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THE CONCEPT OF VOLUNTARY FEED INTAKE AND SATISFACTION IN RUMINANTS: A REVIEW

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Abstract

This review dealt with the concept of the feed intake of cattle, sheep and goats. Because ruminants, especially small ruminants, are normally fed ad libitum, voluntary feed intake is crucial in the feeding tactics and strategies aimed at optimal production. The review highlighted the common factors that influence feeding intake. The voluntary feed intake of ruminants varies as a function of the characteristics of the feed, the animal and its environment. The control mechanisms for the feed intake of farm animals generally can be envisaged as operating at three levels, namely at metabolic level, the concentration of nutrients and metabolites or hormone secretions. In ruminants, the control of intake is at the level of the digestive system and the characteristics of the food. The quantity of digesta in the digestive system may determine whether or not the animal ingests more food. The activities involved in feeding are complex. Such activities include: the search for food, the recognition of food and movement towards it, the sensory appraisal of feed and the initiation of eating and digestion. In the alimentary tract, the feed consumed is digested and the nutrients are then absorbed and metabolized. All these processes can influence feed intake. The characteristics of the feed, animal factor, size of the animal, pregnancy, lactation, environmental factors, climate, day length, water consumption and ill-health are the major factors affecting feed intake and satisfaction in ruminants.

Key words: Voluntary feed intake, Ruminants, Satisfaction

Introduction

The consumption of feed is the first step in the process which converts feed into valuable products like milk and meat for human consumption. The amount of feed ruminants voluntarily consume profoundly influences the efficiency of this conversion process. The productivity of ruminants depends on their ability to consume and extract usable energy from available feeds. Ruminants are known for their ability to breakdown fibrous materials of plant origin to meet their nutritional requirements for maintenance, growth, foetal development and other production functions. According Baumont *et al.* (2000), intake is the maximum quantity of feed that can be eaten by an animal when this is supplied *ad libitum* as the sole feed. Illius *et al*. (1996) viewed intake as a "psychological" phenomenon, involving the integration of many signals and reflects the flexibility of a biological system evolved to cope with variability in food supply, composition and animal states. So, plant properties, associated, for example, to the presence of toxins, the taste or smell, are important parameters impacting diet selection and the ingestive behavior of grazing ruminants and so the intake's level (Provenza *et al*., 2003b). Several theories were developed to explain the factors that influence feed intake and satisfaction in farm animals. This paper reviews some of these theories/ or findings with particular reference to ruminant animals.

Feeding behaviour and the control of intake

Intake is influenced primarily by hunger, which is distressing, and by satiety, which is generally pleasurable. Forbes (1995) postulated that "ruminants eat that amount of feed which leaves them with the most comfortable feelings". The regulation of feed intake and dietary choices combines the short-term control of feeding behaviour related to the body homeostatic regulation and long-term control that depends on nutritional requirements and body reserves (Faverdin *et al.*, 1995). Feed factors act mainly on the short-term control. Ruminants fed forages *ad libitum* eat for 5 to 10 hours per day and spend a similar time ruminating. During a main meal, the rate of intake is highest at the beginning and then decreases continuously as satiation proceeds until satiety. Moseley and Antuna-Manendez. (1989) reported that the rate of intake, especially at the beginning of the meal, seems to be a key factor for understanding variations in voluntary intake between forages.

Behavioural bases for the varied diets of ruminants

The origin of food preference

Learning about foods involves neurological, morphological and physiological changes (Distel and Provenza, 1991). The mechanisms used by non-ruminants for selecting a diet are often similar to those used by ruminants (Provenza, 1995). At conception, nature (natural selection) provides each individual with a set of genetic instructions for its morphological and physiological development. To facilitate survival, nature has constructed genotype in ways that enable nurture (experience) to structure individual. The brain determines the structure of the experience, but experience also determines the structure of the brain. It was reported by Baumont *et al*. (2000) that at the beginning of the meal, motivation to eat forage expresses sensory and nutritive properties of the feed that were learned from previous experience.

