Feeding Behaviour in Dairy Cows

Motivational Aspects

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Abstract

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In this thesis I summarise and discuss the results of studies regarding motivational aspects on feeding behaviour in dairy cows. Questions addressed concern how feeding duration and rumen fill in cattle influence some behavioural variables reflecting frustrated feeding motivation, such as stereotypies and behaviours related to feed-searching, and also how rumen fill and feeding duration relate to oxytocin and cortisol. We have also investigated if operant conditioning is a useful method to measure and quantify the motivational strength to obtain roughages with different characteristics and sensory qualities. The aim was to test the hypothesis that oral manipulation of feed is a behavioural need in cattle, irrespective of rumen load.

Low rumen content and long eating time had the effect that the cows spent a rather short time with behaviours related to feed-searching and showed low levels of stereotypies. The cows with long eating time had a larger oxytocin release during the afternoons compared with the cows with short eating time. The cows with high rumen content and short eating time spent relatively more time with behaviours related to feed-searching and with stereotypies. The cortisol concentration in the morning sampling period was higher in the treatment with short eating time compared with the cows with long eating time.

The studies with operant conditioning showed large individual differences between cows in their motivation to work for feed in general. The results also showed that cows have individual preference for one specific side.

It can be concluded that oral manipulation of feed is a behavioural need in cattle irrespective of rumen load. A short duration of feeding behaviours combined with a low rumen load seriously impairs the welfare of cattle. The results imply that there are physiological mechanisms, possibly in the form of oxytocin, involved in the motivation of feeding. I also conclude that operant conditioning could be a fruitful method to measure and quantify feed preference of dairy cows. However, the results only reflect the preference of the individual animal, and a complete mapping according to side preference must be done of each individual included in the experiment.

The practical implication of these studies is to provide all cows with sufficiently long eating time, preferably by constant access to roughage.

Keywords: Feeding, behaviour, stereotypies, motivation, dairy cows, oxytocin, cortisol, operant conditioning.

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Contents

List of original papers

The present thesis is based on the following four papers, which will be referred to in the text by their Roman numerals:

I. Lindström, T., & Redbo, I. 2000. Effect of feeding duration and rumen fill on behaviour in dairy cows. *Applied Animal Behaviour Science*, 70 (2), 83-97.

II. Lindström, T., Redbo, I. & Uvnäs-Moberg, K. 2000. Plasma oxytocin and cortisol concentrations in dairy cows in relation to feeding duration and rumen fill. *Physiology and Behavior*. In press.

III. Lindström, T., Redbo, I. & Dockens III, W. S. 2000. Individual differences in cows' motivation to obtain a specific feed resource. Submitted to *Journal of Animal Science.*

IV. Lindström, T., Redbo, I. & Dockens III, W. S. 2000. Measuring feed preferences in cows by operant conditioning. Submitted to *Applied Animal Behaviour Science.*

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Introduction

From ecological and ethological points of view, feeding behaviour is the animal's selection and ingestion of feeds required for growth and maintenance (Le Magnen, 1985). Consequently, feeding is the behavioural part of the physiological process we call 'nutrition'. In the wild, feeding behaviour is preceded by and dependent on food-seeking behaviour. The basic determinant of this food-seeking is the physiological mechanism which properly governs the feeding behaviour and urge for animals to seek and to eat food. The animal's food selection and the amounts eaten are governed by the metabolic demand, and therefore supplies of carbohydrates, fats, and proteins from the environment are required to cover the energy expenditure. Thus, the motivation underlying food intake is that of obtaining energy (Toates, 1986).

Motivation of feeding behaviour

There is more than one interpretation of the word 'motivation' in the behavioural literature. However, 'motivation' has most commonly been used as a process that affects the direction, vigour, and persistence of goal-directed behaviour that refers to the strength of the tendency to engage in a behaviour taking into account both internal and external factors (Toates, 1986).

An external factor that might stimulate motivation is often called an incentive, for example the hedonic properties, or palatability, of the feed that might stimulate motivation for feeding. Motivation for feeding may also be stimulated by sight and sound of other animals eating, and of the delivery of fresh feed (Forbes, 1995). Physiological parameters of the body are the internal factors stimulating motivation. Internal motivation often results in a behaviour explained by sensory reinforcers that affect behaviour in different ways: as a reinforcement for merely performing a behaviour per se (self-reinforcing effect) (Herrnstein, 1977), as well as a conventional reinforcer, i.e. feed. When a predator stalks, its prey could serve as an example of a behaviour with a self-reinforcing effect, as both stalking and capturing of the prey serve as reinforcers for the behaviour. The prey as a food reinforcer does not emerge until the prey is eaten.

Changes in either internal or external state might change the motivation, but nonetheless, none of them should be regarded as dominant (Toates, 1986). The tendency to seek food may be of similar intensity whether due to high motivation for feeding in the absence of food or low motivation for feeding in the presence of food (Forbes, 1995). This means that both an external incentive and an internal physiological state jointly play a role in determining the motivation for feeding. However, the environmental cue probably influences the decision on when to seek food. Cue strength is dependent upon the distance to the food, hence, if food is far away we call it low cue strength of food (Toates, 1980). It has been shown in experiments with rats (Toates, 1980), that the tendency for feeding is dependent on the animal's physiological state (rate of deprivation) and the appropriate cue strength. The combination of a low rate of deprivation and high cue strength might give the same feeding tendency as a high rate of deprivation and low cue strength. This means that either combination of energy state and cue strength may result in the same motivational tendency as, according to Toates (1980), the motivational tendency is the product of cue strength and deficit.

Factors affecting the motivation to feed

Hunger and satiety

According to Le Magnen (1985), satiety is the state during which, from the end of one meal to the occurrence of the next, an animal does not eat, i.e. is not stimulated to eat. This means that satiety is a passive state of no hunger. The process of 'satiation' is the mechanism that leads to satiety. Satiation is brought about by chewing and swallowing the food, by its accumulation in the stomach and passing through the intestine. An animal usually stops feeding long before the concentration of nutrients in the bloodstream has reached peak level and before tissue needs are satisfied. Thus, satiety is a function of information at several levels; oral, gastric and post-ingestive (Toates, 1986).

