range between 20 and about 40 min would lead to the same values for the various parameters of the meal pattern, because the number of intervals in this range is extremely low in all animals, criteria higher than 20 min would inevitably result occasionally in attributing the meal state to an animal that actually is in the interval state.

It remains to consider whether criteria shorter than 20 min might possibly be valid, for the breaks in the survivorship curves for non-feeding intervals, on which the 20-min criterion is based, are not very sharp. For this purpose we must also take into account whether different criteria lead to different conclusions as regards major issues like the correlation between M size and the length of the adjacent MM intervals (cf. le Magnen, 1969). Anticipating more detailed analysis of the latter issue in Chapter 4, Fig. 2.6. shows the changes in correlation between meal size and interval duration when criteria are varied from 8 to 92 min in steps of 4 min. For the present discussion the main point arising from Fig. 2.6. is that in the range of criteria between 20 and 50-70 min the correlations remain at a rather constant level, but when lower criteria are used (1) the correlation between M size and the preceding interval increases in most animals and (2) in some individuals also the correlation between M size and the following interval markedly changes (some further points arising from Fig. 2.6. will be discussed in Chapter 4). Under certain realistic assumptions such changes

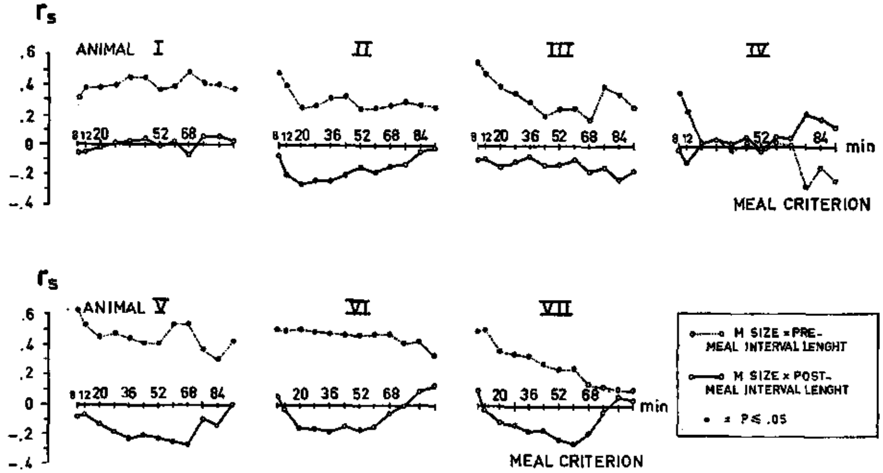

FIG. 2.6. Spearman rank correlation coefficients between meal size and length of the adjacent MM intervals when the meal criterion is varied from 8 to 92 min (only daylight data).

in the correlations can actually be expected as a consequence of lumping between-meal intervals with some within-meal intervals, and complete meals with some fragments of meals. In sum, to make a sharp distinction between the meal and interval states in the cows, a meal criterion neither lower, nor higher than 20 min is preferable.

Fig. 2.2. shows that with a 20-min criterion there is hardly any overlap between the distributions of within-meal and between-meal interval lengths. In other words, meal and interval state alternate in a very distinct manner in cattle. Judging from the available literature, this distinction is not so sharp in other meal-eating mammals, e.g. the mouse and rat (Wiepkema, 1968; Levitsky, 1970). In some birds, e.g. the fowl, pigeon and zebra finch, even the clustering of the feeding events is less marked (Duncan et al., 1970; Zeigler et al., 1971; Slater, 1974); meals or some analogus unit are defined in these cases with very low criteria ($\leqslant 2$ min) and the daily number of those units is much higher than that of meals in cattle (Fig. 3.1.), rats or mice.

To explain why cattle eat in meals would require a detailed study of the time pattern of feeding and other activities within the meal (cf. Wiepkema, 1971). This lies outside the scope of the present paper, but two of the above results are worth mentioning in this context. Firstly, it was found that the distribution of feeding bout length fitted rather well the exponential, random model (Fig. 2.3.). Secondly, the distribution of the within-meal intervals revealed that the longer the non-feeding interruptions are, the lower is the tendency of the animal to resume feeding. Unfortunately, the data were insufficient for a thorough study of trends in these units in the course of a meal, but it was established that the longer non-feeding interruptions (8-20 min) occurred more frequently in the later part of the meal. This shows that within-meal trends in the duration of one or both units must exist, which indicate that the motivation for feeding wanes towards the end of the meal.

Temporal order of meals and rumination bouts

Feeding and rumination are not involved in a rigid sequential patterning (Fig. 2.4.); meals alternate with a varying number of rumination bouts. It is striking that practically every between-meal interval contained rumination, while rumination never occurred within a meal. Yet the longest non-feeding pauses within a meal are certainly long enough to contain a very short MR interval plus a very short rumination bout plus a short RM interval, but these long pauses were rare and the combination of three short units is unlikely (Fig. 2.5.). This may account for the absence of rumination within meals (however, see also assumption 6, p. 53).

Duration of meals, rumination bouts and intervals

The distributions of the duration of these units will reflect the joint effect of the autonomous and interactive factors in the rhythms of feeding and rumination.

The distributions of M duration (Fig. 2.5.) and of MM length (Fig. 2.2.) vary considerably in form between animals. However, in the case of M duration this variation can largely be ascribed to differences between the individual diurnal rhythms of feeding. In animals with an approximately exponential survivorship curve for M duration (nos. I, III, IV), a relatively large number of (small) meals occurred during the night (cf. Fig. 3.2.). When these meals are excluded from the distributions, the survivorship curves in all individuals are convex, indicating that at least during daylight the rate of decay of meals increases progressively with meal duration.

The differences between animals in the form of the MM interval curves (Fig. 2.2.) cannot be explained in this way. These curves reveal that in all animals meals are followed by some period (longer than 20 min of course) in which initiation of another meal is very improbable. One may surmise that the initial low rate of decay of the intervals beyond 20 min is caused by interaction with rumination, which as we have seen, starts rather soon after nearly every meal, but later chapters will present some arguments against this view.

The MR interval distributions (Fig. 2.5.) reveal that meals are followed by a short period of no rumination. Such a 'lag' for rumination also exists in sheep (Pearce, 1965a). I shall discuss in Chapter 6 what factors affect the length of the lag.

The survivorship curves for rumination bouts and their intervals (Fig. 2.5.) indicate that R bouts generally persisted for at least 5 min and R/R intervals for at least 15 min. As already stated, the intervals were much longer on the average when they contained feeding. It is unlikely that feeding is allowed to start only in the longer intervals because MR intervals are much shorter on the average than RR intervals. It is more probable that feeding has priority over rumination and that this is the reason why the occurrence of meals prolongs the intervals between rumination bouts. This hypothesis will be further considered in later chapters.

The RM interval distributions show an excess of short intervals in four animals (Fig. 2.5.). This may indicate that rumination induces a temporary facilitation of feeding. Another possible explanation is that meals may start at any moment, irrespective of whether the cow is ruminating or not. Under that condition an excess of short RM intervals will arise (see p. 32). We shall see in later chapters that the latter hypothesis is probably correct, but the former one cannot be disproved at present.

To sum up, we have seen in this discussion that some of the behaviour measures utilized are not randomly distributed in the sense that they do not conform to a first-order Markov process. However, even in cases which do fit this model, there are several reasons why the conclusion that behaviour is random would not necessarily be correct (cf. Delius, 1969). Firstly, the duration of the unit may yet depend on what kind of units precede it and how long these units are. Secondly, when data pooled for the whole day suggest randomness, non-randomness may yet be revealed when diurnal rhythmicity is taken into account, as shown above for M duration. These two points will be examined in more detail in Chapters 3 and 4.

3. DAILY TOTALS AND DIURNAL PATTERNS OF FEEDING AND RUMINATION

3.1. Introduction

This chapter specifies some further characteristics of feeding and rumination that must be taken into account in any model of these behaviours. Two aspects will be discussed:

(1) the amount of food eaten, and the amount of time spent on meals and on rumination per 24 hours, the way in which these amounts are divided into meals and rumination bouts, and some correlations between these measures;
(2) the diurnal rhythmicity of feeding and rumination and the influence thereon of the light-regime.

3.2. Material

The data used came mainly from the basic experiment (p. 2). The effect of the light-dark cycle was examined in two animals, one of the FH-breed (no. VIII) and one of the MRY-breed (no. IX), in the following way: both animals were maintained at first on a 16-8 light-dark cycle for 27 days, subsequently for 18 days on a 10-14 cycle, and finally on a 16-8 cycle again for 18 days. The other conditions were the same as in the basic experiment. Data were analyzed only for the later part of each experimental period (10-12 days), when the animals were habituated to the light-regime.

3.3. Results

3.3.1. *Daily amounts of feeding and rumination*

Table 3.1. gives for each animal the mean and standard deviation of daily food intake, total time spent on meals and on rumination bouts per day, and daily number of these units. There is considerable variation between the animals in the various measures. Of course, from Table 3.1. we can also calculate mean duration of M, R, and MM and R/R intervals (compare Figs. 2.2 and 2.5.).

Table 3.2. shows some relevant correlations. Firstly, daily food intake and total rumination time were positively correlated. Secondly, in four animals daily intake correlated significantly positively with mean M size. Rather different, but low correlations were found between daily intake and the number of M. This difference may be due to the fact that in all animals daily number of M was strongly negatively associated with M size ($-.91 \leqslant r \leqslant -.38$). Thirdly, in general daily rumination time correlated positively with mean duration of R, but in the animals in which this effect was weak, it also correlated

Table 3.1. Means and standard deviations of some measures of the daily feeding and rumination patterns.

animal	number of days	daily food intake(kg)		daily meal time (min)		daily number of M		daily rumination time (min)		daily number of R	
		$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
I	32	16.7	1.9	359	49	8.9	1.8	551	41	15.5	1.4
II	26	13.2	.9	303	43	8.4	.7	493	28	14.3	1.6
III	12	16.3	1.0	392	46	9.6	1.7	498	21	13.5	1.5
IV	17	17.0	.7	362	29	11.4	1.8	493	43	11.6	1.7
V	17	18.5	1.5	292	37	7.1	1.1	579	34	10.8	1.4
VI	28	11.0	1.1	248	29	5.9	1.0	496	25	16.9	1.2
VII	25	10.3	1.0	353	32	6.9	.9	464	34	15.5	1.2

Table 3.2. Correlation coefficients between some measures of the daily feeding and rumination patterns.

animal	daily food intake x daily rumination time	daily food intake x mean M size per day	daily food intake x daily number of M	daily rumination time x mean R length per day	daily rumination time x daily number of R
I	+.30*	+.66***	−.38*	+.61***	−.05
II	+.41*	+.53***	+.28	+.03	+.45*
III	+.55*	+.11	+.17	+.55*	−.30
IV	+.10	−.04	+.21	+.28	+.38
V	+.48*	+.46*	−.10	+.45*	−.06
VI	+.71***	+.20	+.42*	+.31	+.38*
VII	+.57***	+.72***	−.38*	+.66***	+.08

*$p \leqslant .05$ ***$p \leqslant .005$

positively with the number of R. When in the above correlations total meal time was used instead of the amount of food eaten, generally the same results were obtained, but the positive correlation with total rumination time disappeared in the majority of animals and was much weakened in the remaining ones, no doubt because meal time comprises both feeding bouts and interruptions of meals.

3.3.2. *Diurnal fluctuations*

To examine diurnal patterns of feeding and rumination the day was divided into periods of two hours. For each measure of behaviour (Figs. 3.1. and 3.2.) the period-to-period variation was tested against the within-period variation between days in an analysis of variance (Weber, 1967). In all animals, significant ($p \leqslant .05$) diurnal fluctuations were established in all measures, except in R duration in animal II.

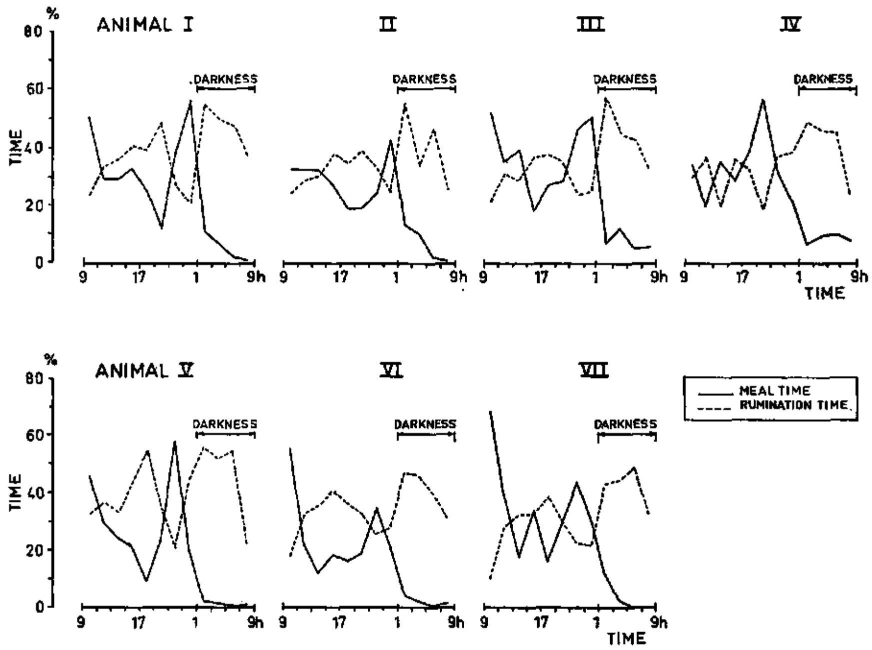

FIG. 3.1. Mean percentage of time spent on meals and on rumination bouts in the various two-hour periods.

Fig. 3.1. shows strong diurnal fluctuations in total time spent on meals and rumination bouts per two hours. Feeding showed two main peaks: one in the beginning of daylight and one at the end. The evening peak was higher in four animals. In all of them feeding was strongly reduced during the night.

Rumination in general showed the reverse fluctuations. Only towards the end of night, time spent on rumination decreased while feeding was maintained at a constant low level.

Fig. 3.2. shows how the diurnal fluctuations in total time spent on meals and on rumination originate from changes in length of M and MM intervals, and R and R/R intervals, respectively. M duration tends to vary in parallel with total meal time, i.e. it is high in the beginning and at the end of the day. Meals were brief during the night. The fluctuations in MM length were the reverse of those in M duration. Very long intervals occurred during the night, particularly in some animals (nos. V, VI, VII). Clearly, both changes in M and MM interval length contribute to the diurnal rhythmicity of time spent on meals.

The fluctuations in R length were of small amplitude in comparison to those in M duration. There was hardly any difference in mean R length between day and night in any animal. R/R interval length fluctuated much more, in the main parallel to M duration. However, during the night interval length did not decrease so strongly.