Taste – Feedback interaction

The dynamic interplay between nature and nurture is illustrated by the taste-feedback interactions associated with food preference. It involves interaction between taste and post-ingestion feedback, which are determined by an animal's physiological condition and a plant's chemical characteristics (Provenza, 1996). Of course, taste (as well as smell and sight) allows animals to discriminate among feeds and is a source of hedonic sensations. But other factors, especially post-ingestion feedback, calibrate a food taste with its homeostatic utility. These biochemical mechanisms identify foods adequate in nutrients, thereby increasing an animal's preference. Taste-feedback interaction occurs automatically, in the absence of any cognitive association or memory of the feedback event, every time food is eaten. Thus, after food ingestion, preference changes even if an animal is deeply anesthetized (Provenza *et al*., 1994), tranquilized (Forthman, 1984) or when its electro-cortical activity is depressed (Buresova and Bures, 1973).

The Role of experience in taste-feedback interactions

Animals acquire preferences for familiar foods and they are reluctant to eat novel foods or familiar foods whose flavours have changed (Provenza, 1995). Animals search for preferred foods in unfamiliar environments and show the greatest decreases in intake when they are offered novel feeds in novel environments (Burrit and Provenza, 1996). Accordingly, familiarity controls preference. When animals become ill after eating a meal of familiar and novel feeds, they avoid their novel feeds. Novelty can override temporal contiguity when illness develops after feeds in sequence. For instance, lambs typically avoid eating feeds in succession unless one of the feeds is novel in which case they avoid the novel feed regardless of sequence (Provenza, 1993).

Sensory specific responses

Sensory-specific satiety is a term used to refer to the decrease in preference for the taste of feed as it is consumed (Roll, 1986). The controversy over the relative importance of sensory or feedback specific responses is misguided because both are always involved (Provenza, 1995). Feedback begins before eating as the sights, sounds and odours associated with foods cause the release of saliva and other digestive enzymes, gastrointestinal and pancreatic hormones and the neurotransmitters involved in eating. Taste and feedback (presence and absence) are inevitably in interplay any time feed is taken into the mouth. The level of intake can be conditioned by other characteristics of the forage, such as flavor (taste and smell), appearance, texture and by the post-ingestive feedback occurring after its intake, i.e. “if forage tastes good, animals tend to eat it more” (Baumont, 1996). The flavor feedback interaction depends directly on the chemical characteristics of feed, animal nutritional status and animal past or recent experiences.

Nutrient-specific responses

The nutrient concentrations of forages are factors of interest in the regulation of feed intake. Animals prefer feeds or combinations of feeds that contain a variety of nutrients in appropriate proportions, presumably because they are the most satiating. The idea of nutrient-specific satiety is based on the premise that preference depends on an animal’s physiological condition relative to a feed’s chemical characteristics (Provenza, 1996). Once an animal’s requirement for a particular nutrient is met, preference declines for feeds with high concentrations of that nutrient. For instance, lambs fed diet high in energy subsequently prefer feed lower in energy and higher in protein; those fed diet high in protein subsequently prefer feed high in energy (Wang and Provenza, 1996). This hypothesis is consistent with the notion that the ratio of protein to energy is important in the feed preferences of ruminants (Eggan, 1977). The energy protein balance of the diet can therefore influence the level of intake and the diet selection. According to Kyriazakis *et al*. (1993), lambs that can select between pairs of diets, varying between 7.8 and 23.5% of crude protein, present a maximal level of intake with the diets containing between 14.1 and 17.2% of crude proteins. According to these observations, a judicious forage supplementation could contribute to improve diets nutritional balance and so, to increase the total voluntary intake (Vazquez *et al*., 2000).On a "requirement theory" basis, the animal eats in order to maximize its production potential under some constraints such as its gut volume and diets quality (Yearsley *et al.*, 2001). According to this theory, intake regulation would be based on the meeting of energy needs (Kyriazakis, 2003). In this way, Faverdin *et al.* (2007) has demonstrated that intake is positively linked to body weight and to the level of the production of dairy cows and so linked to the animal requirements. According to Provenza (1995), ruminants, like other mammals, develop preferences for feeds that are richer in energy. Animals increase intake to meet their nutritional needs. Deficits or imbalances of amino acids cause decreases in intake. Feed intake in cattle, sheep and goats is reduced due to phosphorus deficiency in diet and the reduction in feed intake depends on the severity of the deficiency (Ternouth, 1991). Other nutrients whose deficiencies are liable to restrict feed intake in ruminants are sulphur, sodium and cobalt (Mc Donald *et al.*, 1995).

