Factors Affecting Feed Intake and Its Regulation Mechanisms in Ruminants
A Review
Gebreegziabher Zereu

Department of Animal and Range Sciences, College of Agriculture, Wolaita Sodo University, Ethiopia

*Corresponding author: wedizereu24@gmail.com

Rec. Date: Feb 27, 2016 05:54
Accept Date: Mar 28, 2016 08:59
Published Online: April 07, 2016
DOI 10.5455/ijlr.20160328085909

Abstract
Feed intake is one of the main determinant factors of ruminant performance. However, it is affected by different sets of factors that can be grouped under three categories; 1) feed related factors (include feed chemical and physical characteristics, associative effects between dietary components, nutrient balance and amount of anti-quality factors), 2) animal related factors (such as physiological status, size and genotype of the animal) and 3) environment related factors (like temperature, housing and prevalence of diseases). Ruminants try to satisfy their nutrient requirements for maintenance and other productive purposes from different feed sources because it is unlikely that feed/s contain the exact amount of nutrients required by animals. This consumption of different feeds to balance nutrient intake by ruminants may lead them to over or under consumption of one or more nutrients. Both under and over feedings are not required by the animals and therefore they should have mechanisms to regulate their intake. Ruminants feed intake regulation mechanisms have been perceived and described differently by scholars—theories of intake regulation. But, these intake regulation theories fall under three categories: 1) physical feed intake regulation—states fill effect resulted from destination of the gastrointestinal tract causes the animal to stop or start feeding; 2) metabolic or chemostatic feed intake regulation—states the presence of nutrients, metabolites and hormones in the circulating blood signals the animal to stop or continue on feeding; 3) cost benefit model of feed intake regulation—states animals continue feeding to get nutrient they require and stops to avoid the detrimental effect of by-products of metabolism (free radicals), but this theory have been criticized by different scholars. However, it has been proved that, the different signals in intake regulation are working in integrated way controlled by the central nervous system.

Key words: Feed Intake, Intake Regulation, Ruminants

Introduction

Livestock play vital roles for human being. They utilize and convert grains and roughages feeds in to human utilizable forms, although the incorporation of food grains in livestock feeding is not efficient use of limited resource where there is world food shortage (Gillespie and Flanders, 2010). Feeding of grains to animals imparts computation with human for food, and hence there is an interest to reduce the amount of grains in the diet of animals especially in ruminants because ruminants are able to utilize fibrous feeds (Forbes, 2007a). In the global livestock production system, ruminants are economically most important (Pittroff and Soca, 2006), because they transform large quantities of plant materials which do not have direct value as human food into the form that can be used directly (Gillespie and Flanders, 2010). Ruminants are able to utilize forage-based diets and can thrive in situations that are difficult, even to survive, for non-ruminant animals; because of the unique digestive and metabolic mechanisms they have (Forbes, 2005). Their voluminous stomachs harbor and provide suitable environment to microorganisms that are capable of digesting fibrous materials such as cellulose (Dijkstra et al., 2005). Such pre-gastric fermentation enables ruminants’ to utilize large proportion of energy from roughage feeds than that can be utilized by their own enzymes alone and convert non-protein nitrogen to high biological value in the form of microbial protein (Allen, 1996). Therefore, ruminants are processing plants that convert plant materials (fibrous feeds) which human and monogastric animals are unable to utilize directly, that would otherwise be wasted, into highly nutritious human food.