To unravel the interaction between feeding and rumination, fluctuations in

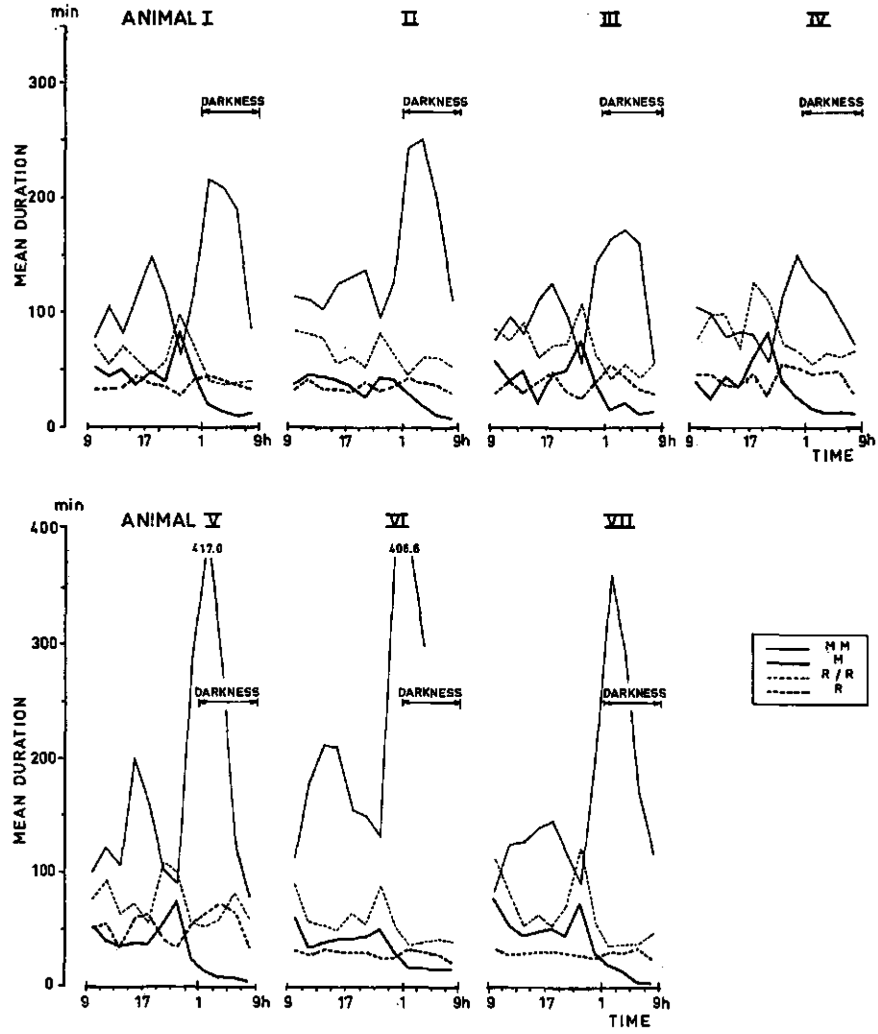

FIG. 3.2. Mean duration of meals, rumination bouts, and MM and R/R intervals, started in the various two-hour periods.

MR, RR, and RM lengths should be considered as well. These fluctuations were of relatively small amplitude or showed hardly corresponding patterns in the various animals. For the lumped data of all animals, they will be considered again in the next chapter. For the present discussion it suffices to state that MR, RR and RM interval lengths are fairly constant over the day.

Fig. 3.3. shows the effect of changing the light-dark cycle on the feeding and rumination rhythms. On the 10-14 cycle the feeding peaks retained the same relation to the light period as on the 16–8 cycle, but on a 10–14 cycle rather

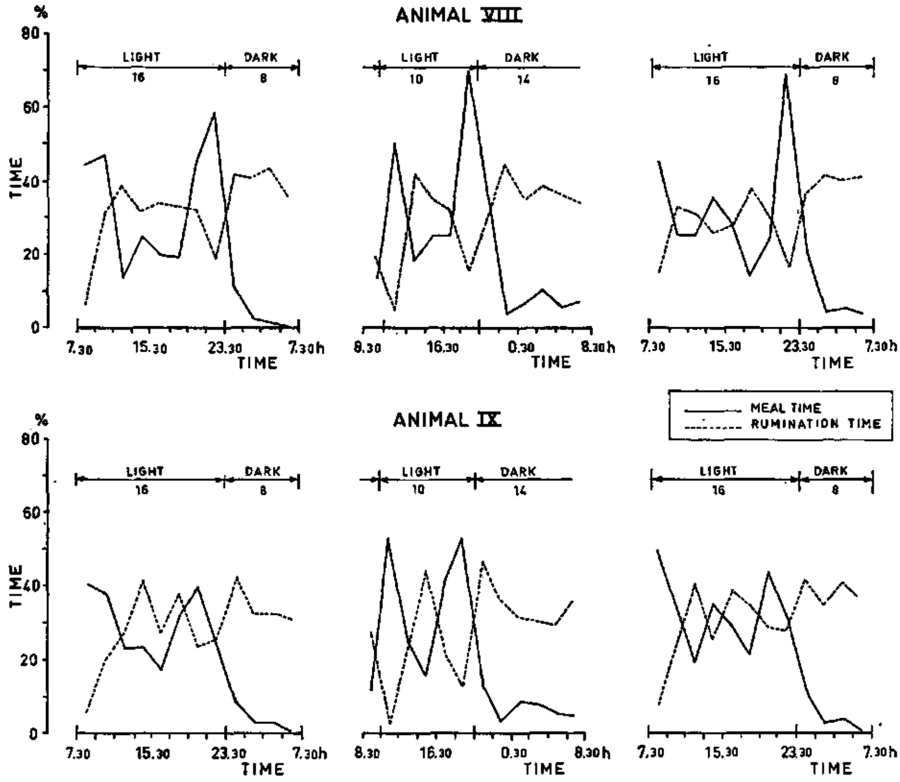

FIG. 3.3. Mean time spent on meals and rumination bouts in the various two-hour periods on the different light-dark cycles.

more feeding occurred during the night. The strong inverse relation between meal and rumination time was not affected by changing the cycle.

3.4. DISCUSSION

Daily amounts of feeding and rumination

The values in Table 3.1. for daily intake, total daily meal and rumination times, and numbers of M and R, are in the range of values found in the literature and need no further comment (cf. Hafez et al., 1969; Porzig, 1969), but it may be mentioned that the differences in food intake between animals were not obviously related to differences in body weight. Further, it is worth stressing that cows spend so much time on feeding and rumination (our animals: 12–15 hours per day).

Table 3.2. reveals some further points relevant to a model of feeding and rumination. Firstly, daily food intake and total rumination time are positively

correlated, as also shown by other workers (e.g. Ruckebusch, 1970). This indicates that facilitatory relations may exist between feeding and rumination. We shall come back to this point in the Chapters 5 and 6. Secondly, in most animals daily food intake increases with meal size rather than number of meals. This may reflect the way in which cattle ensure that daily intake matches caloric expenditure, but this point can be decided only by experimental manipulation of expenditure (cf. le Magnen, 1967). Thirdly, variation in daily amount of rumination originates generally from variation in R length alone; number of R contributed significantly in only two animals. This point is considered again in Chapter 6, where the need for rumination is manipulated.

Diurnal fluctuations

Feeding as well as rumination show marked diurnal rhythms due to fluctuations in the interval lengths of both behaviours, and in meal duration in the case of feeding (Figs. 3.1. and 3.2.). Moreover, the patterning of these diurnal cycles is strongly dependent on the light-dark regime (Fig. 3.3.) as also suggested by studies on grazing cattle (Hafez et al., 1969; Porzig, 1969).

Feeding has two main peaks, one in the beginning and one at the end of the day, while it is strongly reduced during the night (Fig. 3.1.). In our experiment the morning peak coincided with the supply of fresh food, but a morning peak also appears under more constant food conditions (unpubl. observations; Hafez et al., loc. cit.). In periods with more feeding, meals are larger and MM intervals shorter than when feeding is at a low level (Fig. 3.2.). This finding may provide a useful pointer for physiological analysis of the feeding motivation.

The diurnal fluctuations in the amount of rumination (Fig. 3.1.) are mainly opposite to those in feeding, as also reported, e.g., by Skouri (1967) and Geoffroy (1974). This might be expected because the two behaviours are mutually exclusive and much time is spent on each. However, there is no reason to assume diurnal fluctuations in the motivation for rumination because the length of both rumination bouts (Fig. 3.2.) and RR intervals remain fairly constant over the day. In contrast, R/R interval length fluctuates strongly and largely parallel to M duration. This makes it likely that feeding has priority over rumination and actually causes the diurnal fluctuations in the latter. This point will be examined further in the following chapters.

The diurnal fluctuations, particularly in the measures for feeding, have consequences for the subsequent analyses. To avoid complications due to trends in the data (cf. Delius, 1969) at least four periods should be distinguished: the beginning, middle and end of the day, and the night.

4. TEMPORAL CORRELATION BETWEEN UNITS WITHIN SHORT SEQUENCES

4.1. Introduction

In this chapter a further step is made in the analysis of the feeding and rumination patterns under ad lib. conditions. From the behaviour protocols of the basic experiment (p. 2), various types of short sequences of meals, rumination bouts and intervals are selected and for each type the following questions are examined:

(1) Are durations of the units within the sequence correlated and,

(2) if so, are these correlations dependent on the time of day?

At the end of this chapter, I shall put forward a preliminary model of feeding and rumination, based on the ad lib. data, which will serve as a basis for further experimentation.

4.2. Results

Multiple regression analysis was employed to determine the correlation between durations of units within each sequence. In this analysis the following model has been used:

$$Y = a + b_1X_1 + b_2X_2 + \dots b_nX_n$$

to explain the variation of the dependent variable Y from the variation of the independent variables $X_1 \dots X_n$ (Weber, 1967). Student's t-test was used for testing the significance of the partial regression co-efficients $b_1 \dots b_n$. In each case the percentage of variance of Y was calculated, that was associated with the X-variables. The significance of this percentage was tested with Fisher's F-test (Weber, 1967).

In our case, multiple regression analysis was seriously complicated because the requirement for independence of the X-variables was not always met. The partial regression co-efficient of Y on one X-variable may then be strongly dependent upon the other X-variables in the model. Moreover, one X-variable may then account for nearly the same percentage of variance of Y as a whole set of X-variables, which individually would correlate significantly with Y. To avoid these complications in the interpretation of results, I first calculated the regression co-efficients of Y on each of the X-variables separately and also the percentages of variance of Y, associated with these individual variables. Subsequently, the X-variables were joined in the multiple model and the fraction of variance of Y associated with that model was calculated.

The regression analyses were carried out separately for different periods of the day in order to check for diurnal changes in the relationships. The length of the periods was adjusted to the pattern of diurnal fluctuation in the variables, as presented in Fig. 3.2. The sequences were attributed to the period in which the last unit of the sequence started, except in the case of the sequence M – MM – M (see below).

The data of the seven animals were pooled after correction for individual differences in the mean values of the variables. This pooling was necessary to obtain a reasonable number of degrees of freedom for testing the estimated parameters; it was permissible because analyses of individual results showed that there was at least qualitative correspondence between all experimental subjects.

Sequence M – MM – M

The analyses were made for each period of two hours separately. Only the last six hours of the night were taken together as one period. The sequences were attributed to the period in which the first M started, not the second. This ensured that the first (relatively large) meal of each experimental day was assigned to period no. 1.

Table 4.1. presents mean durations of the units in the various periods and the percentage of time spent on rumination during the MM intervals. In all animals M duration was strongly positively correlated with M size ($+.84 \leqslant r \leqslant +.95$; $p \leqslant .005$), so that it suffices to use one of the two measures in the subsequent analyses. As the special point of interest here is the time pattern of the meal and interval states, I shall use M duration and not M size. Values of MM length are much lower in Table 4.1. than in Fig. 3.2., because in the former the (long) intervals ended by the first M of the next day are not included. The percentage of rumination time during the interval fluctuates within narrow limits from period to period. This might be expected in view of the high positive correlation between MM length and total rumination time during that interval, seen in the individual animals ($+.72 \leqslant r \leqslant +.96$; $p \leqslant .005$)

Table 4.2. shows the dependence of MM length upon the preceding M. Only

Table 4.1. Mean duration of the units in the sequence M – MM – M and mean percentage of time spent on rumination during MM.

2-h period no.		*n*	first M min	MM min	second M min	total rumation time during MM %
day	1	190	50.4	100.5	40.4	44.4
	2	131	40.5	118.2	42.7	44.8
	3	117	42.1	115.5	38.9	49.4
	4	117	36.6	128.3	42.5	50.5
	5	95	43.4	131.8	54.0	44.6
	6	100	46.1	99.7	54.6	47.6
	7	129	61.1	107.3	29.2	45.1
	8	81	33.6	135.5	20.1	54.8
night	9	36	18.1	134.5	10.1	48.4
	10–12	49	11.8	101.1	11.2	49.6

Table 4.2. Dependence of MM on the preceding M.

	2-h period	regression of MM on preceding M	
	no.	b	% variance
day	1	+.03	.0
	2	+.05	.0
	3	+.50*	4.2*
	4	+.55*	4.0*
	5	+.06	.1
	6	+.01	.0
	7	+.64*	5.3*
	8	+.09	.1
night	9	+.29	.2
	10–12	+1.45	5.4

* $p \leqslant .05$

in the middle and at the end of day significant, positive regression co-efficients were found, but the percentages of associated variance were small.

Total rumination time during the MM intervals also hardly correlated with the preceding M. The correlations were very similar to those found for the interval length; they are not presented in the table, therefore. Rumination time and interval length together did not correlate better with the preceding M than each of these variables alone. This indicates that also the percentage of time spent on rumination during the interval was not substantially affected by the preceding M.

Table 4.3. shows the dependence of the second M in the sequence on the preceding M, MM interval, and total rumination time during that interval. The two successive meals were only significantly correlated in the periods 7 and 8, i.e. around the end of the evening peak. The relationship was negative. During most of the day M, was positively correlated with the preceding MM interval. This relationship accounted for up to about one fifth of the variance of M. Around the beginning and middle of the evening feeding peak (sequences starting in periods 5 and 6) the positive correlation decreased and it even became negative at the end of this peak (period 7). During night all correlation disappeared.

M duration was rather similarly correlated with total rumination time during the preceding MM interval as with that interval itself. Interval length and rumination time together accounted for hardly more of the variance of M than one of them alone. These results indicate that neither absolute amount of rumination in the preceding interval, nor the percentage of time spent on it, are of importance for explaining the subsequent M duration in addition to interval length. Altogether, in any one period no more than about one fourth of the variance of M was associated with duration of its preceding units in the sequence.

Table 4.3. Dependence of M on the preceding MM and M, and on total rumination time during MM.