The sensory action of food passing the mouth *per se*, cannot induce satiety, which has been demonstrated by sham-feeding rats, dogs and monkeys (Kraly et al., 1978). This phenomenon has also been shown in dairy cows (Baile & Della-Fera, 1981). Cows in which the boli were removed from the rumen continued to eat for much longer times and consumed larger quantities of feed than during normal feeding. From this, the authors conclude that it is unlikely that exhaustion of salivary glands or fatigue of jaw muscles limits or acts as a control for feed intake. Another method that has been used is to introduce food directly into the stomach without passing the mouth/throat. This makes it possible to separate the effects of stimulation in the mouth/throat region from the effects of change in stomach content. With this method it has been shown that oral factors play a role in the cessation of feeding (Hinde, 1970) and that both oral and gastric factors in dogs operate and co-operate to regulate food intake during a meal (Janowitz & Grossman, 1949).

The most obvious conditions that stimulate hunger and eating are energy deficit and weight loss induced by food deprivation (Le Magnen, 1985). Eating is initiated by a combination of systemic or metabolic stimulation and sensory stimulation, i.e. the palatability of the food. Eating leads to changes at post-absorptive level, but before these changes occur, the filling during the meal achieves satiety due to a negative feedback counteracting the initial positive feedback of the hunger-dependent palatability. It is known that palatability has a major influence on feed intake in ruminants, and that the sense of taste is highly developed in cattle (Albright, 1993).

There is a lot of evidence that homeostasis and the rate of glucose utilisation play a role in generating the hunger signal (Le Magnen, 1985). Numerous studies with *ad libitum* fed rats have demonstrated that feeding is linked to the complex mechanism that controls the supply of glucose to the tissues and maintains the blood glucose on a constant level. However, glucose as a metabolite controlling feeding is valid for monogastrics, but according to Dowden & Jacobson (1960), Simkins et al. (1965), Baile & Mayer (1970), and Baile & Della-Fera (1981), there is little evidence that glucose concentration or utilisation rate has a significant role in controlling feeding in ruminants.

Learning

Learning refers to a process of permanent change in behaviour as a consequence of experience. Much effort has been made to relate all examples of learning to one or two basic types. There are, however, two different types of situations in which learning is commonly studied (Hinde, 1970), namely in the distinction between classical, or Pavlovian, conditioning and operant conditioning used by Skinner. In establishing the laws of classical conditioning, Pavlov employed the reflex arc as a model (Schwartz & Gamzu, 1977). Under a variety of conditions, Pavlov showed that stimuli could be made to trigger or elicit particular reflexes. With this model it was easy to explain salivation, but more difficult to explain stimulus which triggered, for example, feeding. A new learning principle was required to explain behaviours that appeared voluntary and unelicited. This principle was Thorndike's law of effect (Bower & Hilgard, 1981). This law states that classes of behaviour can be controlled by their own consequences. Skinner highlighted the importance of the law of effect in learning and the distinction between the two kinds of learning. With his invention, the Skinner box, he could demonstrate the principles of operant conditioning: the animal is asked to make some response, e.g. to produce an effect and to perform a function to obtain or avoid certain consequences. Ferster & Skinner (1957) developed schedules of reinforcement to take advantage of the close linkage between cause and immediate consequences.

It is well known that animals use their sight, smell and taste to identify the appropriate feeds (Forbes, 1998) and that they learn from each other and from their own experience what to eat (Provenza & Balph, 1987). Animals also have the ability to associate the sensory properties of foods with the metabolic consequences of eating the foods (Forbes, 1995). If a food is very toxic, the animal retains a memory of the food's sensory properties for a lifetime and avoids that food, but foods with milder metabolic effects are retained for short periods allowing the animal to relearn about the metabolic effects of that food (Forbes & Kyriazakis, 1995). It is also stated that animals can select a diet appropriate to their metabolic needs as long as the foods are clearly different by taste or colour and that animals have the opportunity to learn the nutritional difference between foods (Forbes & Kyriazakis, 1995; Provenza & Balph, 1987). In the absence of any direct sensory cues, many animals can use spatial memory to locate sources of food, or to choose between foods (Kovalcik & Kovalcik, 1986). It is also known that animals can remember the likely spatial position of appropriate foods, based on previous experience (Forbes, 1998). Implicated here are the processes of (a) forming a memory of recently ingested food, (b) monitoring the consequences of ingestion, and (c) feedback modulation of incentive value (Toates, 1986).

Competitive behaviours

Animals can only perform one behaviour at a time, even if stimuli appropriate for more than one behaviour are present (Toates, 1980). This means that there must be a decision-making process to determine which activity the animal performs at any given time. If the motivation for feeding is high the animal goes on feeding until the motivation is lowered and the motivation for another behaviour dominates, meaning that the animal might switch from one behaviour to another. This phenomenon is called behavioural inhibition (Toates, 1980) and was introduced by Hinde (1970), who stated that when two types of behaviour are present, the causal factors for one behaviour will be reduced in strength and cancelled by inhibition arising from the causal factors for the other behaviour. A feeding tit, alarmed by the appearance of a flying predator, and hence abandoning its food, could serve as an example of this (Hinde, 1970).

Another factor involved in time-sharing between behaviours is the mechanism of persistence. One possible device for ensuring persistence is positive feedback of the behaviour *per se* (Toates, 1980). Suppose the tendencies for eating and drinking are roughly equal, but feeding takes control. If the start of feeding actually increases rather than decreases feeding tendency, the animal will persist eating for a while until the tendency for drinking gets stronger than the tendency for eating.

When discussing persistence of behaviours, McFarlands 'trajectory model' could be used (Toates, 1980). This model represents a state-space approach to motivation (Sibly & McFarland, 1974), in which the animal's changes in behaviour can be viewed as a system of interacting variables. The state of the internal environment can be described in terms of a finite number of physiological state variables, each of which can be represented on an axis in a diagram. Thus, with thirst placed, e.g. on the y-axis, and hunger on the x-axis, any state of simultaneous hunger and thirst could be described in this diagram, as well as the switches between these two behaviours. The possible behaviour trajectory following the satiation of hunger and thirst could then be shown.