Toxin-specific responses

Toxin causes a decrease in preference for food, but toxins do not necessarily prevent ruminants from eating a food, especially if the feed contains needed nutrients (Wang and Provenza, 1996b). Different toxins often differ in their effects on herbivours and herbivours have assorted physiological mechanisms to counter the effects of various toxins (Mc Arthur *et al.*, 1991). The degree to which a feed is avoided following a meal depends on the dose of the toxin (Ralphs and Cheney, 1993).

Physical constraints on voluntary feed intake by ruminants

As a result of diverse supporting evidence, the theory that physical distention in the gastro-intestinal tract limits voluntary dry matter intake has been widely accepted (Forbes, 1995). Voluntary dry matter intake of low digestibility feeds is thought to be limited by physical distention in the gastro-intestinal tract, which presumably diminishes as digestibility increases. The reticulorumen is generally regarded as the site in the gastro-intestinal tract at which distention limits intake with high-fill diets (Baile and Forbes, 1974).

The regulation of intake appears mediated by different signals under the form of metabolites and hormones emitted by the central nervous system and the peripheral organs like liver, pancreas intestinal tracts and that can be regarded as mediators of appetite (Rhind *et al.*, 2002). The role of leptin (hormone secreted by fatty cells), of cholocystokinine (hormone secreted by the intestinal mucous membrane) and of insulin in the control of satiety in ruminants has been widely documented (Forbes, 2003). In the same way, during the digestion process, the rumen environment (pH and osmolarity) can also explain the variation of voluntary intake (Faverdin, 1999).

The hepatic oxidation hypothesis

The hypothesis that feed intake is regulated by the oxidation of fuel in the liver has evolved as advances have been made by several groups. The idea that the liver is involved in the regulation of food intake was introduced by Russell (1963), who proposed that the feeding behaviour of dogs was influenced by glucoreceptors in the liver following Meyer's suggestion that feed intake is regulated by changes in blood glucose concentration (Meyer, 1953).

The propionate regulation of feed intake

Propionate is the primary glucose precursor for ruminants but can also be oxidized and stimulate the oxidation of other fuels (Allen *et al*., 2005). Besides increasing the amount of Volatile Fatty Acid (VFA) produced, increasing ruminal starch fermentation also increases propionate infusions (Allen, 2000). Intake depression by propionate is greater than the other major fermentation acids (acetate and butyrate) when fused into the vein of sheep and the infusion of propionate into the mesenteric vein of steers reduced feed intake, whereas acetate infused at similar rates did not (Elliot *et al.*,1985). The liver is involved in the regulation of feed intake by propionate because the depression of feed intake by propionate infusion in sheep was eliminated by severing the nerves connecting the liver to the brain (Anil and Forbes, 1988). Of fuels metabolized by ruminant liver, propionate is likely a primary signal to terminate meals because its flux to the liver increases greatly during meals (Benson *et al*., 2002). Ruminant liver has high activity propionyl COA systhetase (Ricks and Cook, 1987). As a result, propionate is extensively metabolized by ruminant liver, but there is little net metabolism of acetate (Reynolds, 1995), thus explaining differences in feed intake depression by the infusion of propionate compared to acetate. These observations are consistent with the hepatic oxidation hypothesis.

The Effects of Insulin and Glucagon on feed intake

The most important hormonal regulators of both lipid and carbohydrate metabolism are insulin and glucagons. Despite the fact that adipose tissue in early lactation cows is relatively insensitive to insulin, a low dose of insulin three days postpartum decreased plasma non-esterified fatty acids (NEFA) and triglyceride concentrations and increased feed intake of dairy cows (Hayirli *et al.*, 2002). However, higher doses of insulin caused hypoglycemia fail to decrease NEFA concentration and did not increase feed intake. Administration of exogenous glucagons stimulates insulin secretion and offers the advantage of preventing hypoglycemia because glucagons directly stimulate gluconeogenesis. The subcutaneous administration of glucagons decreased plasma NEFA concentration and tended to increase feed intake over control after 7 days of treatment (Nafikov *et al*., 2006).