2-h period	regression of M on						
	preceding M		preceding MM		preceding rumination time		these variables together
no.	*b*	% variance	*b*	% variance	*b*	% variance	% variance
day 1	–.03	.1	+.17*	15.8*	+.37*	20.6*	21.5*
2	+.10	.7	+.17*	15.5*	+.41*	26.1*	26.8*
3	+.05	.3	+.18*	20.3*	+.34*	24.0*	24.6*
4	+.04	.1	+.22*	20.5*	+.34*	16.8*	20.9*
5	+.22	2.7	+.27*	10.6*	+.27*	3.8*	14.9*
6	–.06	.2	+.17*	6.1*	+.27*	5.0*	6.6
7	–.29*	19.5*	–.06*	6.2*	–.13*	9.0*	22.1*
8	–.11*	4.8*	–.01	.7	–.02	.3	6.9
night 9	+.02	.3	+.01	.7	+.02	1.5	2.2
10–12	+.10	.8	+.03	2.7	+.03	1.0	4.5

* $p \leqslant .05$

Sequence R – RM – M

In the analysis of this sequence the same periods were considered as above. Of course, sequences which ended on the first M of the next day were omitted again. Mean durations of the units in the various periods are shown in Table 4.4. Only sequences with a short R and RM interval could be assigned to period no. 1. In the other periods, mean R and RM lengths were rather constant, in spite of the strong fluctuations in M duration (the suggestion that R is somewhat longer during night is not statistically reliable).

The results of the regression analyses are presented in Table 4.5. The relationship between RM interval and preceding R lengths was positive and not evidently subject to diurnal changes, but the percentage of associated variance was rather low. The M at end of the sequence was not dependent on the preceding RM interval and only in some periods during the day and night it was slightly positively correlated with the preceding R.

Sequence M – MR – R

Again the same periods were considered. Mean durations of the units in each period are presented in Table 4.6. Mean MR length as well as mean R length were rather constant over the day.

Table 4.7. shows the relationships between the units. Considering the M at the beginning of the sequence as dependent variable, weakly significant correlation with the MR interval was found in two, and with R in only one out of the total of ten periods. In all periods except 10–12, R length was inversely related with the preceding MR interval.

Table 4.4. Mean duration of the units in the sequence R – RM – M.

	2-h period no.	*n*	R min	RM min	M min
day	1	27	29.3	4.6	33.6
	2	126	34.2	15.9	41.0
	3	108	34.1	14.9	43.8
	4	109	33.5	12.2	37.5
	5	95	36.2	13.5	43.4
	6	96	33.0	15.6	45.0
	7	123	30.1	13.7	62.9
	8	93	32.8	15.2	34.0
night	9	62	39.1	12.4	19.8
	10–12	129	40.6	13.9	12.8

Table 4.5. Dependence of RM and M on preceding units in the sequence R – RM – M.

2-h period	regression of RM on		regression of M on				
	preceding R		preceding R		preceding RM		both variables
no.	*b*	% variance	*b*	% variance	*b*	% variance	% variance
day 1	+.22	13.8	+.42	4.2	+.35	1.0	4.3
2	+.34*	6.3*	+.28*	4.2*	−.01	.0	4.2
3	+.18	2.7	+.39*	6.8*	−.05	.1	6.8*
4	+.07	.5	+.14	.8	+.23	2.4	3.0
5	+.28*	8.7*	−.20	1.1	−.01	.0	1.2
6	+.19	3.7	−.05	.1	−.12	.6	.6
7	+.42*	11.7*	−.10	.2	+.08	.2	.5
8	+.29*	5.3*	+.01	.0	+.01	.0	.0
night 9	+.20*	6.2*	−.04	.1	−.29	4.5	4.5
10–12	+.34*	11.2*	+.12*	4.8*	−.04	.6	6.3*

* $p \leqslant .05$

Table 4.6. Mean duration of the units in the sequence M – MR – R.

	2-h period no.	*n*	M min	MR min	R min
day	1	134	51.7	25.8	36.6
	2	114	39.5	23.9	38.2
	3	93	40.3	26.5	35.8
	4	132	42.0	22.5	40.7
	5	90	37.2	22.7	38.7
	6	95	37.6	26.2	35.1
	7	72	56.6	25.6	36.1
	8	142	56.3	22.4	37.4
night	9	95	31.4	18.6	42.4
	10–12	138	15.6	29.3	39.8

Table 4.7. Dependence of MR and R on preceding units in the sequence M – MR – R.

2-h period	regression of MR on		regression of R on				
	preceding M		preceding M		preceding MR		both variables
no.	*b*	% variance	*b*	% variance	*b*	% variance	% variance
day 1	−.24*	8.1*	+.14*	3.6*	−.36*	16.5*	17.2*
2	+.01	.0	−.05	1.0	−.22*	5.9*	6.8*
3	+.02	.1	−.11	2.7	−.38*	20.3*	22.7*
4	−.06	.7	+.06	.7	−.25*	6.9*	7.3*
5	−.09	3.1	+.05	.6	−.30*	5.9*	6.1
6	−.03	.2	−.02	.2	−.15*	4.0*	4.2
7	−.17*	6.2*	+.01	.1	−.02	.1	.1
8	−.06	2.6	+.04	.8	−.23*	3.2*	3.6
night 9	−.03	.9	+.02	.1	−.37*	4.7*	4.7
10–12	−.02	.0	+.06	.2	+.13	1.8	2.1

* $p \leqslant .05$

Sequences of R and RR

As Fig. 2.4. shows, the number of R within an MM interval varied strongly, particularly in some animals. However, the following discussion is restricted to sequences with only one, two, or three rumination bouts (called sequence A, B, and C, respectively), because those with a higher number of bouts were too rare for meaningful analysis.

Fig. 4.1. illustrates the mean durations of rumination bouts and RR intervals

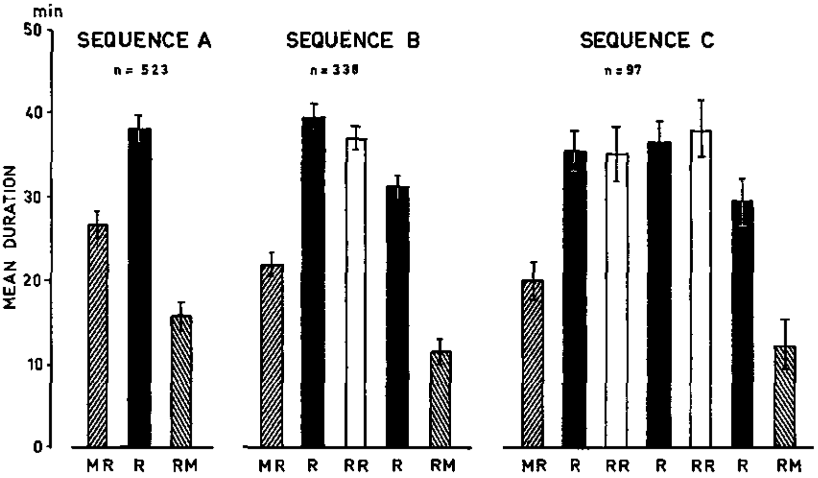

Fig. 4.1. Mean duration of rumination bouts and their adjacent MR, RR and RM intervals in sequences with one, two and three bouts per MM interval.

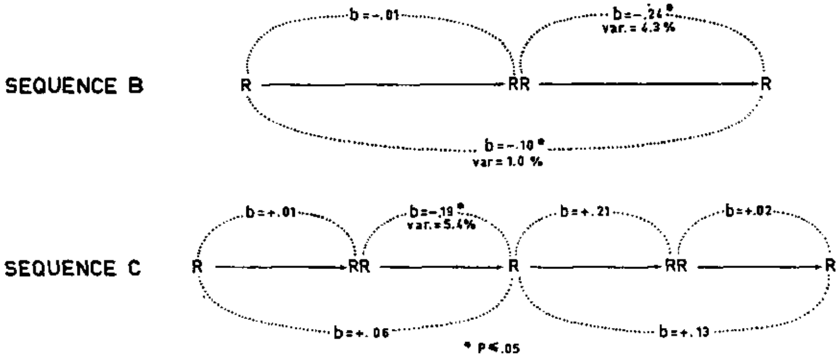

FIG. 4.2. Dependence of R on the preceding RR, and of RR on the preceding R, in sequences with two and three rumination bouts per MM interval.

in the three sequences (together with those of the terminal MR and RM intervals, which will prove of interest in the discussion below). As regards R and RR intervals, two points deserve mention: Firstly, the only R in sequence A was about as long as the first R in sequence B, and the first and second R in sequence C were only a little shorter. In contrast, the last R in sequences B and C was much shorter than the preceding one(s). Secondly, mean length of RR intervals was about equal in the latter two sequences. The correlations between successive R and RR intervals in the sequences B and C are shown in Fig. 4.2. For this purpose data of the various periods were lumped as the period-to-period fluctuations in R and RR lengths were of small amplitude. The second R in both sequences was significantly negatively correlated with the preceding RR interval, but in sequence C not the third R. In none of these cases R was significantly related with the following RR interval. Moreover, only in sequence B a weak, but significantly negative correlation was found between successive R's.

4.3. DISCUSSION

Before discussing the organization of individual sequences the following remarks should be made. Firstly, whatever unit was chosen as the dependent variable in the regression analysis, variation in its duration was usually only for a small part associated with duration of the preceding units. Clearly, deterministic models would not be appropriate (cf. Panksepp, 1973) and the temporal patterning of feeding and rumination must be treated as a stochastic process. Secondly, units which were further apart in a sequence generally correlated less well than adjacent units. For this reason it was not fruitful to deal with still longer sequences. Finally, the regression analyses consider only linear relationships. They do not lend themselves to comparison of the shapes of distributions. For the latter purpose I compared the survivorship curves of successive units in several cases that seemed relevant to me, but this never led to other conclusions than those based on the regression analyses.

Relations within the sequence M – MM – M

First of all, from the fact that duration of M and the following MM interval were hardly correlated (Table 4.2.), it can be concluded that diurnal rhythmicity remains by far the main factor from which we can predict MM interval length (Fig. 3.2.). In contradiction to this result, Fig. 2.6. indicates a negative relationship between meal size and following interval length in at least four animals. This difference is due to the fact that in Fig. 2.6. data of the various daylight periods were pooled. Namely, mean duration of M and that of the following MM interval in the various periods are negatively correlated ($r_s = -.50$; Table 4.1.). This correlation, due to diurnal rhythmicity, overshadows the correlations within the 2-hour periods when the data are lumped. This effect reveals the great importance of dividing the 24-hours into homogeneous periods for statistical analysis of sequences.

Duration of M is much better correlated with the preceding MM interval, but this relationship is subject to marked diurnal changes (Table 4.3.). During the main part of daylight meals are longer when the preceding intervals are also longer. This effect wanes, however, during the first part of the evening feeding peak, probably because at that time M size is at its maximum level anyway. The correlation even becomes negative in the later part of the evening peak. Successive meals also become negatively correlated then, so that in this period we see that the longer the preceding M and MM intervals are, the shorter is the following M. Now it should be realized that the second M begins later on the average, according as the two units preceding it are longer. Therefore, the fact is simply that the later the start of the following M, the smaller this meal will be. This pattern can be ascribed entirely to the diurnal rhythmicity in M duration (Table 4.1.; Fig. 3.2.). Hence, it seems probable that the changes in correlation between M and the MM interval in the course of the day, are due exclusively to the diurnal rhythm of the feeding motivation. Taking into account, moreover, that there is no correlation at all during the night, we may conclude that only when motivation is at a relatively constant and not too low level, marked positive correlations between M and the preceding MM interval may arise.

From this, it can be explained why in animal IV meal size and preceding interval length not positively correlate when all data for daylight were pooled (Fig. 2.6.). In this animal the evening feeding peak occurred very early. M and the preceding interval were positively correlated before that peak, but negatively during the remaining part of daylight. Lumping of the data of these periods caused these effects to cancel each other. This finding illustrates again the necessity of dealing with homogeneous periods in the analysis of time patterns.

The fact that total rumination time during the MM interval has no relation to duration of the subsequent M other than what might be predicted from the relation between MM duration and rumination time, indicates that the limited variation of rumination does not immediately affect the amount of feeding.

Neither was there evidence that the size of a meal influences the proportion of rumination during the next MM interval. In other words, while augmenting effects of feeding on rumination, and *vice versa*, are very likely (Freer et al., 1962; Pearce and Moir, 1964; Welch, 1969b; Ruckebusch, 1970), these effects hardly have a short-term influence on the course of rumination or feeding under ad lib. conditions.

To sum up, the main outcome of this discussion so far are the following two points. Firstly, the analysis shows that pooling data of the whole day and/or night, as is common use in the literature (e.g. le Magnen and Tallon, 1966; Duncan et al., 1970), may produce misleading results: lumping data of periods with different mean meal and MM durations give rise to correlations that differ in strength and even in sign from those extant within homogeneous periods (Fig. 2.6.). To some extent this difficulty may be met by correcting for differences in the means, or by using ratios between the variables (Panksepp, 1973), but such correction is effective only if the correlations within the homogeneous period to be lumped has the same sign. In the opposite case, no correction is feasible. Secondly, apart from the complications due to diurnal rhythmicity, cattle differ strongly from other vertebrates in the correlations between meal size and the length of the adjacent between-meal intervals. In guinea pigs (Hirsch, 1971) and pigeons (Zeigler et al., 1971) no clear correlation was found between these measures, whereas e.g. in rats (le Magnen and Tallon, 1966; Thomas and Mayer, 1968; Panksepp, 1973), domestic fowl (Duncan et al., 1970) and zebra finches (Slater, 1971) a positive correlation was found between meal size and post-meal interval length, but again hardly any correlation between meal size and length of the preceding interval. In our cattle the opposite result was obtained: meal size correlated positively with length of the preceding interval, but hardly with length of the gap to the next meal. This finding is not compatible with the view that in cattle the next meal begins because food ingested at the previous one has been used up (cf. Le Magnen, 1969). Rather, it suggests that the meal tends to stop once a fixed level of repletion is reached. It will be interesting to investigate at the physiological level what factors are responsible for this. One factor already proposed in this context, at least on roughage diets, is the degree of filling of the reticulorumen (Campling, 1970).

Relations within the sequence R – RM – M

The shorter R is, the shorter will be the interval to the next feeding (Table 4.5.). Taken together with the form of the RM interval survivorship curves (Fig. 2.5.), this fact hardly leaves room to doubt that ongoing rumination may be broken off under the influence of the state variables that promote feeding. This presumed inhibitory effect of the feeding state is in no way associated with the duration of the following M, for RM interval length was rather constant over the day and not correlated with M duration in any period.

Relations within the sequence M – MR – R

M duration hardly affects the length of the interval to the next R (Table 4.7.).

Only when meals are very large (morning and evening feeding peaks), rumination follows sooner according as the meal is larger. Consequently, MR interval length is rather constant over the day (Table 4.6.). Taken together with the fact that M and R length are hardly correlated, these results suggest that the ending of a meal is not affected by state variables promoting the occurrence of rumination. Rather, the animal satiates itself first and thereafter rumination is permitted.

On the other hand, there is a relation between MR and R length: if latency of rumination is short, it is probable that the ensuing rumination bout will be relatively long.

Relations within sequences of R and RR

Fig. 4.1. reveals several important aspects. Firstly, in the case of MM intervals with two or three rumination bouts, the final R is shorter than the others. This indicates that, as already suggested above, ongoing rumination may be inhibited under influence of the state variables promoting feeding. Further examination showed that the reduction of R length was independent of duration of subsequent M. This suggests that the inhibition is not dependent on the level of the state variables as manifest in M duration.