The amount and type of feed consumed are the two most important, out of the many, factors that determine ruminant productivity (Preston and Leng, 1987). Intake of digestible and metabolizable nutrients determines animal performance (Huhtanen et al., 2008). Throughout the world, ruminant production systems are based on forages but forages alone are unable to promote required levels of animal production due to their limitations in feeding values (Wilkins, 2000). Regardless of the greater capacity of digestive tract they posses, there are many circumstances in which ruminants do not eat sufficiently and unable to meet their nutrient requirements (Forbes, 2005). This problem of under-feeding is prominent in ruminants when they are provided with highly fibrous, bulky feeds and this results in severe deficiency of essential nutrient/s (Forbes, 2000; Forbes, 2007a). On the other hand, excessive intake is undesirable from economic point of view (McDonald et al., 2002; Forbes, 2007a) and risks of toxicity (Forbes and Provenza, 2000). Hence, animals should have some mechanisms to regulate their intake, not to under or excessively consume. Therefore, the aim of this review is to discuss and compile information on the importance of feed intake, factors affecting it and its regulation mechanisms in ruminants. This will help livestock researchers and producers to have a general understanding on this topic. Various research journals, review articles and text books were reviewed and the information was summarized.
Importance of Feed Intake

Feed intake refers to the quantity of feed consumed by an animal or group of animals in a given period of time during which they have free access to that feed (Forbes, 2007a). Animal productive efficiency is largely dependent on daily rate of feed intake (Illius et al., 2000) and if an animal consumes more feed each day its daily production has increased which in turn increase the overall efficiency of production process due to the reduction of maintenance costs as productivity rises (McDonald et al., 2002). This can be further elaborated, as forage intake increases, availability of total energy and other nutrients to the animal increases, while the proportion of dietary energy for maintenance decreases (Dougherty and Collins, 2003). High efficiency of forage energy utilization is achieved at or near ad libitum feeding and increased forage intake should be ensured in order to achieve higher production goals (Weston, 1996). On the other hand, very low intake will result in body weight lose, reduced level of production (growth or milk secretion) and poor reproductive performance (Forbes, 2007a; Tahir, 2008) and in under fed animals maintenance requirement becomes a very large proportion of the metabolizable energy of the food and hence resulting in lower feed conversion efficiency (Forbes, 2007a).

Animals usually continue to eat until they get the amount of nutrients that satisfy their energy needs, including continued fat deposition in adults (Forbes, 2007a). However, over feeding can result in excessive fat accumulation (McDonald et al., 2002; Forbes, 2007a). Excessive intakes of feed, which brings fat accumulation, should be avoided for two reasons: i) low sale value of fat because of consumers’ interest and ii) because fat is high in energy content and low in water content, it is expensive to produce (Forbes, 2007a). Therefore, feed consumption must be matched with required/expected level of animal production (Forbes, 2007a).

By integrating knowledge of the relationships between feed intake and feed characteristics, the intake of metabolizable energy (ME) can be manipulated, and for example, feed of low ME can be given to animals if their nutrient requirements are relatively low and thereby reducing feed cost (Forbes, 2007a). On the other hand, feeds with high ME contents can be offered to animals if their nutrient requirements are high due to some physiological needs. In general, knowledge of food intake is important for diet formulation, for the prediction of animal performance, for the design and control of production systems and for the assessment of animal–resource interactions in grazing ecosystems (Illius et al., 2000).

Factors Affecting Feed Intake in Ruminants

Variations in forage feeding value is largely (70%) determined by its intake, while the rest (30%) is accounted by its nutritive value (Dougherty and Collins, 2003). Therefore, it is important to determine the factors affecting forage/feed intake. According to McDonald et al. (2002), factors affecting feed intake in
ruminants can be grouped under three categories; i) animal related factors, ii) feed characteristics iii) environmental conditions.

**Feed Related Factors**
Nutritive value of a given feedstuff is a function of its DM intake and its ability to supply the nutrients required by an animal for maintenance, growth and reproduction (Teferedegne, 2000). Physical and chemical characteristics (Forbes, 2007a), sward structure (in grazing ruminants), nutrient balance, associative effects and anti-nutritional factors can affect feed intake.

**Physical and Chemical Factors**
Physical factors refer to these characteristics of a feed that affect intake by influencing gastrointestinal volume following ingestion and the rate at which that occupied volume is reduced via digestion and onward passage (Romney and Gill, 2000). The cell wall contents of forages, where high percentage (35-80%) of organic matter (OM) is concentrated, has a major impact in this respect, as these structures are slowly digestible and occupies large portion of the gut than the cell contents (Romney and Gill, 2000). Besides, forage characteristics like DM content and particle size, and resistance to fracture can affect ease of prehension and thus intake rate (Inoue et al., 1994).