Summary of the factors affecting feed intake and satisfaction in ruminant nutrition

The characteristics of the feed

The quality of feed

The quality of the feed depends mainly on its energy and protein content and to a lesser degree on the type of feed available and the quantity consumed. Animals eat more feed if the feed already eaten passes quickly through the digestive system. Highly fibrous feeds spend a long time in the digestive components to be extracted. The longer it takes the feed in the digestive tract the less the intake. There is a positive relationship between the digestibility of feed and their intake. Intake is closely related to the rate of the digestion of diets and digestibility, i.e. feeds that are digested rapidly, and are also of high digestibility, promote high intakes. The faster the rate of digestion the more rapid is the digestive tract emptied and the more space is made available for the next meal. Forage dry matter content can influence voluntary intake. If dry matter of forage is lower than 20%, as in young grazed grass, the volume of water in the rumen increases with subsequent decrease on the intake level in spite of a high forage digestibility (Meissner *et al.*, 1995). Plant maturity also causes variation on intake. When plant is over grown and protein content decreases cell walls and tissues lignification increase with, as a consequence, an increase of forage retention time in the rumen, limiting voluntary intake (Arthington *et al*., 2005).

Nutrient deficiency in feeds influence intake. For example, protein or nitrogen deficiency can reduce the activities of microorganisms, which results in reduced feed intake. The physical characteristics of the forage, such as dry matter content and particle size, and resistance to fracture are known to affect the ease of prehension and thus intake rate (Inoué *et al.*, 1994). With dried forages, relative preferences for mixtures with varying proportions of long and short particles were closely related to the differences in intake rates (Kenney and Black, 1984). Discrimination between the different mixtures decreases as the intake rates of the feeds being compared increase. Accordingly, the preference for short particles is more pronounced in slowly ingested forage like straw than in rapidly ingested hay. Small ruminants are also sensitive to the particle size of concentrates. Ground feeds with a large percentage of fine particles (<0.5 mm) are clearly less well accepted than coarse ground feeds (Morand-Fehr *et al.*, 1994). The preference for coarse particles may be due to greater ease of prehension. The water content in feed modifies dry matter intake very little except with ground cereals that can be changed into compact pastes with high water content (Baumon *et al.* 2000).

The Animal factor affecting intake in ruminants

The capacity of rumen

The capacity of the rumen is a critical factor in determining the feed intake of ruminants. Intake is restricted by the capacity of the rumen wall to signal the degree of ‘’fill’’ to the brain, but what constitutes the maximum and hence critical ‘’fill’’ of the rumen is uncertain. Reticulorumen is the primary control point for the physical limitation to intake. The quantity of roughage eaten by the animal is directly related to its rate of disappearance from the reticula-rumen. lntraruminal additions of water during eating did not affect the feed intake of cattle or sheep (Campling and Balch 1961) presumably because water rapidly leaves the rumen. These findings are important with regard to forage moisture content and its effect on dry matter intake. Considerable evidence is available showing, with predominantly roughage diets, voluntary intake is limited by the capacity of the reticulo-rumen and by the rate of the disappearance of digesta from this organ (Ellis, 1978).

Voluntary feed intake is limited by physical conditions within the gut and particularly by the amount of digesta in the reticulo-rumen. The fill gut capacity, in relation to forage characteristics, can be considered as the main factor of the regulation of voluntary intake. Intake appears limited by the maximal volume that the digestive tract can reach (Allen, 1996), even if herbivores are able to progressively modify the volume of their rumen and increase the transit rate of digesta when the quality of forage decreased (Schettini *et al*., 1999).

The Size of the animal

As the animal grows, feed intake follows approximately and proportionately to metabolic body weight. According to Holmes *et al*. (1961), the voluntary intake of grazing animals has been related to body size and to metabolic body size. Intake seems to be related to fasting heat production, which is itself related to metabolic weight in sheep than in cattle. When animals become excessively fat, their intake tends to stabilize, i.e. not to increase as body weight continues to increase. This may be due to abdominal fat deposits reducing the volume of the rumen, but may also be a metabolic effect. Conversely, in very lean animals intake per unit of metabolic body weight tends to be high. Arnold *et al*. (1964) noted that as thin sheep become fat, intake decreases and intake and liveweight are negatively related. Langlands (1968) reported that thin sheep grazing with fat sheep make compensatory gain by increasing intake by 20% or more on a per unit of liveweight basis. Allden (1968) also found young sheep compensated for previous periods of under nutrition by eating more per unit liveweight than sheep which were previously well fed.