The fact that in MM intervals with only one R (sequence A in Fig. 4.1.), this rumination bout does not differ in length from the first R of sequence B, or the first two of sequence C, is compatible with this conclusion, for there are few MM intervals that do not considerably exceed the time needed for an undisturbed R together with its MR and RM intervals (Figs. 2.2. and 2.5.). Indeed, Fig. 4.1. shows that, as one might expect, MR and RM intervals actually tend to be longer in sequence A than in B or C.

Secondly, the first R after feeding has the same length as the following bout if this one is not disturbed by feeding (see sequence C; Fig. 4.1.). As is clarified in Fig. 4.3., this means that the meal has caused the phase of the rumination

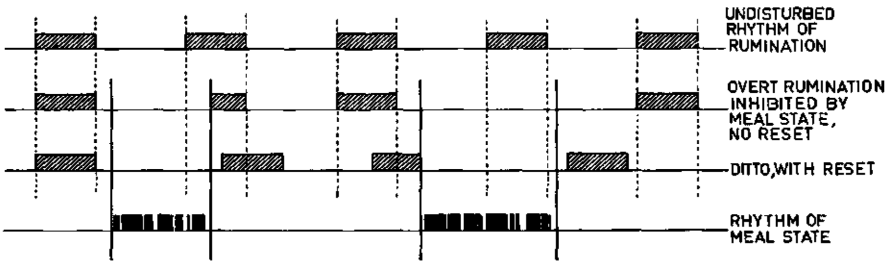

FIG. 4.3. Diagram to clarify the concept of phase reset of the rumination rhythm. Vertical lines indicate beginning and end of the meal state, vertical broken lines beginning and end of overt rumination in the case that the rumination rhythm is completely undisturbed. Black blocks denote F bouts, hatched blocks R bouts. If there is no reset of the rumination rhythm, 'fragments' of R bouts may be seen after a meal. Alternatively, if the phase of the rumination rhythm is reset after feeding, the first R following a meal has the same length as all other R bouts that are not disrupted by the meal state.

rhythm to be reset (unless no reset takes place, but rumination is postponed till that moment after the end of the meal at which the first complete R would have started if this meal had not taken place; however, the MR length data exclude this possibility). Thirdly, rumination has a rather stable periodicity, for in the various sequences in Fig. 4.1. mean durations of the successive undisturbed rumination bouts and RR intervals are fairly constant. This suggests that the motivation for rumination does not wane with the performance of this behaviour in the course of the intermeal interval. If so, duration of an R will have little or no effect on the length of the subsequent RR interval and R. This is confirmed by Fig. 4.2.

The second R in sequences with two and three bouts was negatively related with the preceding RR interval (Fig. 4.2.). Taken together with the analogous relationship found above between R and the foregoing MR interval, this suggests that the same conditions which promote an earlier start of rumination also promote its longer continuation. Hence, it is likely that MR and RR interval length will change in the same direction if the amount of rumination is manipulated. This will be examined in Chapter 6.

4.4. PRELIMINARY MODEL

As a basis for designing further experiments I shall now put forward a preliminary model of feeding and rumination incorporating the following assumptions, which appear plausible in view of the facts presented so far:

(1) Over periods of several hours, feeding has an independent rhythm in the sense that naturally occurring variations in rumination during that period does not affect the pattern of feeding.

(2) The feeding rhythm is characterized by an alternation of 'meal' and 'interval' states.

(3) Rumination similarly has a basic rhythmicity, not affected by short term variations in foregoing food intake; but this rhythm is subject to two limitations that will now be specified.

(4) Overt manifestation of rumination is inhibited whenever the feeding rhythm is in the meal state.

(5) When feeding has interfered in this way i.e. after a meal, the phase of the rumination rhythm is reset.

(6) At least for several hours, the rumination rhythm maintains a rather constant periodicity within the limits just specified, because the need for rumination does not readily wane with its performance.

It should be noted that these assumptions rest on observations in the ad lib. condition. One aim of the remaining part of this study will be assess to what extent the same assumptions hold under a wider range of conditions. In Chapters 5 and 6 this will be done for 5 out of the 6 assumptions (the exception being number 2).

To demonstrate that these 6 assumptions together constitute a model of feeding and rumination behaviour, and not a mere list of unconnected statements, I shall now show that by combining several of these assumptions we can make a prediction as to the distribution of RM interval duration, whereas this prediction cannot be derived from any single one of these assumptions.

In order to simplify the discussion let us assume for the time being (in contradiction to assumption 5) that there is no fixed phase relation between the feeding and ruminating rhythms. In that case, the meal state is equally likely to set in at any point of an rumination bout or an RR interval, so that a fraction

$$\frac{\text{mean R duration}}{\text{mean R + RR duration}}$$

of all RM intervals will start while an R is in progress (assumption 4). In these cases the duration of the RM will be determined by the survivorship of the non-feeding interruptions within a meal (assumption 2). On the other hand, when the meal state sets in while an RR interval is in progress, the resulting RM will contain an extra (non-meal state) component ranging in duration from zero to the maximum duration of an RR interval (assumption 6). These considerations result in a predicted shape of the survivorship curve of RM intervals, exemplified by Fig. 4.4. (which is based on mean duration of 40 min for R and 60 min for RR, and a mean lag of 3 min between onset of the meal state and the start of feeding).

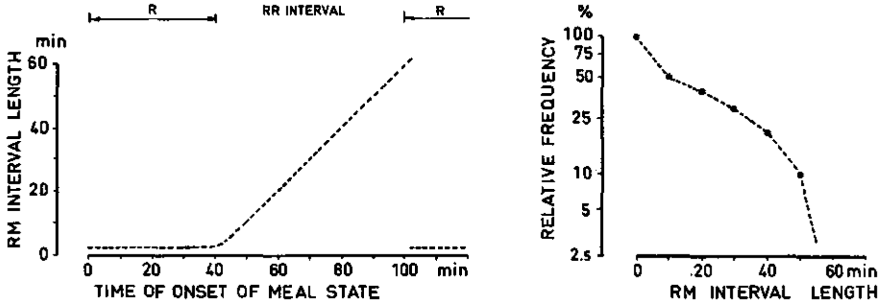

FIG. 4.4. Left: Hypothetical diagram showing the length of the RM interval as a function of time lapse between the start of rumination and the onset of the meal state, assuming that (1) R and RR length are 40 and 60 min, respectively, (2) rumination is inhibited as soon as the meal state sets in, and (3) 3 min pass between the onset of the meal state and the start of overt feeding. Right: Survivorship curve for RM length under these conditions, under the further assumption that the meal state is equally likely to begin at any point of an R or RR. To make the survivorship curve comparable with later curves, a class width of 10 min has been used for RM duration.

If we want to check this prediction, caution is required in view of the additional assumption of the absence of fixed phase relations between feeding and rumination. The postulated reset (assumption 5) probably invalidates this assumption for the ad lib. condition. Therefore, the prediction will be tested in a later chapter under conditions of restricted feeding (Chapter 6), but it may already be stated here that the outcome of this test is in agreement with the prediction of our model in certain cases. In the other cases the observed deviation from the prediction will lead to an interesting extension of the model, not to a fundamental revision.

In view of the reset phenomenon, it is not surprising that the survivorship curves for RM under ad lib. conditions (Fig. 2.5.) deviate from the prediction in Fig. 4.4. However, even these curves fit in with the model in one respect, which is independent of the reset: the course of the first part of the RM survivorship curves in Fig. 2.5. closely resembles that of the FF intervals within a meal (Fig. 2.3.) as indeed one would expect if the duration of this class of brief RM intervals is governed by the factors determining the length of the interruptions of meals.

Similarly, the above model predicts a positive correlation between duration of the final R before a meal and the subsequent RM, even under ad lib. conditions. We have already seen that this prediction comes true. Moreover, when reset plays no role, the model can predict mean duration of the final R.

5. THE EFFECT OF SHORT-TERM PREVENTION OF RUMINATION

5.1. INTRODUCTION

In this chapter I shall examine the following two elements of the preliminary model discussed above (p. 31):

(1) The animal will give priority to feeding whenever the causal factors both for feeding and rumination are sufficient to give rise to their corresponding behaviour.

(2) The state variables for feeding are relatively independent of rumination, in so far that the amount of rumination does not clearly influence the size of the subsequent meal.

These assumptions will be studied by preventing the animals from ruminating for some time and analyzing the effect of this treatment on subsequent feeding.

5.2. METHOD

Two adult cows were used, both of the MRY-breed (nos. X and XI). They were kept under the same conditions as in the basic experiment (p. 2) except that the food, hay wafers, was produced from another crop of hay.

In each animal rumination was prevented once per two or three days during a 3-hour period beginning two hours after light on (11.00–14.00 h). This was achieved by restricting the jaw movements with a closely fitting leather muzzle. The muzzle allowed normal regurgitation of gases from the reticulorumen, but of course no feeding. For that reason feeding was also prevented on the control days by closing the mangers during the three hours mentioned. In animal X rumination was prevented on 9 out of 25 days and animal XI on 11 out of 25 days.

5.3. RESULTS

The effect of three hours prevention of rumination on the feeding and rumination patterns is shown in Fig. 5.1. (p. 36). Differences between prevention and control days were tested statistically only over two periods: from the end of deprivation to the end of the light period (14.00–01.00 h) and over the whole 24 hours (Table 5.1.). This was permissible because there were no important differences between the two conditions imposed for the successive one-hour periods.

The feeding pattern was not changed by the prevention of rumination, neither in the distribution over the day (Fig. 5.1a.), nor in the total time spent on meals or mean M duration (Table 5.1.). Under both experimental conditions

TABLE 5.1. Total meal and rumination time, and mean duration of meals and rumination bouts on prevention (p) and control (c) days.

period			total meal time (min)			duration of M (min)		
			$\bar{x}_c$	$\bar{x}_p$	t	$\bar{x}_c$	$\bar{x}_p$	t
14.00–01.00 h								
	animal	X	222.3	210.4	+.82	58.6	53.5	+.81
		XI	266.2	258.3	+.60	53.6	56.0	−.69
09.00–09.00 h								
	animal	X	318.1	313.6	+.45	57.9	52.6	+.94
		XI	355.2	349.4	+.40	50.8	52.5	−.41

period			total rumination time (min)			duration of R (min)		
			$\bar{x}_c$	$\bar{x}_p$	t	$\bar{x}_c$	$\bar{x}_p$	t
14.00–01.00 h								
	animal	X	190.5	212.3	−3.73***	34.1	39.9	−2.62***
		XI	201.5	225.9	−3.04***	28.7	30.3	−1.12
09.00–09.00 h								
	animal	X	474.4	417.4	+6.21***	33.4	37.6	−2.90***
		XI	522.0	465.9	+8.74***	30.3	31.0	− .74

*** $p \leqslant 0.005$, Student's t-test

feeding was strongly increased in the period immediately following the prevention period which was evidently caused by the three hours of food deprivation (cf. Fig. 3.1., basic experiment).

The prevention of rumination resulted in significantly more rumination in the period 14.00–01.00 h, but during the following night rumination had reverted to the normal level. The increase was first seen after a period of feeding (Fig. 5.1b.). Over the 24 hours the animals compensated only partly for the prevented rumination: in all they ruminated about one hour less than on control days (Table 5.1.).

For the interpretation of this experiment it was important to examine in more detail what behaviour the animals performed immediately after feeding was allowed by opening the mangers. On days when rumination was prevented, the muzzles were removed just before. In most cases the animals started feeding immediately or rather soon.

animal	mean latency of feeding after opening the manger (min)			mean total ruimination time during that latency (min)			mean duration of the following M (min)		
	control days	prevention days	U^a	control days	prevention days	U^a	control days	prevention days	t^b
X	12.0	3.8	39	6.8	1.3	57	77.3	73.1	+.22
XI	.9	3.5	38*	.8	2.9	41	78.9	81.5	−.29

[a] Mann-Whitney U test (Siegel, 1956); [b] Student's t-test; * $p < .05$

In animal X neither the latency of feeding, nor the amount of rumination during that interval differed significantly between prevention and control days. In contrast, in animal XI the first measure increased a little on prevention days, but total rumination time during this interval again was not significantly changed. In neither animal the duration of the subsequent M was changed by the prevention of rumination.

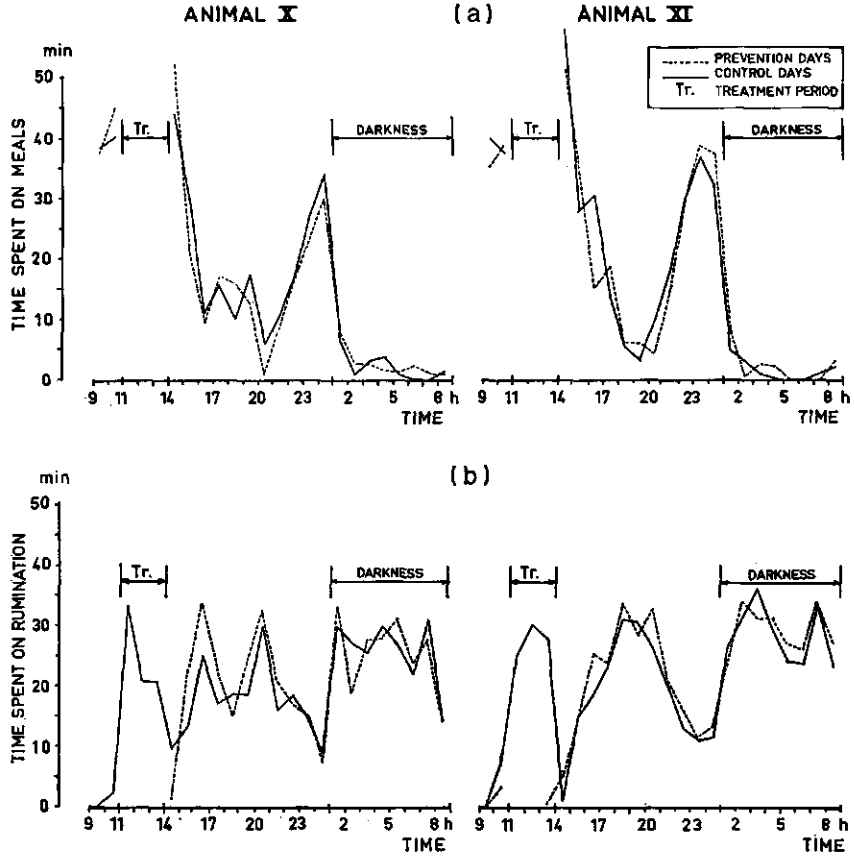

FIG. 5.1. (a) Mean time spent on meals and (b) mean time spent on rumination bouts in the various one-hour periods.

5.4. DISCUSSION

In this experiment rumination was prevented for some hours in order to raise the motivation for this behaviour. Unfortunately, it was impossible to prevent rumination without restricting feeding at the same time. The treatment was kept very short, therefore, to interfere as little as possible with feeding.

After the treatment, rumination was increased so that we may accept that the motivation for this behaviour was heightened indeed. The increase was seen, however, only after a period of feeding (Fig. 5.1.). Nevertheless, it is likely that the higher urge to ruminate existed already from the end of deprivation. Further proof for this was obtained from an additional experiment with one cow. That experiment was similar to the present one but feeding was prevented two hours longer. The prevention of rumination resulted in an increase of total rumination time during this two-hour period of 18.4 min

($p < .05$; Student's t-test). This increase began as soon as rumination was allowed again.