Hormones

Numerous hormones are involved in the complex hunger-satiety system, but in the studies presented in this thesis we have chosen to focus on two hormones; oxytocin and cortisol.

The pituitary hormone oxytocin is well known for its contribution to milk ejection. However, results from recent years of research show that oxytocin also has interesting behavioural effects, e.g. to exert anti-stress-like effects characterised by calmness (Uvnäs-Moberg, 1997). Oxytocin is also released in response to feeding in dairy cows (Svennersten et al., 1990), and in calves (Johansson, 2000). There are also indications that oxytocin is released by the presence of food in the mouth, oesophagus or stomach (Uvnäs-Moberg et al., 1985), that feeding duration might have an effect on oxytocin release (Johansson, 2000) and that oxytocin can be released by stimulation of peripheral nerves originating in the gastrointestinal tract (Stock & Uvnäs-Moberg, 1988).

Another interesting character about oxytocin is that it might have an immediate increasing effect on cortisol levels, followed by a sustained decrease of cortisol (Pettersson et al., 1999). In dairy cows fed during milking, it is suggested that the level of cortisol might be suppressed by the high oxytocin levels during milking (Johansson et al., 1999).

The glucocorticoid cortisol is also known to be released in response to feeding (Willett & Erb, 1972) and milking (Wagner & Oxenreider, 1972; Gorewit et al., 1992) in dairy cows, even though cortisol is most known for its physiological effects in connection with stress (Munck et al., 1984), metabolism and immunity (Lefcourt et al., 1993; Leal & Moreira, 1997; Moon Hong Kil, 1998). It has also been reported that cortisol might be released as an anticipatory response to forthcoming feed (Willett & Erb, 1972).

Consequences of low feeding duration

Cattle on pasture spend 7-9 hours daily grazing and about the same amount of time ruminating the ingested feed (Hafez & Bouissou, 1975). Today, most of the dairy cows in Sweden still pass their days during the stable period in tie-stall housing systems, although there is an obvious trend towards different loose housing systems. The feeding of dairy cows in tie-stall housing systems is often accomplished within a rather short time, compared with the duration of eating and ruminating among cows on pasture. Even though the cow's physiological needs are most often fulfilled in modern dairy systems, the duration of feed intake is low compared with natural conditions.

An animal highly motivated to perform feeding behaviours, but restricted from doing so, may show different kinds of displacement behaviours, due to the frustrated feeding (Redbo, 1992b). It has been shown in numerous studies with cattle (e.g. Redbo, 1990; Redbo et al., 1996; Redbo & Nordblad, 1997) that restricted feeding leads to both a development as well as an increase in behavioural disturbances, such as stereotyped oral behaviours. Behaviours related to feed-searching, i.e. nosing or licking the empty feed-trough or on the floor, or fittings close to the trough, often adjoin a bout of stereotypies (Redbo, 1992a). Taken together, this means that behaviours related to feed-searching and stereotypies in cattle could be used as markers for frustrated feeding behaviours.

A need to behave?

The question whether animals have behavioural needs has been discussed among scientists for years, and in 1989 Ted Friend stated that "the existence of behavioural needs is now accepted". Friend (1989) defines behavioural needs as behaviours that are motivated largely by internal stimuli and, if an animal is prevented from performing them for prolonged periods, the individual's welfare may be compromised. In 1993, Jensen & Toates made an investigation of the question whether there exist needs to perform particular behaviours when the physiological needs of the animal are taken care of. The authors argues for a holistic approach to the motivational control of behaviour. They conclude that a behavioural need generally has been used to describe "the need to perform a specific behaviour pattern whatever the environment is like and even if the physiological needs which the behaviour serves are fulfilled". Jensen & Toates also state that according to current theory, behavioural need would be to perform a behaviour pattern fitting some or all of the following three criteria: it is mainly caused by internal causal factors, its tendency is gradually built up while it is not being performed and the mere performance of the behaviour pattern is rewarding. Jensen & Toates argue that "animals do possess needs with regards to their behaviour, i.e. prevention of performance of species-specific behaviour may cause signs of reduced welfare".

According to Friend (1989), an animal's need to perform a particular behaviour can be estimated using different techniques: (1) observation under 'natural' conditions, (2) observation of overt behaviour under structured or restricted conditions, (3) requiring an animal to work for the opportunity to perform specific behaviours, (4) controlled behavioural deprivation followed by open-field testing, (5) quantification of physiological responses.

One way to measure an animal's motivation is to use operant conditioning techniques, in which the animal is asked to choose between commodities by pressing a lever or key. This enables us to 'ask the animal' which commodities they prefer (Baldwin, 1983). The major benefit of using operant conditioning to measure feeding motivation lies in its precision because the intensity of the operant response is thought to closely reflect the motivation to obtain the reinforcer (Day et al., 1996). Operant conditioning has been used to assess the importance of different commodities, e.g. Dawkins (1983) made hens choose between food and litter under different levels of food deprivation. The technique has been used to quantify the environmental requirements of domestic animals, e.g. pigs (Matthews & Ladewig, 1994; Ladewig & Matthews, 1996), sheep and calves (Bell & Sly, 1977; Baldwin & Start, 1978), mice (Roper, 1975) and hens (McAdie et al., 1993; Gunnarsson et al., 2000). The method also makes it possible to obtain quantitative measures of preference for diverse variables (Arave, 1995). Petherick and Rutter (1990) used operant conditioning with hens to quantify their motivation to get to a feeder or nest-box, and Ramonet et al. (2000) used the method to measure feeding motivation in pregnant sows.