Feed intake and pregnancy

The pregnancy state is also a factor controlling voluntary intake. In the predictive equation of Faverdin *et al.* (2006), the intake capacity of dairy cows is proportional to the lactation state, age and maturity of cow and to a “pregnancy indicator” that explains the decrease of intake during the last weeks of pregnancy. Two factors influence feed intake in pregnant animals. Intake increases during foetal development. This is because the foetus needs high nutrients but in the later stages of pregnancy the effective volume of the abdominal cavity is reduced as the foetus increases in size and so is the space available for expansion of the rumen during feeding. As a result, intake is depressed, especially if the diet is predominantly roughage.

Feed intake and lactation

Intake increases at the onset of lactation. It is believed that the increase, which is mainly physiological in origin, but may also be a physical effect resulting from the reduction in fat deposits in the abdominal cavity. In early lactation, the dairy cow loses weight which is replaced at a late phase of lactation when milk yields are falling while the intakes of dry matter remain high. Feed intake is related to the kind of production, e.g. different kinds of goats eat different amounts of feed as percentage of their body weight. Dairy goats take in 5-8% per day while meat goats do not get above 3% (Carl and Kees, 1991).

The Environmental factors affecting the feed intake of ruminants

Among environmental constraints, temperature, photoperiod and distance from the drinking water source are the main factors that limit the voluntary feed intake, especially in grazing animals.

Grazing animal

The Intake of pasture herbage meets the animal needs without undue energy expenditure. This is determined by three factors, namely: bite size (quantity of dry matter harvested) at each bite, bite rate (number of bite per minute) and grazing time. For these factors to be achieved, the grasses/pasture must be suitably distributed. Sward characteristics, in terms of blade morphology, such as hair occurrence, thickness of cuticle, leaves size, stems physical properties and dead materials ratio can stimulate, limit or inhibit animal foraging behavior (Provenza, 2003a) These parameters have a huge influence on bite size and intake rate. In relation to grass characteristics, bite size varied from 10 to 400 mg MO for sheep and from 70 to 610 mg MO for cattle. Under grazing, there is a close relationship between leaf proportion, green leaf mass (Smit, 2005), sward density (Prache *et al*., 1997) and dry matter intake. According to Benvenutti *et al*. (2006), stems can have a barrier effect on bite size and instantaneous intake rate. The higher is stems density, the smaller is the bite area and the slower is the biting rate. This leads to a decrease of the instantaneous intake rate. Boval *et al.* (2007) confirmed that stem length and stem proportion in the sward have a negative impact on biting rate with a correlation of, respectively, -0.67 and -0.40. Sward composition, in terms of plant species, can also influence the level of intake. Indeed, compared to grasses, legumes are often associated to higher level of intake (Ribeiro *et al*., 2003). Assoumaya *et al*. (2007) explained that forage legumes are faster reduced in small particles than grasses and that less time is needed to take and masticate a similar bite than for grass.

Feed intake and climate

The climate, too, is of importance in determining the feed intake of animals. During the digestion of feed, heat is produced, which must be dispersed through evaporation or moisture and by direct heat transfer to the surroundings. If the humidity of the air or the ambient temperature is high, the animal finds it difficult to lose its heat through evaporation. As a result, it can digest less feed and therefore less feed intake.

Day length and intake

Day length also has effects on feed intake though not in all animals. This effect is most evident in deer. It also affects sheep. Intake in sheep is reduced as days get shorter, but to a much lesser than do deer. Cattle seem not to be affected by day length.

Feed intake and water consumption

If there is sufficient water to meet the requirements of an animal, it will take in less feed. It needs the water for the digestion of its feed and for the dispersion of heat via evaporation.

Ill-health and intake

Ill-health can reduce the intake of ruminants. Both internal and external parasites infestation tend to reduce intake.

Conclusion

Voluntary feed intake is a complex system which develops along three dimensions: animal, forage (or the ration) and the environment (including management). The control of feed intake depends, at the same time, on plant characteristics in relation to gut capacity, to the animal's requirements and nutrient concentrations of forages, to the post-ingestive feedback of the intake and the learning process, to the morphological characteristics of grazed plants and on the environment, such as climate, abundance and the frequency of feed resources, etc.

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