In spite of the higher motivation for rumination, the feeding pattern was not markedly affected, neither as regards latency of feeding after deprivation, nor as regards duration of the subsequent meal or the further course of feeding. This supports the earlier hypothesis that the cow gives priority to feeding whenever the causal factors for the two behaviours are in conflict.

In this experiment it was also possible to study some aspects of the facilitatory influences of rumination on feeding. The extra amount of rumination during food deprivation on control days did not enlarge the size of the subsequent meal, nor did it affect the further course of feeding in any way (p. 35, Fig. 5.1a.). This confirms that it is not critical for individual meal size whether the animal ruminates more or less beforehand, nor does a difference of about one hour in total daily rumination time have a noticeable effect on total food intake on the same (or following) day.

6. THE EFFECT OF RESTRICTED FEEDING

6.1. INTRODUCTION

Accepting that feeding has priority over rumination, and that the causal factors for feeding are relatively independent of rumination, I shall now examine some other elements of the preliminary model put forward on p. 31. Specifically the following questions will be considered:

1. How does the rumination rhythm respond to changes in the amount of food eaten?
2. Is it true that, for a given level of food intake, the rumination rhythm is fairly constant over prolonged non-feeding periods, indicating that the need to ruminate does not readily wane with the performance of this behaviour?
3. Can rumination be inhibited by state variables promoting feeding responses, even in the absence of food itself?
4. What is the influence of meal size on the phase reset of the rumination rhythm?

For studying these questions two experiments have been designed, both involving restriction of feeding time and the second also the amount of food given.

6.2. EXPERIMENT I

6.2.1. *Method*

In two animals, the nos. IV and V of the basic experiment, feeding was restricted (by closing the manger) to two periods per day: from 06.30 to 09.00 h and from 17.00 to 19.30 h. Total length of these periods was roughly the same as total daily meal time under ad lib. conditions. In each period an equal amount of fresh food was supplied. The total amount was so adjusted that the animals left some 10 percent of the food supplied uneaten every day. The further conditions were the same as in the basic experiment, except that a 13–11 light-dark cycle was maintained (lights on at 06.30 h, the time of beginning the morning feeding period).

Before the experiment started, the animals were habituated to the restricted feeding schedule. Nevertheless, this schedule imposed a considerable degree of food deprivation on these cows, compared with the ad lib. conditions (Table

TABLE 6.1. Mean food intake per feeding period and per day on the restricted feeding schedule.

animal	number of days	mean intake in the morning (kg)	mean intake in the evening (kg)	mean daily intake (kg)
IV	20	4.9	6.8	11.7
V	19	5.9	6.9	12.8

6.1.; compare Table 3.1., but note that the basic experiment was carried out about a year earlier than experiment I). In the evening they consumed a larger amount of food, on most days even all food supplied in this period. In animal IV a total of 20 daily recordings was obtained and in animal V a total of 19.

6.2.2. *Results*

Within-day changes in total rumination time, and R and RR duration

Fig. 6.1a. shows when the animals ate and how much time they spent on rumination in the various one-hour periods. Feeding was always started as soon as the mangers were opened and it continued during the greater part of the feeding periods. Around the end of these periods or somewhat later, rumination started. Amount of rumination per hour was rather constant in the course of the non-feeding periods, almost until the end of these periods. There were no differences between day and night.

Fig. 6.1b. shows the within-day fluctuations in the length of R and RR. The fluctuations in both measures deviate from randomness within each non-feeding period in each animal ($p \leqslant .05$; *F*-test, Weber, 1967). The length of R fluctuated in a peculiar manner. In the course of the non-feeding periods it increased

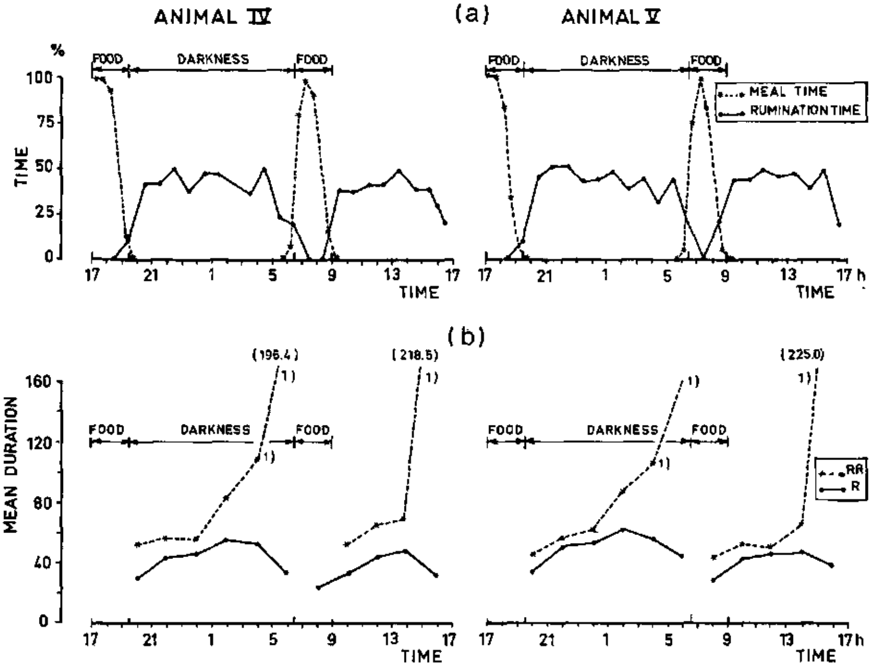

FIG. 6.1. (a) Mean time spent on meals and rumination bouts per two hours. (b) Mean duration of rumination bouts and RR intervals started in the various two-hour periods.

1) Both RR and (long!) RmR values are included in these averages.

at first but decreased during the last 2 (to 4) hours when the mean time spent on rumination was also going down. The initial increase in R length did not cause a trend in total rumination time, because RR length increased at the same time. Both during day and night, this interval length increased through the whole non-feeding period, though very gradually in the first six hours after feeding. The final parts of the interval curves in Fig. 6.1b. must be left out of consideration, because the RR values are mixed there with RmR values.

Distribution of R length

For reasons that will appear in the Discussion (p. 51) I will compare the survivorship curve for R length under the restricted feeding with that under ad lib. conditions (basic experiment). As Fig. 6.2. shows there was in both animals indeed some excess of short bouts in the latter case. However, the differences between the survivorship curves were not significant (one-tailed two-sample Kolmogorov-Smirnov test; Siegel, 1956), not even when the two curves in each animal were shifted along the abscissa to correct for differences in mean R length between the samples.

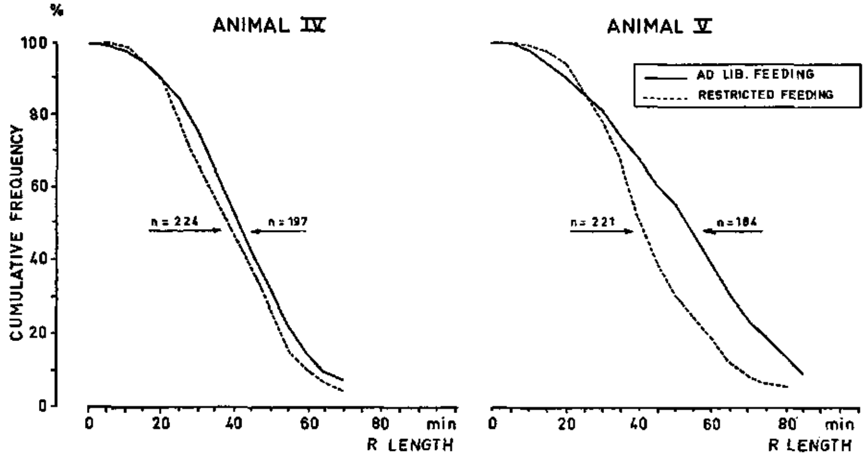

Fig. 6.2. Survivorship curves for R length under restricted feeding and ad lib. conditions (note ordinate scale non-logarithmic).

Distribution of RM and MR length

Fig. 6.3. presents the survivorship curves for the RM and MR intervals. The data of the animals were pooled as the distributions were very similar in both individuals. The shape of the RM curves is very different in the morning and evening. In the evening there was a marked shortage but in the morning an excess of short intervals, compared with the exponential model. On the other hand, in the range of intervals between 10 and 50 min the curves of both periods have about the same slope. Beyond this range they cross, indicating that there were relatively more large RM intervals in the morning than in the evening.

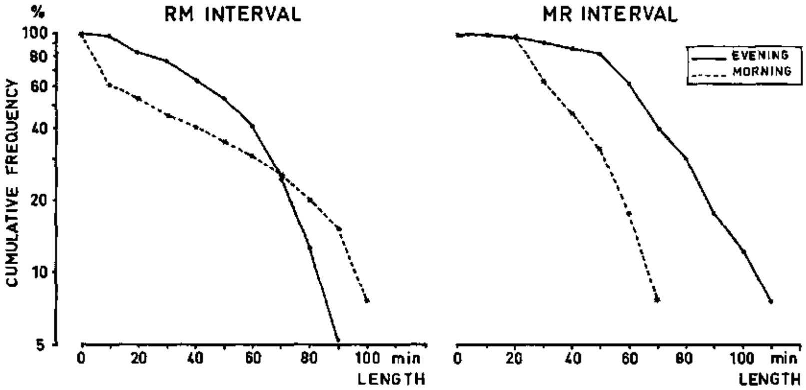

FIG. 6.3. Survivorship curves for the lengths of RM and MR intervals adjoining the morning and evening feeding periods.

Given this fact, one might expect in view of what has been said on p. 32 that RR intervals will also be longer before the morning than before the evening feeding. Fig. 6.1. shows that such is indeed the case.

The survivorship curves for MR intervals suggest that these intervals are composed of two very distinct phases: a period immediately following feeding in which rumination is very improbable, and a subsequent period in which the probability of resuming rumination is high, fairly constant, and independent of the time of day.

6.3. EXPERIMENT II

6.3.1. *Method*

On the basis of the results of experiment I it was decided to make a further experiment, also with restriction of feeding to two periods per day, but different from the foregoing on the following points: (1) besides hay wafers another food was used, long hay, which requires more rumination; (2) the amount of food given was restricted to different levels; (3) more animals were used, four on each diet, but the various regimes were presented to each animal for much shorter periods; (4) on some days hay wafers were fed ad lib.

The experiment was made in a room with four cowstands for individual feeding. The windows of the room were not shuttered, but with the aid of additional artificial lighting the period of darkness was maintained at 9 hours (from 20.00 to 05.00 h). For recording the feeding time a wooden flap was constructed at the entrance of each manger. During feeding the animal pressed the flap against a microswitch which caused an on-off signal to a 20-channel Esterline Angus event recorder (chart speed 75 cm/h). The records of rumination were also made on this recorder, using the same technique as in the basic experiment.

Hay wafer experiment. The group of four cows used in this experiment consisted of two animals from previous experiments (nos. VIII and IX) and two others, one of the FH-breed (no. XII) and one of the MRY-breed (no. XIII). The hay wafers were of nearly the same chemical composition and feeding value as the food used in the basic experiment (p. 2). The food was given either ad lib. (AL) or during only two periods of two hours and a half per day, from 06.30 to 09.00 h and from 17.00 to 19.30 h. Equal amounts of food were given in both periods, but the total amount was varied. At the highest level (HL) the animals could eat as much as they wanted during the restricted feeding periods. At the medium level (ML) the animals were given 80 per cent of their HL daily intake and at the low level (LL) 60 per cent. The amount actually eaten per day can be read from Fig. 6.4. The feeding regimes were presented to each animal in the following succesion: AL – HL – ML – HL – LL – HL – AL. Normally each regime was continued for one week. The recordings were started then on the third day so that at most five days of recordings were taken per regime and per animal. However, with the changeover from ad lib. to restricted feeding and *vice versa*, some extra days were taken without recordings. Moreover, due to technical difficulties I had to depart from the scheme sometimes. In all the numbers of recording days were:

animal	regime			
	AL	HL	ML	LL
VIII	10	13	5	5
IX	9	12	5	5
XII	12	13	5	5
XIII	10	12	5	5

Long hay experiment. A group of four cows was used, consisting of three animals already used before (nos. VIII, IX, X) and another of the MRY-breed (no. XIV). Except that long hay[2] was given, this experiment differed from the preceding one on the following points: (1) in view of the results obtained with hay wafers only restricted regimes were used, in the order: HL – LL – HL – ML – HL; (2) the HL regimes were continued for 10 days, the ML and LL regimes for 14 days; (3) the recordings were started on the fourth day; (4) the feeding periods were extended to three hours, because the eating rate was low. The following numbers of recording days were obtained:

animal	regime		
	HL	ML	LL
VIII	21	10	10
IX	18	10	9
X	21	9	10
XIV	21	10	10

---

[2] The chemical composition and feeding value of this food were as follows: dry matter 82.1%, sand 5.1%; in dry matter: 15.9% crude protein, 34.1% crude fiber, 8.4% ash, 8.2% digestible crude protein and 360 gr starch equivalents/kg.

Both in the hay wafer and long hay experiment the animals were habituated to the feeding schedule before the recordings started. This I concluded from the fact that daily food intake and total rumination time manifested no trend during the experimental periods.

In the statistical analysis the data of individual animals were kept separate in the first instance. However, all data obtained with the same regime were pooled because there were no significant differences within regimes between successive periods on the same diet.

6.3.2. *Results*

Daily amount of rumination

Fig. 6.4. shows the relationship between daily food intake and daily rumination time for the hay wafer and long hay diets. The amount of rumination was strongly positively dependent on food intake on both diets. The relationship was clearly linear in both cases. The animals ruminated much more per kilogram of long hay than of hay wafers, which was not surprising as the latter food consisted of much smaller particles.

Fig. 6.5. shows how daily amount of rumination depends on duration of R and R/R intervals. On both diets duration of R was strongly positively correlated with the amount of rumination, and on the hay wafer diet R/R length negatively. On long hay, however, this interval length remained more or less

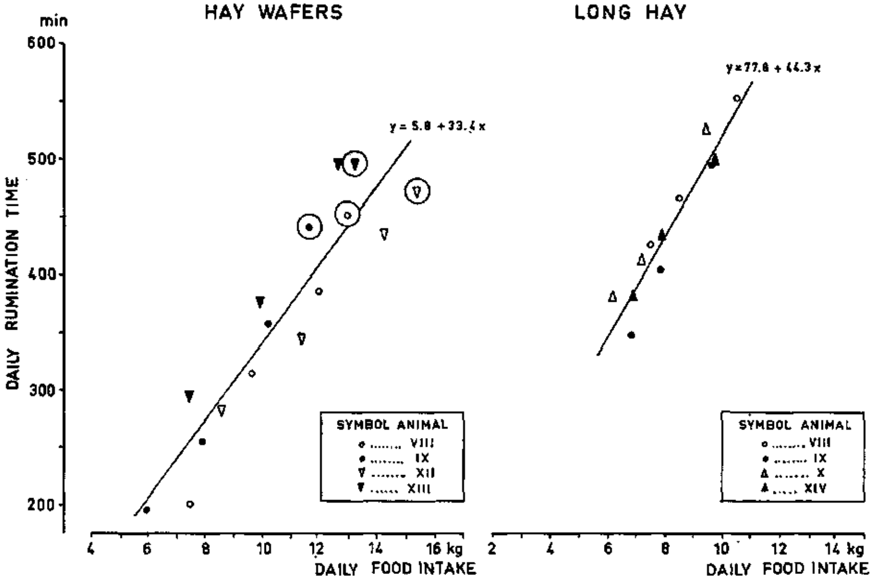

FIG. 6.4. Relationship between mean daily rumination time and mean daily food intake, calculated per regime and per animal. The encircled symbols concern ad lib. feeding.