Operant conditioning has also been used in cattle where preferences for different feeds have been investigated. Matthews & Temple (1979) trained dairy cows on several pairs of concurrent variable-interval schedules with different types of feed, while Moore et al. (1974) made an operant conditioning study with Jersey cows in order to record the pattern of responses of the cows under four different schedules. A concentrate mixture of crushed barley and corn meal was used as reinforcement. Klopfer et al. (1981) determined the relative palatability of 20 feeds by exposing cows to all possible pairs of the feeds, and Arave et al. (1983) used heifers in an operant conditioning procedure to evaluate the animal's preferences among commercial dairy meals and pellets.

Objectives

The objectives of the present thesis can be summarised in the following points:

- To examine how feeding duration and rumen fill in cattle influence (a) some behavioural variables possibly reflecting frustrated feeding motivation, and (b) its relation to some physiological mechanisms, and thereby testing the hypothesis that oral manipulation of feed is a behavioural need in cattle, irrespective of actual rumen load.

- To investigate if operant conditioning is a useful method to measure and quantify the motivational strength for feeding roughages with different characteristics and sensory qualities, and to measure feed preferences in dairy cows.

Material and Methods

All studies were carried out at Kungsängen Research Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden. The experimental procedure, including the blood sampling reported in Papers I and II, was approved by Uppsala Animal Ethics Committee.

Papers I and II

Animals and experimental design

Twelve rumen-fistulated lactating dairy cows of the Swedish Red and White Cattle Breed were used and subjected to 4 different treatments:

A: Low rumen content + long duration of eating
B: High rumen content + short duration of eating
C: High rumen content + long duration of eating (=positive control)
D: Low rumen content + short duration of eating (=negative control)

Each animal passed through all treatments in one of four different orders. Each treatment lasted for 3 days, followed by a two-week recovery period when the cows were kept in accordance with ordinary management and feeding routines, before a new 3-day experimental period started. All cows were housed in the same barn in individual stalls with an empty stall or a solid partition in between them. All cows were milked twice daily.

Feeding

All experimental cows were fed a mixture of 60% grass clover silage, 5% grass hay and 35% concentrate in individual amounts calculated according to their individual milk production. The energy concentration in the mixture varied during the two years between 11.7 and 12.0 MJ metabolizable energy per kg dry matter. One day before the experiment started the feed was restricted to 75% of normal individual feed amount for all 4 treatments. The cows were fed individually in troughs twice a day. Amounts of leftovers were recorded during the whole experimental period. All cows had free access to water in individual bowls and the water consumption was recorded individually during the experimental days. All cows had free access to salt lick.

Rumen content was transferred from cow A to cow B through the rumen fistulae to obtain treatments A and B. Cows in treatment A were offered 150% of normal feed amount to eat orally (in principle *ad libitum*) but rumen content was regulated to stay at 75% of normal feed allotment. Cows in treatment B were offered 50% of normal feed amount to be eaten orally, while 50% (in the form of rumen content from cows in A) was filled directly into the rumen. Cows in C received 150% of normal amounts, while cows in D only received 50% to eat. Transfer of rumen content from cow A to cow B was made 3 times a day (07.00, 10.00 and 13.00 h) and at 16.00 h rumen content was extracted from the rumen from cow A without passing it to cow B.

Behavioural registrations

The cows were videotaped both under normal conditions (24 hours) two days before the onset of the treatments, and on the third day of the experiment, in all four treatments. From these videotapes the following behaviours were analysed according to their duration and frequency: *eating* – when the cow was obtaining feed from the trough or from the floor in her mouth or when chewing or swallowing feed; *ruminating* – chewing or regurgitating already swallowed feed; *behaviours related to feed-searching* – nosing or licking the empty feed-trough, or on the floor, or fittings close of the trough; *licking salt* – licking on the saltlick; *stereotypy* – when the cow consistently rolled its tongue outside or inside her mouth or chewed on a bar in an unvaried, repeated and stereotyped manner; *total standing* – when the cow was standing up on all four legs irrespective of any other activities, *total lying* – when the cow was lying irrespective of other activities; *other active* – included all other behaviours except eating, ruminating, behaviours related to feed-searching, and stereotypy.

Blood sampling and analyses (Paper II)

Blood samples were collected on the third and last experimental day from cows in treatments A and B. The day before the blood collection started, the cows were fitted with permanent jugular catheters that were brought up to the withers, from where the samples could be taken with minimum disturbance of the animal. Samples were taken around milking and feeding during the morning and afternoon. In this way we obtained 12+12 samples from each cow. The samples were immediately placed on ice and centrifuged for 20 min, after which the plasma was frozen and stored at –80°C until assay.

All blood samples were radio immunoassayed for oxytocin according to Stock & Uvnäs-Moberg (1988). The concentrations of cortisol in the blood samples were analysed with radio immunoassay technique using a commercial kit (Coat-a-count, Diagnostic Products Corporation, USA). Only blood samples from year two were analysed for cortisol concentration.

Statistical analyses

Statistical analyses and methods used are described in detail in each separate paper. The analyses of behavioural data were performed using MINITAB (1996) and SYSTAT (1998), while analyses of physiological data were conducted using the Mixed Procedure of SAS (1995) and MINITAB (1996).

Papers III and IV

Animals

Twelve non-lactating, pregnant dairy cows of the Swedish Red and White Cattle Breed were used in an experiment with gradually increasing Fixed Ratio (FR) levels (Paper III) and in an extinction test (Paper IV). All cows were experimentally naive when starting the experiment with FR schedules. The extinction test was carried out after the FR test.

In a side preference test (Paper IV) another seven non-lactating dairy cows were used and four of these cows also participated in a concurrent schedules test (Paper IV). When starting the side preference test all cows were experimentally naive, but in the concurrent schedules test the cows were well adapted to the experimental equipment since this test was carried out after the side preference test.

Feeding

During the experimental periods all cows were fed for maintenance and for the growth of foetus according to Swedish standard recommendations of dry cows (Spörndly, 1999). All experimental cows were fed with standard grass/red clover silage (~4 kg dry matter per cow and day) in the morning and in the afternoon, and after the experimental session each day the cows were provided with straw (~1 kg per cow and day). The standard silage used at Kungsängen Research farm is chopped and a mixture of timothy (*Phleum pratense*), meadow fescue (*Festuca pratensis*) and red clover (*Trifolium pratense*). On experimental days the cows were feed deprivated since 05.30 h in the morning. They had free access to water except during the experimental sessions.

Experimental equipment

The experimental equipment used was an appropriate modification of a "Skinner box" with solid walls, into which the cow was led manually on a halter. In the front of the box there were two square metallic nose plates operating two metallic nets covering two buckets containing the feed. The cow could see and smell, but not obtain the feed in the bucket, due to the covering nets. A minimum response force of 1.5 N was required to press the nose plate, and when pressing the plate the net was retracted and the feed could be obtained. The nose plates were inoperative during reward delivery. The nets and the changing of buckets were pneumatically operated.

Experimental feeds

Using the "Skinner box" three different feeds were evaluated as sole silages in a test with fixed ratio schedules: red clover (*Trifolium pratense)*, white clover (*Trifolium repens*) and perennial ryegrass (*Lolium perenne*). In the subsequent extinction test, the same red clover and the same white clover were used.

In a side preference test hay or standard silage was used, while in a test with concurrent schedules, perennial ryegrass or lucerne *(Medicago sativa)* as sole silages were used.

All silages were used in full length, they were stored as plastic-covered bales and they were well preserved and had good aerobic stability. Every reward the cows obtained in these tests consisted of 40 grams of the experimental feed.

Training and experiments

By shaping, the cows were trained to operate the apparatus, i.e. to press one plate, on fixed ratio schedules starting with FR 1 up to FR 20. During this training period the reinforcement consisted of either hay or standard silage.

In the experiment with gradually increasing FR levels (Paper III), one nose plate was used. The experiment started on FR 20 and the workload for the same experimental feed was increased with 20 presses each day until the cow ceased pressing or reached the upper limit FR 180. This upper limit was set for practical reasons, since the time for the experiment was restricted by the time the cows were dried-off. Registrations made during each session were number of reinforcers, number of responses, and number of extra responses, i.e. responses that were made beyond the required responses.

Both in this test, and in the subsequent extinction test, only one feed was tested per session, and the reinforcement consisted of 40 grams of the feed. Each experimental session lasted for 20 minutes and was always conducted at the same time in the morning for the individual cow.

The test with FR schedules was followed by a training session on FR 20 schedule in order to recover normal response patterns before the subsequent extinction test. The extinction test (Paper IV) was accomplished during three consecutive days with the same feed on a FR 10 schedule using one nose plate. When the cow entered the box the net was opened so she could obtain the first "reward" of feed without pressing the nose plate. Afterwards she could obtain another four reinforcers by pressing the plate on a FR 10 level. After these five reinforcers the pressing resulted in empty buckets until she either ceased responding or paused for 10 minutes. This was our limit for interrupting the test session as leaving the cow in the test box for long periods after cessation of responding might have negative consequences on conditioning. Only one feed was tested per session and every reinforcer the cows obtained consisted of 40 grams. Numbers of empty buckets, numbers of responses and numbers of extra responses (i.e. responses that were made beyond the required responses) during each extinction session were recorded.

In the side preference test (Paper IV), the cows were working with two nose plates; initially only the right plate was operative, but in the next session only the left plate was operative. After this, the side preference tests started with concurrent schedules (FR 1 on both sides), allowing the cow to switch back and forth at any time. The same feed was used both to the right and to the left, although some individual cows got hay and some got silage. The test was accomplished during 10-14 days per cow, with one session each day, and each session lasting for 20 minutes. According to the procedure used by Matthews & Temple (1979), a change-over delay of 5 seconds was arranged after each change from one response plate to the other. Frequencies of responses on the left nose plate and right nose plate, respectively, were recorded. We also noted which nose plate each cow preferred to start responding on. For 4 cows the schedules were altered to intermittent reinforcement during some of the test sessions in order to investigate the impact on subsequent sessions.

In the test with concurrent schedules (Paper IV) the cows were presented to ryegrass on the left and lucerne on the right in the "Skinner box" on a FR schedule (FR 20, 25, 30, 45, 65 and 80). The test was accomplished with one session per day, lasting for 20 minutes. Even in this test, a change-over delay of 5 seconds was arranged after every change from one response plate to the other according to the Matthews and Temple (1979) procedure. Numbers of rewards with ryegrass and lucerne, respectively, were recorded and slopes of best-fit straight lines were calculated.

Statistical analyses

Statistical analyses and methods used are described in detail in each separate paper. All analyses of correlation in Papers III and IV were performed using MINITAB (1996). Differences in the extinction test between the two feeds in numbers of empty buckets, number of responses, and numbers of extra responses (Paper IV) were calculated using SYSTAT (1998). The procedure Mixed in the SAS (1997) package was used to analyse differences between FRs, cows and feeds (Paper III).

Results

Papers I and II

Even though the experiments were accomplished during two consecutive years, the two experimental periods were analysed separately, since the results in duration of rumination in treatment A differed significantly between years. However, a comparison between treatments A and B clearly showed the same response pattern in both years, even though the magnitude of the figures for duration of rumination differed between years.

Effects of low rumen content and long eating time

Since the cows in this treatment (A) were provided the mixture given in the experiment *ad libitum*, they spent long time eating and had high numbers of eating bouts. As a consequence of the long and frequent eating, they spent rather short time with behaviours related to feed-searching and showed a low level of stereotypies. In spite of the long duration of eating, the cows in this treatment spent rather short time ruminating, due to the extraction of rumen content. The A cows also spent more time licking the salt lick than the cows in B.

Compared with a normal day, the A cows spent more time eating and standing on the experimental day, while they spent less time with behaviours related to feed-searching, stereotypies and rumination on the experimental day. The A cows had more bouts of eating and licking salt on the experimental day, but the number of bouts of ruminating was lower on an experimental day than on a normal day.

The cows with long eating time (treatment A) had a larger oxytocin release during the afternoons compared with the cows in B, since the response area under the concentration/time curve for the A cows was larger in the afternoons in both years. One hour after the rumen content transfer from the A cow to the B cow, the oxytocin levels were lower in the treatment with low level of rumen content (treatment A) than in cows with filled rumen (treatment B).