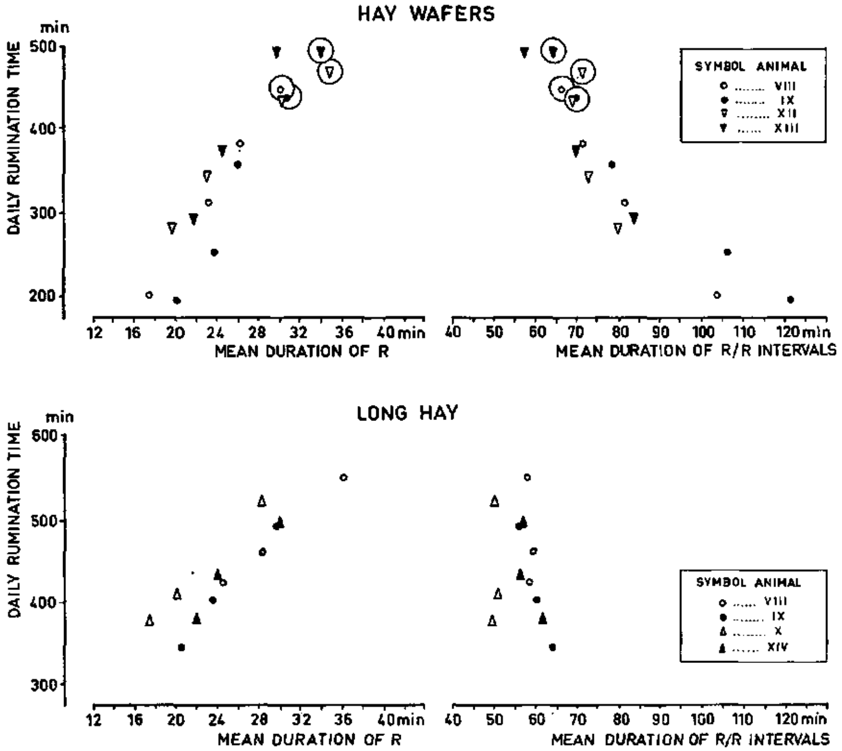

FIG. 6.5. Relationship between mean daily rumination time and mean duration of rumination bouts and R/R intervals, calculated per regime and per animal. The encircled symbols concern ad lib. feeding.

the same for the three regimes. The latter difference between the diets can possibly be ascribed to the mean level of the variables, i.e. the data for the two diets may form two parts of one and the same curvelinear relationship. The variation in R/R length on the hay wafer regimes was largely due to changes in length of the RR and not the RmR intervals (Fig. 6.6.).

In the wafer experiment, the ad lib. data fit in rather well with the trends observed in the data for restricted feeding (Figs. 6.4. and 6.5.). This is especially striking if one looks at the data of the individual animals. Apparently, the daily amount of rumination is primarily dependent on the amount of food consumed per day and not on the temporal distribution of feeding within the day. Because of this finding I thought it unnecessary to include an ad lib. regime in the long hay experiment.

Within-day changes in total rumination time, and R and RR durations

Mean time spent on rumination in every two-hour period as well as mean

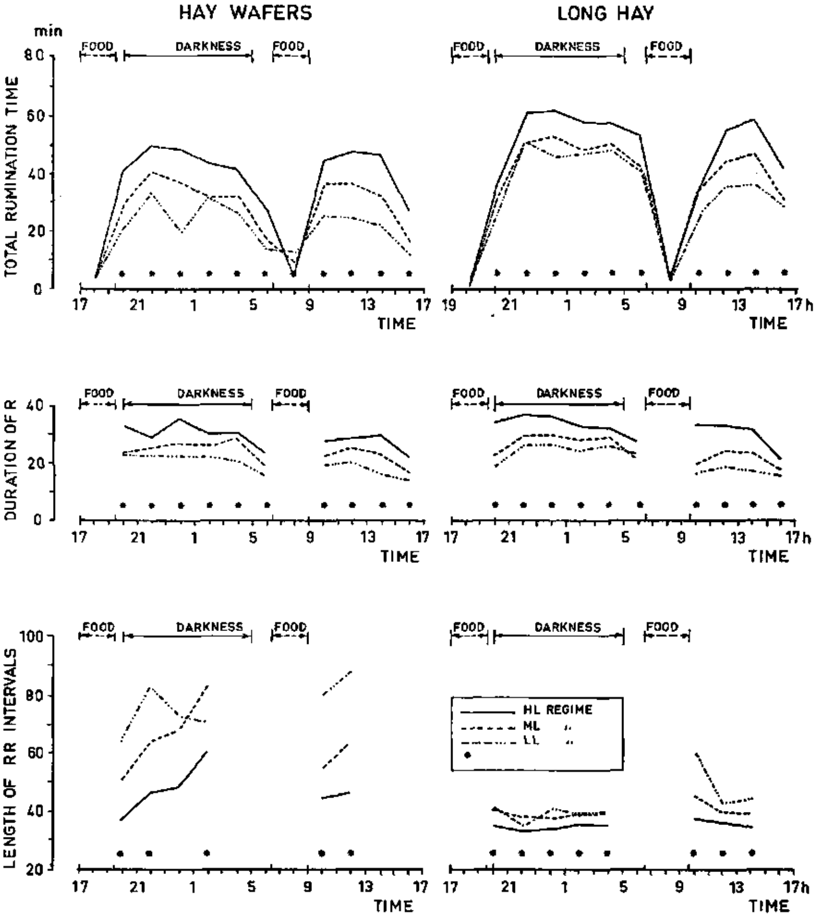

FIG. 6.6. Differences between HL, ML and LL regimes in mean time spent on rumination per two-hour period and in mean length of rumination bouts and RR intervals started during these periods. The * symbol indicates that at least the two extreme values in that two-hour period differ significantly ($p \leqslant .05$; Student's *t*-test).

length of R and RR intervals started during these periods is shown for each restricted feeding regime in Fig. 6.6. The data of the animals were pooled because the results in the individual cows corresponded reasonably well. Further, because only seldom an R or RR interval started within the feeding periods, those bouts and intervals were omitted from the graphs. Finally, the interval curves were restricted to the first part of the non-feeding periods in which no RmR intervals started yet.

Fig. 6.6. shows that the feeding regimes affected all these variables significantly in nearly all two-hour periods. Because in most two-hour periods total rumination time was highest for the HL regimes and lowest for the LL regimes,

the daily patterns of the fluctuations of the variables were about the same for all regimes. For long hay mean RR length did not increase in the course of the non-feeding periods, in contrast with that for the hay wafer regimes.

Distribution of R length

Analogous to experiment I (p. 40) the survivorship curves for R length on the AL and HL regimes of hay wafers were compared. In neither animal the curves for the two regimes crossed (compare Fig. 6.2.). Also transforming the scale of the survivorship curves to account for the differences in mean R length between the regimes did not result in any meaningful difference between the shapes of the curves.

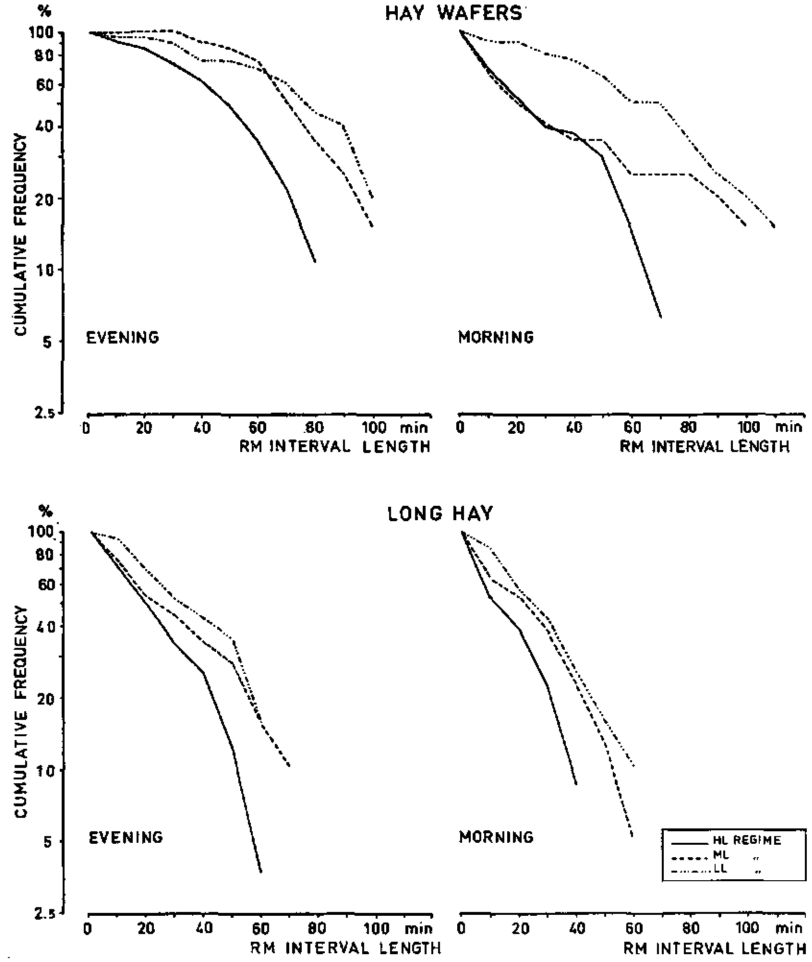

FIG. 6.7. Survivorship curves for RM lenght in the morning and evening on HL, ML and LL regimes.

Distribution of RM and MR length

For the restricted regimes of both diets the survivorship curves for RM and MR intervals are shown in the Figs. 6.7. and 6.8., respectively. Data of the various animals were pooled as the individual results corresponded in the main. Some irregularities in the curves due to this pooling will be disregarded in the present discussion (cf. Fig. 6.3.).

Fig. 6.7. shows firstly that the RM intervals were longest on the LL regimes and shortest on the HL regimes. Secondly, these intervals were much longer on the average on the hay wafer than on the long hay diet. Thirdly, compared with the exponential model, a straight line, there was in the evening a marked shortage of short RM intervals on the hay wafer regimes, but not on long hay. On the other hand, in the morning there was an excess of short intervals on the HL and ML regimes of long hay, but not markedly on the corresponding hay wafer regimes. Fourthly, the LL regimes of both diets resulted in some shortage of short RM intervals, in the morning as well as the evening.

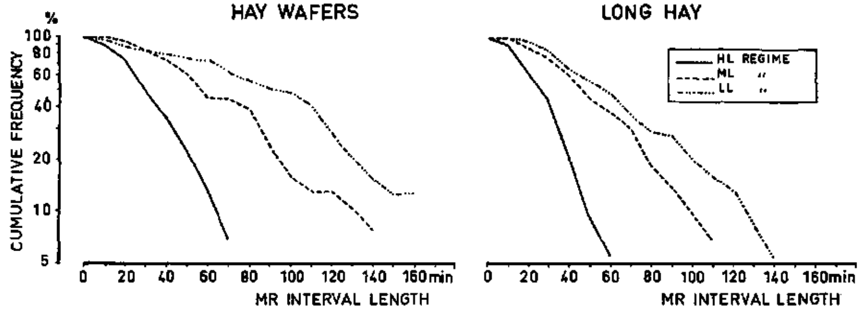

FIG. 6.8. Survivorship curves for MR length on HL, ML and LL regimes.

The survivorship curves for the MR intervals (Fig. 6.8.) were made for the pooled morning and evening data of all animals. These two sets of data agreed rather well although the intervals were longer on the average in the evening. Mainly due to pooling, the survivorship curves were not so markedly composed of two parts, an initial flat part and a further steep part, as those presented in Fig. 6.3. for experiment I. Nevertheless, the curves in Fig. 6.8. suggest that both the lag for rumination after feeding is shorter, and the probability of rumination beginning in the subsequent time-steps is greater, according as the intake in the preceding feeding period is higher.

6.4. DISCUSSION

Let us now consider what answers can be given to the questions raised in the introduction, and to what adjustments of the preliminary model these answers lead.

Dependence of rumination on amount of food eaten

Experiment II demonstrates that rumination increases when more food is eaten, and when the food particles are coarser (Fig. 6.4.). Similar relations had been established before (e.g. Freer et al., 1962; Pearce, 1965a; Skouri, 1967; Welch and Smith, 1969a and b; Ruckebusch, 1970), but my data reveal some interesting further points.

(1) In the range of food intake studied the relation between daily rumination time and daily food intake was clearly linear (Fig. 6.4.). Although it seems obvious to conclude from this that a fixed amount of rumination is needed per kg of diet ingested (as also suggested by Freer *et* al., 1962), in fact this conclusion is correct only for the hay wafer diet. Unexpectedly, in the case of long hay more rumination per kg is performed when total intake is less, as can be seen from the large intercept on the Y-axis indicated by the regression equation. A similar relation is reported by Welch and Smith (1969b) for sheep fed long hay. These workers also demonstrated that the decelerated increase in total rumination time with increasing food intake was independent of the time available for rumination.

(2) Although Fig. 6.4. indicates that mean daily amount of rumination can be explained almost wholly from mean daily food intake, the day-to-day variation in total rumination time under ad lib. conditions correlated far from completely with daily intake (Table 3.2.). This might be due to the fact that food intake on one day influences rumination on one or more subsequent days, but also on the restricted regimes in experiment II daily rumination time varied considerable while food intake was almost constant. Obviously, variation in the daily amount of rumination must stem from other factors than food intake alone.

(3) The hay wafer experiment reveals that the distribution of food intake over a day is not critical for the relation between intake and daily amount of rumination.

(4) In the effect of food intake on the rumination rhythm, there was a marked difference between the two diets (Figs. 6.5. and 6.6.). On hay wafers RR interval length decreased when more food was eaten but on long hay RR was about equally short irrespective of the level of intake. This suggests that some minimum RR interval length is already reached at a very low level of long hay intake. Indeed, at low levels of this diet the cow probably ruminates more than is strictly necessary for digestion because, as Welch and Smith (1969b) have shown, the relative lagging of the amount of rumination at higher intake levels is not due to lack of available time.

Changes in rumination rhythm in the course of the non-feeding periods

The preliminary model, based on ad lib. observations, assumes that neither total rumination time, nor R or RR length shows a trend in the course of the non-feeding periods. Is this also true for restricted regimes?