The cortisol concentration was lower during the morning sampling period in treatment A compared with treatment B, and the level was also lower in A before milking in the afternoon than after the milking.

Effects of high rumen content and short eating time

The cows in this treatment (B) had the shortest eating times and lowest numbers of eating bouts together with the cows in treatment D. Consequently, they spent rather long time with behaviours related to feed-searching and with stereotypies and the frequencies of these two behaviours were also higher in B than in A. The cows in B spent longer time ruminating and had more ruminating bouts compared with the cows in A.

Compared with a normal day, the cows in B spent less time with eating on the experimental day, but more time with rumination and behaviours related to feed-searching. The frequency of rumination as well as of behaviours related to feed-searching were higher on an experimental day than on a normal day.

The cows with short duration of eating (treatment B) showed lower levels of oxytocin concentration in the afternoon than the cows with long duration of eating (A). This treatment (B) also resulted in lower figures of oxytocin concentration before feeding than after feeding in the afternoon. The rumen content transfer that was made in the morning gave higher oxytocin levels in the cows with filled rumen (B) compared with the cows with low level of rumen content (A). Even when the oxytocin concentration was compared within treatment B, the level was higher after the rumen content transfer had been completed than just before it had commenced.

The cortisol concentration in the morning sampling period was higher in this treatment (B) with short eating times compared with the cows with long eating time (A). The B cows also seemed to have a higher cortisol level at the start of blood sampling in the morning, while the cortisol level was lower just before the milking in the afternoon compared with after the milking.

Effects of high rumen content and long eating time

The cows in this treatment (C) spent long time eating and ruminating, while they spent considerably short time with behaviours related to feed-searching and stereotypies. Even the frequencies of stereotypies and behaviours related to feed-searching were low in this treatment.

Effects of low rumen content and short eating time

The cows in D had the highest figures of stereotypies and behaviours related to feed-searching compared with all the other treatments.

Papers III and IV

Differences between feeds

In the test with gradually increasing fixed ratio (FR) schedule (Paper III) there were no differences between the three evaluated feeds (red clover, white clover and ryegrass silage) in numbers of responses, in numbers of extra responses or in the slope of the best-fit straight lines for the feeds. However, there was a significant correlation between the numbers of extra responses and slope of the best-fit straight line for ryegrass.

In the extinction test (Paper IV) there were no significant differences between the two feeds in numbers of empty buckets, in numbers of responses or in numbers of extra responses. In the same test there was, however, a significant correlation between numbers of empty buckets and numbers of extra responses in both red and white clover.

In the concurrent schedules test, the slopes of the best-fit straight lines for ryegrass were shallower than those for lucerne.

Differences and similarities between individual cows

In the test with gradually increasing fixed ratio (FR) schedule (Paper III), there was a significant difference between individual cows and a significant interaction between cow and FR. The same test showed that there was a significant negative correlation between extra responses for red clover and low milk production.

The extinction test showed that in numbers of empty buckets, seven of the cows that were presented to red clover first in the test had higher figures for red clover.

In numbers of extra responses six cows that got red clover first in the test also responded more for red clover.

In the side preference test, five of the cows made their first response on the right plate in their first session when both plates were equally operative during the whole session, while the two remaining cows started with the left plate. Three of the cows started responding to the right in most of the sessions, while four cows started responding to the left in most of the sessions. Some of the individual cows showed a relative consistency in side preference, while others were more flexible. The results from these tests show that a/ cows have individual preference for one specific side, b/ it is possible to alter this preference by training, and c/ this training effect is short-lasting after which the cow may return to its preferred side.

General discussion

Identifying a behavioural need for feeding

Can feeding behaviour be considered a behavioural need in cattle? With behavioural variables (Papers I and II), physiological parameters (Paper II) and the operant conditioning technique (Papers III and IV), we have tried to reveal the answer to this question.

When using the term "need", I agree with Hughes & Duncan's (1988) opinion that there will be degrees of need with a continuum running from "no need" to "critically important need". When trying to assess the needs of animals, Jensen & Toates (1993) have argued for a holistic approach to the motivational control of behaviour, meaning that the total behavioural system is analysed. Jensen & Toates (1993) also state that preventing an animal from carrying out a certain behaviour in a given situation might cause signs of suffering.

In Paper I we have used stereotyped oral behaviours, together with behaviours related to feed-searching, as markers for frustrated feeding motivation. The latter behavioural category has been defined as non-stereotyped nosing and licking in or around the feeding site or trough. Stereotypy level has previously been found to be negatively correlated with duration of feeding (Redbo, 1990) and restricted feed amounts have been found to significantly increase the stereotypy levels in dairy cows (Redbo et al., 1996). The relation between restricted feed amounts and stereotypies has also been proposed to be an effect of the thwarting of feeding and foraging behaviours occurring in tetherstalls for cattle (Redbo, 1992a). It has also been shown that the development and performance of stereotypies in cattle is strongly related to feeding motivation (Redbo et al., 1996) and to feeding duration (Redbo & Nordblad, 1997).

These tendencies were also seen in Paper I, since the cows in treatments A and C (with long eating times) spent approximately the same time eating and had the lowest levels of stereotypies compared with the cows in treatments B and D (with short eating times). Interestingly, the behavioural observations in Paper II showed that cows with long duration of feeding behaviours (treatments A and C) combined with short duration of stereotypies had higher levels of oxytocin concentrations in the blood plasma compared with cows with short duration of eating and filled rumen (treatment B). It has been shown in earlier studies that oxytocin is released in response to feeding in dairy cows (Svennersten et al., 1995) and is also released by the presence of food in the mouth, oesophagus or stomach in sows and dogs (Uvnäs-Moberg et al., 1985). It has also been demonstrated in rats that oxytocin has behavioural effects, e.g. to exert anti-stress-like effects characterised by calmness (Uvnäs-Moberg et al., 1994; Uvnäs-Moberg, 1998). The time spent feeding found in treatments A and C (Paper I) was almost on the level found for freely grazing cattle (Hafez & Bouissou, 1975), and might be sufficiently long to allow negative feed-back on motivation for feeding.

In Paper I, the cows in treatment D had a short duration of eating and low level of rumen fill, and they also showed the highest levels of stereotypies as well as of behaviours related to feed-searching. Thus, this treatment probably constitutes the worst possible condition for the cows among the four treatments used.

However, we wanted to examine not only how feeding duration would influence behavioural variables possibly reflecting frustrated feeding motivation, but also how rumen fill influences the feeding motivation. Thus, to be able to correctly interpret the effect of a long or a short eating duration on the wellbeing of the cow, the effect of oral feed intake must be separated from the effect of rumen load. By using rumen fistulated cows we could achieve this separation.

The results in Paper I show that even though the rumen content of the A cows was extracted, these cows spent approximately the same time eating as the cows in treatment C, indicating that rumen fill is not the only factor that governs feed intake in cattle. The results in Papers I and II indicate that eating, chewing and swallowing of the feed *per se*, induce an oxytocin release in cattle irrespective of rumen load, as cows with long duration of eating had higher levels of oxytocin in the blood plasma, even if they had low rumen fill, compared with cows with filled rumen. It has been suggested (Johansson, 2000) that increased oxytocin response might be linked to the act of feed intake itself, and that sensory nerves within the oral cavity could be activated to induce this effect. However, satiety cannot be induced solely by food passing the mouth, which has been demonstrated by sham-feeding rats, dogs and monkeys (Kraly et al., 1978). Rats that were offered solid or liquid food in a sham-feeding situation continued to eat for several hours. After an enormous meal they took a short break, and soon after, they continued the sham-feeding or sham-drinking. This phenomenon has also been shown in dairy cows by Baile & Della-Fera (1981). Cows in which the boli were removed from the rumen continued to eat for much longer times and consumed larger quantities of feed than during normal feeding.

Throughout the years, several studies that involved manipulation of rumen load have been carried out to determine the voluntary feed intake and to increase the knowledge of appetite regulation in ruminants. Carr & Jacobson (1967) added polyethylene cubes or water to the rumen, and removed ingesta from the rumen in one study. They concluded that bulk or water added to the rumen was not an important factor determining the dry matter consumed, but that removal of ingesta increased the voluntary intake. Campling (1970) removed swallowed hay as it entered the reticulo-rumen, which resulted in longer eating time than normal. This was also found in Papers I and II; the cows in treatment A (from which rumen content was extracted) showed significantly higher levels of both duration and frequency of eating on the experimental day compared with a normal day. In a study with rumen fistulated sheep (Welton & Baumgardt, 1970), the voluntary intake was assessed by diets diluted with different percentages of sawdust. Egan (1972) introduced an impermeable rubber bladder into the reticulo-rumen in sheep to examine the relationship between the intake and the amount of digesta in the reticulo-rumen. When the bladder was expanded with 3 litres of water, the depression in intake was immediate, and the conclusion was that the sheep's intake was influenced by changes that occur when the digesta load was altered. These studies, together with more ordinary studies on voluntary intake in cattle, provide us with interesting knowledge, even though later studies (see e.g. Le Magnen, 1985; Forbes, 1995) have shown that it is more complicated to explain appetite regulation than just to exclude feed.

When a prolonged inability to perform a certain behaviour, e.g. feeding behaviour, results in stereotypies, that behaviour must have extremely strong motivation (Friend, 1989). Even if there has been a selection for traits specifically adaptive in captivity, behavioural characteristics needed in the wild have not been lost (Tennessen, 1989). According to Dawkins (1990), captive animals often suffer in situations in which they are prevented from doing something that they are highly motivated to do. In Paper I, the cows in treatment B, with short eating time and filled rumen, showed relatively high levels of stereotypies and behaviours related to feed-searching, compared with the treatments with long feeding durations, notwithstanding the high rumen load. This was interpreted as a consequence of frustrated feeding motivation. But, do animals need to perform specific behaviours even if their physiological needs are fulfilled? And, if this is the case, how is it possible to measure and quantify this need? According to Friend (1989) one technique to estimate the need to perform a particular behaviour is to observe the animal under "natural" conditions. We tried to achieve this in Paper I, since some of the behaviours were analysed during a normal day which then was compared with an experimental day. The results indicate that motivation for feeding was persistent in treatments with short eating duration, irrespective of rumen load.

It has been demonstrated that cortisol is released in response to stress in cattle (e.g. Adeyemo & Heath, 1982; Echternkamp, 1984; Friend et al., 1985; Lefebvre et al., 1990; Redbo, 1993). It has also been shown that glucocorticoids might be released due to frustration in goats (Carbonaro et al., 1992) and as a consequence of feed restriction or feed deprivation in dairy cows (Samuelsson et al., 1996). In Paper II, we saw this relation between feeding behaviour and cortisol; the cows in treatment B, with short duration of eating, showed higher levels of cortisol in the morning, probably due to hunger, as they had no access to feed during the night. From experiments with rats, it is known that starvation may increase plasma levels of corticosterone (Ventura, 1982). The rumen content transfer that was made in the afternoon (Paper I), probably also affected the levels of cortisol; the cows in treatment A, from which the digesta was exerted, showed higher levels of cortisol soon after the rumen content removal was completed.

Another interesting factor about oxytocin and cortisol is that they might interact, and that both feeding and milking may influence their release (Gorewit et al., 1992; Wagner & Oxenreider, 1972). In Paper II we found an increase in cortisol release in both treatments in the afternoon when comparing levels before, and after milking. This is in good accordance with a study of dairy cows (Johansson et al., 1999) where it is suggested that the level of cortisol in cows fed during milking might be suppressed by high oxytocin levels. In a study with rats (Petersson et al., 1999), it has been demonstrated that after oxytocin administration, an immediate rise of cortisol occurs, followed by a sustained decrease of cortisol. In Paper II, there was an increase in both treatments in cortisol concentrations after milking and feeding in the morning, and this was probably caused by milking.