Total rumination time. I shall not discuss the changes in rumination time per two hours just after and just before the feeding periods. Fig. 6.1. and 6.6. show a tendency in some cases (e.g. during the night on the hay wafer regimes HL and ML) for rumination to decrease in the course of the 8–11 hours long non-feeding periods, also in those parts of these periods where no influence of immediately foregoing or imminent feeding behaviour comes in. However, taking the material as a whole it is a reasonable first approximation to state that over most of the non-feeding periods rumination time per two hours is constant, but positively dependent on the level of food intake. This finding indicates that the need for rumination only slightly wanes with the performance of this behaviour, even when periods between meals are made much longer than they are under ad lib. conditions. This conclusion fits with the hypothesis adopted by Stevens and Sellers (1968) and by Ruckebusch (1970) that, given constant quality of the food, the desire to ruminate is directly related to the volume of the contents of the reticulorumen. This volume does not change rapidly. From my data it cannot be decided whether the rumination level is determined entirely by the level of food intake in the final foregoing feeding period, or whether previous feeding periods contribute as well. However, Welch and Smith (1968 and 1969a) have shown that in sheep, deprived of food, some rumination still occurs on the second day of deprivation. Moreover, when after 48 hours of fasting a single meal of roughage is given, rumination is seen again for 24–48 hours after that meal. It seems likely, therefore, that the need for rumination depends on the integrated food intake over a period of at least one to two days.

Duration of R and RR intervals. The trends in duration of R and RR intervals in experiment I (Fig. 6.1b.) and II (Fig. 6.6.) lead to the following conclusions:

(1) The parameters of the rumination rhythm, i.e. duration of R and RR, responds differentially to the changes in state variables for rumination that occurs during the non-feeding period.

(2) The trend in R length is largely independent of the diet given. R length sometimes increases a little in the first period after feeding but after that it hardly changes with time for many hours. The subsequent decrease may be due partly to waning of the promoting effect of foregoing intake but for another part to interference from feeding. The available data do not permit a choice between these alternatives.

(3) In contrast, the trend in RR length depends strongly on the type of food. The coarser food, long hay, seems to stimulate rumination so strongly that RR intervals have nearly the same length on regimes with high and low intake, and for a long time after the food ingestion.

Inhibition of rumination at the end of the non-feeding periods. According to the preliminary model, rumination is inhibited whenever the animal is in the meal state. I shall now attempt to give a more detailed specification of the conditions that may promote the inhibition of rumination, utilizing data on the length of RM intervals and rumination bouts.

RM intervals. On the restricted regimes, both in experiment I and II, feeding always started as soon it was allowed by opening the manger. It is very unlikely that there never was any need for rumination at that time, for rumination is seen even on the second day of prolonged food deprivation (unpubl. observations; Welch and Smith, 1968). In other words, feeding must have inhibited rumination, at least in a number of cases.

First I shall consider whether the appearance of food may be a necessary condition for the inhibition. If so, rumination will be inhibited only from the time of opening the mangers and not before. The rumination rhythm may be in any phase at the time when feeding begins (because the non-feeding periods are long, a phase link between this rhythm and the time of opening the manger may be ruled out). Under these conditons the distribution of RM length will be similar to the predicted survivorship curve for RM intervals presented in Fig. 4.4. There are sufficient data to check whether this is so in experiment I, and in experiment II for the long hay diet. When the appropriate values for R and RR length (Figs. 6.1. and 6.6.) are substituted, the data agree very well with the model in the morning in experiment I (Fig. 6.3.), and in the morning on the HL and ML regimes of long hay in experiment II (Fig. 6.7.). Therefore, the data are compatible with the view that at least in certain situations the presence of food is required for the inhibition of rumination. More precisely, if inhibition in the absence of food is possible at all in these situations, this happens so rarely as not to be quantitatively noticeable in the data here presented. I conclude that the presentation of food has an overruling influence among the factors promoting inhibition of rumination.

Another condition that may promote the inhibition of rumination appears from the differences in the RM survivorship curves between the morning and evening. The evening feeding was preceded by some period in which we handled the animals and recording equipment. In experiment I about 10 min were used for these preparatory activities and in experiment II up to 25 min. Figs. 6.3. and 6.7. show that on all regimes rumination was more or less strongly decreased during these times in comparison to the model of Fig. 4.4. This suggests that external cues informing the animal that food will soon become available may promote the inhibition of rumination. Because the duration of preparations varied somewhat from day to day, it may be understood that in Figs. 6.3. and 6.7., beyond the initial part, marked concavity was never seen in the survivorship curves, although this would be expected on the basis of the reasoning underlying Fig. 4.4.

Fig.6.7. further shows that on the LL regime of long hay rumination was much more improbable in the period immediately before feeding than on the corresponding ML and HL regimes (the hay wafer data suggest more or less the same, but these data are statistically less reliable). This effect cannot be attributed only to the fact that R bouts are shorter and RR intervals somewhat longer on the LL regime. In other words, in the case of marked food

deprivation either the sensitivity to external cues must be increased, or the state variables for feeding alone inhibit rumination, independent of the presence of food stimuli or external cues.

Fig. 6.7. also shows marked difference in the RM survivorship curves between the two diets. This may be explained at least partly from the differences in R and RR length on the two diets, but one may surmise that feeding is also somewhat less effective in inhibiting rumination when the motivation for the latter is very high. However, the data are not sufficient to establish this point.

Rumination bouts. Whether food stimuli are required for the inhibition of rumination may also be derived from the distribution of R length.

In the ad lib. situation food stimuli are always present, while on restricted schedules this only holds for two short periods per day. In consequence, if food stimuli are necessary for rumination to be disrupted, such disruptions will occur far more often under ad lib. than restricted feeding conditions. However, neither in experiment I (Fig. 6.2.), nor in experiment II (p. 46), a clear excess of short bouts was seen in the ad lib. situation. This finding strengthens the indication that rumination may be inhibited by a meal state occurring in the absence of food.

To sum up, in the range of conditions here investigated the inhibition of rumination by feeding may be promoted either by the actual availability of food or by a state of 'expectancy' induced by external cues informing the animal that food will soon become available. Further, in states of marked food deprivation the inhibition of rumination may be precipitated, but it remains undecided whether this is due to an increased sensitivity to external cues or to direct effects of the feeding motivation, independent of the presence of either food or external cues.

Phase reset of rumination after feeding

For discussing factors that determine the reset of rumination after feeding, two parts of the MR interval must be distinguished: an initial lag during which probability of onset of rumination is zero, followed by a period in which this probability has a finite value. Experiments I and II show that the length of the lag depends on four conditions (compare Figs. 2.5., 6.3. and 6.8.):

(1) the feeding schedule (longer lag on restricted schedules; also reported by Pearce (1965a) for sheep);
(2) the time of day (longer lag in the evening);
(3) the nature of the diet (longer lag on hay wafers);
(4) the level of intake (longer lag for lower levels).

I have no clear explanation for these phenomena but at least two factors may play a role. Firstly, for some time after feeding the receptor areas for rumination near the cardia may not yet be reached by the coarse material in the reticulorumen (Pearce, 1965b). Secondly, rumination may still be inhibited by the state variables for feeding for some time after overt feeding has ceased.

Once the lag period has passed, the further survival of the MR interval will depend on the same factors that govern the survival of the subsequent RR intervals. The following points argue for this view: (1) under ad lib. conditions MR length is rather constant over the day just as RR length (Chapter 4);

(2) in experiment I the slope of the survivorship curves for MR intervals was almost the same in the morning and evening just as mean length of the subsequent RR intervals (Figs. 6.1. and 6.3.; it is very likely, then, that the survivorship curves for RR intervals were also the same for both periods); (3) in experiment II the slope of the MR survivorship curve became steeper with increasing level of food intake and increasing coarseness of the food which again agrees with the effects on mean RR length of the various regimes (Figs. 6.6. and 6.8.).

7. GENERAL DISCUSSION

In this chapter I shall put together the final model of feeding and rumination in cattle resulting from the present study. A few tests of the validity of the model will be suggested, and one or two assumptions will be briefly commented on. Further, some other results of this study will be reviewed which were not incorporated in the model as their inclusion would not lead to a further increase in its predictive power.

FINAL MODEL

Chapters 5 and 6 have demonstrated that various assumptions in the preliminary model (p. 31) hold for a wider range of conditions than ad lib. feeding alone. Utilizing these facts and some further results from these and earlier chapters, the preliminary model can now be transformed as follows:

(1) Feeding has an autonomous rhythm in the sense that at least over periods of several hours the state variables for feeding are wholly independent of the amount of rumination (pp. 28 and 37).

(2) The feeding rhythm is characterized by an alternation of 'meal' and 'interval' states.

(3) A strong diurnal rhythmicity is imposed on feeding which manifests itself in large meals and short intervals during feeding peaks, and small meals and long intervals during periods of low food intake.

(4) Rumination similarly has a basic rhythmicity (Figs. 2.5, 4.1, and 4.2), which is independent of feeding within the limits specified in the following three points.

(5) The state variables for rumination depend on the food intake integrated over a period of at least one to two days (p. 49), so that the last meal taken has a noticeable influence on rumination only if this meal was very large (see assumption 7).

(6) Overt manifestation of rumination is inhibited whenever the feeding rhythm is in the meal state; the inhibition is promoted especially by the presence of food stimuli, but in the case of food deprivation external cues informing the animal that food will become available may be effective as well (p. 50). When deprivation is strong, the state variables for feeding alone may be sufficient to inhibit rumination (either directly, or through increased sensitivity to external stimuli; p. 50).

(7) After feeding has interfered in this way, the phase of the rumination rhythm is reset to a fixed point in the cycle (pp. 30 and 51; however, rumination is resumed sooner when the last meal taken was very large (p. 30), see assumption 5).

(8) The need for rumination wanes only slightly with performance of this

behaviour, so that over periods of up to 6–10 hours the rumination rhythm maintains a rather constant periodicity within the limits specified before.

To test the validity of this model, let us consider the reliability of its predictions. Firstly, this model allows the same predictions concerning the length of the final R before feeding and the RM interval distribution as the preliminary model. Particularly the prediction of the latter has been extensively discussed already (p. 32). Secondly, it can be predicted from the final model that rumination will be subject to diurnal rhythmicity. Because the state variables for rumination depend upon the food intake over the foregoing 24–48 hours (assumption 5) and the need for rumination does not readily wane with the performance of this behaviour (assumption 8), we may expect that the rumination rhythm will have a rather constant periodicity over the 24 hours under ad lib. conditions. However, due to the inhibitory effects of feeding (assumption 6) and the fact that feeding itself has a strong diurnal rhythmicity (assumption 3), diurnal changes will also be imposed on the rumination rhythm, mainly on the length of the non-rumination intervals. Durations of RM and MR intervals will be rather constant over the day, however. These predictions fit the ad lib. data very well (Chapters 3 and 4).

A further possibility of testing the model is an experiment in which the animals are fed ad lib. with, for example, hay wafers. After the animals are habituated to this diet, some polypropylene ribbon is added to the contents of the reticulorumen. This non-nutritive material strongly stimulates rumination (cf. Welch and Smith, 1971). If feeding has strict priority over rumination indeed (assumption 6), the feeding pattern (i.e. M and MM length) will not markedly change during the first one to two days of the treatment, although rumination may be strongly increased. The R bouts will become longer, and the RR intervals more or less shorter. Correspondingly, the RM interval distribution will indicate a greater excess of short intervals (cf. Fig. 4.4), and the survivorship curve for MR intervals a higher rate of decay of these intervals beyond the initial lag for rumination (assumption 7). After this period of one to two days, it is rather likely that food intake will increase, and that further changes in the feeding and rumination patterns will therefore occur.

THE WORKING HYPOTHESES

In the beginning of this paper it has been assumed in advance that feeding and rumination have their own specific state variables (p. 5). In view of the later results, these assumptions seem reasonable in so far that the overt manifestations of these behaviours follow their own rules in the main. On the other hand, it must be realized that the state variables for rumination ultimately depend on food intake (Chapter 6; Welch and Smith, 1969a), and, conversely, rumination is likely to affect the state variables for feeding (cf. Pearce and Moir, 1964), although this could not be established in the short run in the present study.

A POSSIBLE SHORTCOMING

As far it is verifiable by means of the results of the present study, the final model seems to lead to reliable predictions of various aspects of the behaviour output. However, it will not be surprising when the results of the experiment suggested above do not entirely fit the model, because some uncertainty still exists whether the interaction between feeding and rumination is completely unilateral, as suggested in assumption 6. According to this assumption, feeding has priority over rumination, whereas the causal factors for rumination have no influence on the time of overt feeding. Chapters 2, 4, and 5 suggest indeed that feeding has strong priority. Moreover, no indication has been found at all that the state for rumination affects the time of onset or cessation of a meal. On the other hand, Chapter 6 suggests that on restricted feeding schedules the state variables for rumination may hamper the inhibitory effect of feeding on rumination (p. 51). This point indicates that assumption 6 needs further verification.

Unfortunately, the phase-coupling between feeding and rumination under ad lib. conditions due to the reset prohibits a check of the influence of the state for rumination on the start of feeding through analysis of the degree of shortening of the last R bout before the meal and the form of the distribution of RM interval length. Possibly, the fact that under ad lib. conditions very short R bouts were very rare (p. 13) and in some animals no excess of short RM intervals was seen (p. 14), indicates that rumination may indeed retard the onset of feeding to some extent.

In order to check whether rumination may hasten the end of a meal, we should examine whether there is a positive correlation between durations of the final feeding bouts of the meal and the subsequent MR intervals. However, the data of the automatic records were not appropriate for this (p. 4).

SOME FURTHER RESULTS

I shall now briefly discuss some characteristics of feeding and rumination, not considered in the model, although they are important for understanding the causal organization of these behaviours.

Feeding rhythm. The fact that cattle eat in meals implies that food intake in these animals can be treated in terms of the factors that determine size (and duration) of meals, and length of the intervals between them.

At least during daylight, neither meal duration nor interval length are random in cattle, in contrast to, e.g., domestic fowl (Duncan et al., 1970). In this period, the probability of ending a meal gradually increases with the time elapsed since the beginning of the meal, and once the meal has ceased, the probability of resuming feeding is very low for, roughly speaking, the first hour (Chapter 2). A possible explanation for the latter fact is that rumination prevents overt feeding specially in the first period after a meal, but the fact that in the shorter MM intervals, with only one R bout, the MR and RM intervals are relatively long (Fig. 4.1), argues against this view.

Under the conditions of the present study, larger meals were taken when the preceding interval was longer. Apparently, the degree of food depletion that the cow has incurred at the time of beginning a meal is more or less compensated by the size of that meal. Thus, as stated earlier (p. 29), the cow would tend to stop a meal at some fixed level of repletion (which, however, is probably subject to diurnal rhythmicity). In contrast, meal size does not affect the length of the interval to the next meal, so that it is unlikely that a meal starts at some fixed level of depletion.