To measure feeding motivation

Ethologists and psychologists have adopted a variety of approaches to the problem of how to measure an animal's motivation to perform a behaviour (Dawkins, 1990). One method of identifying possible behavioural needs and determining their relative strength is to use operant conditioning. When using these procedures it is possible to study the linkage between cause and consequences of a learned behaviour, and with behavioural measures we can assess and interpret the behaviour. According to Kilgour et al. (1991), operant conditioning has been used in two major ways; to study the animal's perceptual abilities and to assess their needs, and/or preferences.

When we started up our experiments with operant conditioning we wanted to investigate problems and possibilities with the method for measuring feed preferences (Papers III and IV). We also wanted to investigate if extinction in an operant conditioning situation could be used to measure a cow's individual motivation to obtain a specific feed resource (Paper IV).

When using operant conditioning techniques, and relating quantity of reinforcement to a fixed ratio level in a best-fit straight line, as was done in Paper III, the difference between feeds should have been seen in differences in the slope of the best-fit straight line. A difference in slope would reflect a difference in the cow's motivational strength to work for the current feed. In the extinction test (Paper

IV) the difference in motivational strength for the different feeds also should have been seen in the results. However, such a difference, due to different motivational strength, could not be found neither in the fixed ratio test (Paper III) nor in the extinction test (Paper IV), though I must admit that we had expected a difference between the evaluated feeds. The lack of difference was obviously an effect of the large individual differences among cows that was found, and maybe also of far too small differences between the current feeds. It is known that farm animals are capable of choosing a proper diet according to their needs, as long as the feeds offered are clearly different by taste or colour and the animals have the opportunity to learn the differences between the feeds (Forbes & Kyriazakis, 1995). In fact, this was also seen in Paper III and in the concurrent schedules test (Paper IV), as the feeds were differently ranked by the individual cows, showing that the cows were able to differentiate between the feeds. From the feed analyses we know that there was a difference in the structure of the feeds and different levels of water soluble carbohydrates in the feeds, which possibly could explain this difference in ranking.

In the side preference test in Paper IV, we found clear individual preferences for one specific side, meaning that cows have preference for either right or left side when they have the opportunity to choose between two equally strong reinforcers. This phenomenon might be new knowledge to some, but not all researchers, and it is certainly something that is important to consider when planning and accomplishing even more traditional experiments of feed preference, in which the relative amounts of voluntary intake are used to evaluate different feeds. As our results indicate, such studies might be confounded by the cow's preference for either side. If this information is overlooked, we can never be sure to properly interpret the results due to uncertainty which factors have influenced the cow, and thus, what governs her choice. In an experiment with cows on concurrent schedules in an operant conditioning situation, Matthews and Temple (1979) report on the same kind of position bias when a single kind of feed was presented at either alternative. They also state that the position bias might change, even if it did not change markedly in their experiment. In fact, this was what happened in one of our cows in Paper IV. She abruptly altered preference side after three sessions from a right preference to the left side, without any corresponding changes in reinforcement schedules.

An additional result in our side preference test (Paper IV) was that the preference for either side can be altered by training, and furthermore, that this training effect might be short-lasting, meaning that the cow may return to its preferred side. In accordance with Matthews and Temple (1979), we suggest that this position bias found in Paper IV must be assessed and evaluated throughout the experiment, as it might change and thus could not be regarded as constant. McAdie et al. (1996), also report side biases in the responses; hens presented to different kinds of recorded sounds showed a tendency to respond more to the left than to the right, independent of the reinforcer. The authors suggest this bias to be considered as an inherent bias. In the side preference test in Paper IV, the results also indicate that some carry-over effects were involved in the response pattern, since some of the cows preferred to start working on the same side as they were previously trained. This might be due to the fact that the study was relatively short-lasting. Raslear et al. (1988) state that generation of demand curves in rats typically requires a relatively long period of time, sometimes as long as 40 days.

The results in Paper III further support the suggestion that cows should be considered as individuals rather than as members of a group represented by mean values calculated from pooled data. Examples of this were seen in Paper III; some individuals were more motivated to work for feed in general, while others were less motivated to work for any feed. When studying preferences for different feeds it seems to be more fruitful to interpret the results on an individual basis, i.e. each cow should be studied individually and properly mapped out, as we found differences among cows to be larger than differences within cows both in Papers III and IV. Maybe this difference reflects a cow's different behavioural traits. In a study with pigs, Ladewig & Matthews (1996) found large individual differences in the absolute demand for straw, and the authors state that individual variation constitutes somewhat of a problem in most behavioural research.

Kilgour et al. (1991) considers that preference measures should not be taken as sole indicators of an animal's need or welfare requirements, but that they may become useful when combined with other measures. In Paper III, in which we used operant conditioning to measure the cow's motivation to obtain a specific roughage, we found that individual cows in general were differently motivated to work for feed. These results indicate that the behavioural need for feeding might be differently strong between individual cows.

However, determining a specific behavioural need, such as for the performance of a specific action pattern, is often difficult (Friend, 1989), but from what is stated above, together with former results reported in literature, I venture to say that feeding behaviour is a behavioural need in cattle.

Conclusions

- Oral manipulation of feed is a behavioural need in cattle irrespective of rumen load. A low duration of feeding behaviours combined with a low rumen load seriously impairs the welfare of cattle. The results imply that there are physiological mechanisms, possibly in form of oxytocin, involved in the motivation of feeding.

- Operant conditioning may be a fruitful method to measure and quantify feed preference of dairy cows, but it is important to make test series long enough and preferably in a closed environment. Even then the results only reflect the preference of the individual animal. It is also important to make a complete mapping of the side preference of all the specific individuals included in the experiment.

Implications

Based on the experience of the present work, the most interesting issues for further research could be:

- Additional studies on the connection between appetite regulation and physiological parameters, e.g. oxytocin.

- To improve the Skinner box and the operant conditioning technique as a method of measuring feed preference in cattle.

Practical recommendation that could be given from these studies:

- Arrange a sufficiently long time for dairy cows, as well as other cattle, to eat and manipulate with feed. This means that they should have constant access to roughage.

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