According to the reasoning of some authors, e.g. Thomas and Mayer (1968) and Duncan et al. (1970), the latter findings would suggest that in cattle control of meal size is the main element of adjustment of food intake to presumed requirements, but this is not necessarily so. The control of interval length may be equally important on the basis of the results presented so far. Only the fact that four out of seven animals in the basic experiment took clearly larger meals on days with a higher food intake (p. 15) may be used as an indication that controlling meal size is probably more important than controlling interval length in the regulation of food intake. Ultimate proof, however, must be obtained from experiments in which food requirements and caloric density of the diet are varied.

Rumination rhythm. Rumination is a very regular behaviour and may be performed without interruption even for periods of one hour and longer. In this respect it differs strikingly from feeding. When overt rumination is started, it tends to persist for at least several minutes. Beyond this time the probability of ending the R bout increases progressively, although very gradually at first. The bouts are clearly spaced out in time: in the basic experiment the intervals between successive bouts lasted at least 15 min (p. 13).

The length of a rumination bout has no influence on the time of starting the next bout. However, there is a weak tendency for an R bout to become longer according as it starts sooner after the preceding bout. More markedly, R bouts directly following a meal become longer when they start earlier, irrespective of the size of the meal. The first of these three findings is understandable from the fact the need for rumination wanes only slightly with the performance of this behaviour, but for the latter two I have no clear explanation.

The present study gives no evidence that the rumination rhythm itself is subject to circadian rhythmicity. This seems in contradiction with results reported by Gordon and McAllister (1970) for sheep. These authors found that the response of rumination to food intake was different between the light and dark period. However, it is not yet clear from their experiments whether indeed a circadian cycle is imposed on rumination, or whether interference by the feeding state may account for this effect. Also other workers, e.g. Pearce (1965a), Welch and Smith (1969a) and Geoffroy (1974), report marked diurnal changes in the amount of rumination, but in none of these cases it can be ruled out that the observed diurnal changes are due to feeding.

As Chapter 6 has shown, the nature of the diet has a conspicuous influence on the promoting effect of food intake on rumination. Intervals between R bouts are far shorter on long hay than on hay wafers. Although in general the duration of RR intervals decreases when daily food intake increases, a minimum duration of intervals was already reached at a very low level of intake on the long hay diet. Clearly, amount of food ingested and nature of the diet eaten are two different dimensions of the state for rumination.

SUMMARY

For the maintenance of its caloric and nutritional balance, an animal must consume food. The level of intake ultimately depends upon the factors that govern onset and cessation of the successive feeding spells. These factors may be studied either at the purely behavioural level, or at the level of the underlying physiological mechanisms. However, in both cases a detailed specification of the overt behaviour is a prerequisite. This study attempts to present such a specification of feeding behaviour in cattle. However, for explaining the feeding pattern, rumination behaviour has been considered as well.

Units of feeding and rumination behaviour were defined at the level of 'bouts', i.e. uninterrupted performances of these behaviours. In the case of feeding behaviour, clusters of bouts formed higher order units, termed 'meals'. All other behaviour was only considered in terms of 'intervals' between the feeding and rumination bouts. For the analysis of durations of the behaviour units, the first-order Markov process was used as the random model. Deviations from randomness were derived from the frequency distribution of the durations.

The concept of 'state variables' was introduced to refer to the conditions in the animal that determine, together with external stimuli, the likelihood of occurrence of a given behaviour. As working hypothesis it was assumed that (1) there are state variables that specifically promote feeding, and (2) state variables that specifically promote rumination.

The first part of the investigation concerned an analysis of the feeding and rumination patterns of cows fed ad lib. with hay wafers (Chapter 2, 3 and 4). The feeding rhythm in cattle is characterized by an alternation of 'meal' and 'interval' states. In the meal state, the animal is likely to eat, but this may be interrupted by relatively short spells of non-feeding behaviour. In contrast, in the interval state feeding is unlikely. To make a distinction between these two states as sharp as possible, a meal criterion of 20 min seems preferable.

The feeding rhythm is subject to strong diurnal rhythmicity. During the greater part of daylight, the main feeding period, meal size is positively correlated with length of the preceding interval, suggesting that meals tend to stop once some fixed level of food repletion is reached. On the other hand, meal size is not correlated with the length of the interval to the next meal. Therefore, it is improbable that cattle do not start meals until the food ingested at the previous one has been used up. However, the correlations between meal size and length of the adjacent interval change markedly towards the end of the day, probably due to the strong changes in the motivation for feeding at that time.

Rumination occurs in prolonged bouts, which are clearly spaced out in time. Apart from interference by feeding, the rumination rhythm maintains a rather constant periodicity over the day. Furthermore, duration of a bout does not affect the duration of the interval till the next bout, but a weak tendency exists

for the latter to become longer when it starts earlier.

The ad lib. data strongly suggest that ongoing rumination may be broken off under the influence of the state variables for feeding, and further that renewed rumination is prohibited as long as the feeding rhythm stays in the meal state. After feeding has interfered in this way, the phase of the rumination rhythm is reset. The resumption of rumination is rather independent of the size of the foregoing meal.

The percentage of time spent on rumination during a between-meal interval does not affect size of the subsequent meal; nor does meal size affect the amount of rumination during the next interval. However, daily food intake and total rumination time are positively correlated, suggesting that facilitatory relations between the two behaviours do exist on a longer time scale.

On the basis of these results obtained under ad lib. conditions a preliminary model of feeding and rumination in cattle was put forward (Paragraph 4.4). On aim of the following experiments was to assess to what extent the assumptions in this model hold for a wider range of conditions.

In the first experiment it was established that the prevention of rumination during a three-hour period of food deprivation results in an increase of rumination in the subsequent period, but does not change the feeding pattern at all (Chapter 5). This supports the assumption that feeding has priority over rumination whenever the causal factors of the two behaviours are in conflict. Moreover, it indicates that the state variables for feeding are wholly independent of the amount of rumination in the foregoing period of at least three hours.

Subsequent experiments involved the restriction of feeding to two periods of two and a half to three hours a day (Chapter 6). In one experiment the amount of food given was additionally restricted to different levels, both on a hay wafer and long hay diet. The results reveal that the state variables for rumination are strongly dependent on food intake, presumably the intake integrated over the foregoing 24–48 hours. However, amount of food consumed and nature of the diet have different influences on the state for rumination (for, whereas on the hay wafer diet amount of food eaten and length of the intervals between rumination bouts are negatively correlated, a minimum interval length is already reached at a very low level of intake of long hay, the coarser diet).

During the prolonged non-feeding periods, the rumination rhythm maintained a fairly constant periodicity, irrespective of the level of food intake. This indicates that the need for rumination wanes only slightly with the performance of this behaviour. Further, the experiments confirm that overt rumination is inhibited whenever the feeding rhythm is in the meal state. Evidence has also been found that this inhibition is promoted especially by the presence of food stimuli, but external cues informing the animal that food will become available may be effective as well. Finally, the results suggest that after overt feeding has interfered, the rumination rhythm is reset to a fixed phase.

This study was concluded by putting together the final model of feeding and rumination in cattle (Chapter 7). Various predictions that can be made by combining the assumptions in this model fit the data of the described experiments very well. On the other hand, it has been emphasized that the assumption of absolute priority of feeding over rumination needs further verification.

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SAMENVATTING

Voor de handhaving van zijn warmte- en voedingsbalans moet een dier voedsel opnemen. Het niveau van de opname hangt uiteindelijk af van de factoren, die begin en einde van de opeenvolgende eetperioden bepalen. Deze factoren kan men zowel zuiver op het niveau van het gedrag bestuderen als op het niveau van de daaraan ten grondslag liggende fysiologische mechanismen. In beide gevallen echter is een gedetailleerde specificatie van het uitwendige gedrag een noodzakelijke voorwaarde. Het hier beschreven onderzoek tracht een dergelijke specificatie te geven van het eetgedrag bij runderen. Om het eetpatroon te kunnen begrijpen, is echter ook het herkauwgedrag bekeken.

Eenheden van eet- en herkauwgedrag werden gedefiniëerd op het niveau van 'vlagen', i.c. ononderbroken verrichtingen van deze gedragingen. In het geval van het eetgedrag vormden groepjes vlagen, die kort op elkaar volgden, eenheden van een hogere orde, die 'maaltijden' werden genoemd. Al het overige gedrag werd slechts beschouwd in termen van 'intervallen' tussen de eet- en herkauwvlagen. Voor de analyse van de duur van gedragseenheden werd het eerste-orde Markov proces gebruikt als het toevalsmodel. Afwijkingen van dit model werden afgeleid uit de frequentieverdeling van de duur van die eenheden.

Het begrip 'toestandsvariabele' werd geïntroduceerd om te verwijzen naar de omstandigheden in het dier, die, tezamen met de uitwendige prikkels, de waarschijnlijkheid van het optreden van een gegeven gedrag bepalen. Als werkhypothese werd aangenomen dat er (1) toestandsvariabelen bestaan, die specifiek eetgedrag bevorderen en (2) -variabelen, die specifiek herkauwgedrag bevorderen.

Het eerste gedeelte van het onderzoek betrof een analyse van het eet- en herkauwpatroon van koeien, die ad libitum werden gevoerd met hooiwafels (Hoofdstukken 2, 3 en 4). Dit leverde de volgende resultaten op. Het eetritme van koeien wordt gekenmerkt door een afwisseling van 'maaltijd'- en 'interval'-toestanden. In de maaltijdtoestand is eetgedrag waarschijnlijk, maar dit kan voor korte perioden worden onderbroken door ander gedrag. Daarentegen is eetgedrag onwaarschijnlijk, wanneer het dier in de intervaltoestand verkeert. Om een scherp onderscheid te maken tussen deze twee toestanden, lijkt een maaltijdcriterium van 20 minuten het meest geschikt.

Het eetpatroon is onderhevig aan een sterke etmaalritmiek. Tijdens het grootste gedeelte van de dag, de belangrijkste periode van voedselopname, bestaat er een positieve correlatie tussen maaltijdgrootte en lengte van het eraan voorafgaande interval. Dit suggereert dat maaltijden de neiging vertonen pas beeindigd te worden, zodra een of ander vast niveau van verzadiging is bereikt. Anderzijds is de maaltijdgrootte niet gecorreleerd met de lengte van het interval tot de volgende maaltijd. Het is derhalve onwaarschijnlijk, dat runderen wachten met een nieuwe maaltijd, totdat het voedsel, opgenomen tijdens de vorige maaltijd, is verbruikt. De correlaties tussen maaltijdgrootte en lengten van de begrenzende intervallen veranderen echter sterk tegen het einde van de dag, waarschijnlijk ten gevolge van de sterke veranderingen in de motivatie voor eetgedrag, die dan plaatsvinden.

Herkauwen geschiedt in lange vlagen, afgewisseld met lange intervallen. Afgezien van verstoring door eetgedrag, handhaaft het herkauwritme een tamelijk constante periodiciteit over het etmaal. De duur van een vlaag heeft geen invloed op de duur van het interval tot de volgende vlaag. Anderzijds vertoont een herkauwvlaag de neiging wat langer te worden wanneer ze sneller volgt op de voorafgaande.

De gegevens voor ad libitum omstandigheden suggereren, dat herkauwvlagen kunnen worden afgebroken onder invloed van de toestandsvariabelen voor eetgedrag en dat herkauwen wordt belemmerd, zo lang het eetritme in de maaltijdtoestand blijft. Na een verstoring door eetgedrag wordt de fase van het herkauwritme opnieuw ingesteld. Dit geschiedt tamelijk onafhankelijk van de grootte van de voorgaande maaltijd.

Het percentage van de tijd, besteed aan herkauwen tijdens een interval tussen twee maaltijden, beïnvloedt niet de grootte van de volgende maaltijd. De maaltijdgrootte heeft op zijn beurt geen invloed op de hoeveelheid herkauwen tijdens het volgende interval. Dagelijkse voedselopname en totale herkauwtijd zijn echter positief gecorreleerd, hetgeen suggereert, dat er over een langer tijdstraject wel faciliterende betrekkingen tussen beide gedragingen bestaan.

Op basis van deze resultaten, verkregen onder ad lib. omstandigheden, werd een eerste, voorlopig model opgesteld voor eet- en herkauwgedrag bij runderen (Paragraaf 4.4). Een van de bedoelingen van de daarna verrichte proeven was na te gaan of de verschillende aannames in dit model ook gelden voor een ruimer scala van omstandigheden.

Uit de eerste proef bleek dat de verhindering van het herkauwen tijdens een 3 uur durende periode van voedseldeprivatie wel aanleiding geeft tot meer herkauwen in de navolgende periode, maar het eetpatroon in geen enkel opzicht verandert (Hoofdstuk 5). Dit is een ondersteuning van de aanname, dat eetgedrag voorrang heeft op herkauwen, wanneer de causale factoren voor de beide gedragingen in conflict geraken. Bovendien wijst het erop, dat de toestandsvariabelen voor eetgedrag geheel onafhankelijk zijn van de aan herkauwen bestede tijd in de voorgaande periode van ten minste 3 uren.

In de hierop volgende proeven werd de eettijd beperkt tot twee perioden van twee-en-een-half tot drie uur per dag (Hoofdstuk 6). In een der proeven werd bovendien ook de verstrekte hoeveelheid voedsel tot verschillende niveau's beperkt, zowel op een rantsoen met hooiwafels als met lang hooi. De uitkomsten tonen aan dat de toestandsvariabelen voor herkauwen in sterke mate afhankelijk zijn van de voedselopname, vermoedelijk de opname geïntegreerd over de voorgaande 24–48 uur. De hoeveelheid en aard van het opgenomen voedsel oefenen echter een verschillende invloed uit op de toestand voor herkauwgedrag (want, terwijl bij het verstrekken van hooiwafels de gegeten hoeveelheid voedsel en de lengte van de intervallen tussen de herkauwvlagen negatief gecorreleerd zijn, wordt bij het aanbieden van lang hooi – het grovere voedsel –

reeds een minimale intervalduur bereikt bij een zeer laag opnameniveau).

Tijdens de lange perioden tussen de eettijden handhaafde het herkauwritme een tamelijk constante periodiciteit, ongeacht het niveau van de voedselopname. Dit duidt erop, dat de behoefte aan herkauwen slechts in geringe mate afneemt met de uitvoering van dit gedrag. Verder bevestigen de proeven, dat het herkauwgedrag wordt geremd, wanneer het eetritme in de maaltijdtoestand verkeert. Het blijkt, dat deze remming vooral wordt bevorderd door de aanwezigheid van voedselprikkels, alhoewel tekenen uit de omgeving, die het dier er op wijzen dat voedsel beschikbaar komt, evenzeer werkzaam kunnen zijn. Tenslotte suggereren de uitkomsten, dat het herkauwritme opnieuw wordt ingesteld op een vast punt in zijn cyclus, nadat eetgedrag dit heeft verstoord.

Deze studie werd besloten met het opstellen van het model voor eet-en herkauwgedrag bij runderen, zoals dat uiteindelijk uit de beschreven proeven naar voren komt. Verschillende voorspellingen, die kunnen worden gedaan door het combineren van aannames in dit model, blijken goed overeen te komen met de uitkomsten van de verrichte proeven. Wel wordt er de nadruk op gelegd, dat de aanname van een absolute voorrang van eetgedrag op herkauwen nader geverifiëerd moet worden.

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