The DM content of feeds may affect feed intake by influencing the space occupied within the gut (Romney and Gill, 2000). There was a decrease in silages DM intake (DMI) as the water content increased (Tahir, 2008). The particle size of forages may influence mastication, rumen microbial fermentation and the rate of passage and digestion in the gastro-intestinal tract (GIT) and thereby influences productive performance of the animal (Lu et al., 2005). McDonald et al. (2002) stated that, rate of digestion and digestibility of a given food are closely related, but intake is more closely related to the former than the later per se. McDonald et al. (2002) further explained that, rapidly digested foods are highly digestible and promote high intake due to rapid emptying of the digestive tract creating more space available for next meal. According to Roche et al. (2008), dietary fiber content, its digestibility and rate of degradation in the rumen are the most important forage characteristics that determine DMI. Therefore, the neutral detergent fiber (NDF), which is a measure cell wall content, determines the rate of digestion and has negative correlation with the rate at which the feed is digested (McDonald et al., 2002). However, the relationships between DMI and NDF content of fiber are not always consistent, although NDF positively related with resistance to comminution (Romney and Gill, 2000). Besides, not only the amount of cell wall in ruminant feeds, but also its physical form affects intake (McDonald et al., 2002).

Mechanical grinding of roughages can partially destroy the cell wall structural organization thereby increasing rate of ruminal breakdown and increased intake, although fine grinding reduced digestibility
(McDonald et al., 2002). In addition, feeds that are dusty due to very fine grinding cause irritation of the nose and eyes of animals, and hence decrease feed intake (Preston and Leng, 1987). Smell has also an important effect on feed intake, animals may reject without tasting it, and this can be evidenced by reduction of intake of pasture having smell of dung by cattle, although the animal will readily consume if the grass around the dung is cut and carried (Preston and Leng, 1987). This behavior of refusing pasture around dugs has probably developed to protect the animal itself against infestation by intestinal parasites (Preston and Leng, 1987). Moreover, as animals reject unpalatable pasture, it is assumed that such pasture give off volatile materials (Preston and Leng, 1987).

Forage conservation also has an impact on feed intake. Intake of silage or hay is often lower than their corresponding green forage; the former due to the presence of fermentation products like volatile fatty acids (VFA) and ammonia, while the later is due to its low digestibility and its higher rumen fill effect compared with green forage (Baumont et al., 1999). Intake of a given forage species can also be affected by its palatability (Baumont, 1996 cited by Baumont et al., 1999).

**Sward Structure**

In grazing ruminants, the quality of the diet is not the only factor that determines intake. Availability and distribution of forages can have direct impact on short-term intake rate (Garcia et al., 2003). Besides, sward characteristics like plant density and height can influence intake via their effect on ease of prehension and thus bite size, and in such, they could be the major factors influencing daily herbage intake (Hodgson et al., 1991).

**Nutrient Balance**

Intake may also be depressed when the feed is deficient in nutrients that are critical for the activities of rumen microbes like proteins, minerals (like sulphur, phosphorus, sodium and cobalt), vitamins or amino acids (McDonald et al., 2002; Forbes, 2007a). However, animals fed imbalanced diets may increase their intake hopping to compensate the deficient nutrient, but this may result in excessive intake of other nutrient/s (Fisher, 2002). Animals reduce their intake if the dietary imbalance is high (Illius and Jessop, 1996). The balance with regard to energy and protein is most important, as it can determines the integration of many nutritional signals and deficiency of protein can greatly depress intake, while excess protein consumed can simply be metabolized to energy (Fisher, 2002).

**Associative Effects of Feeds on Feed Intake**

Forages provide ruminants with nutrients that satisfy their maintenance requirements with a small amount of weight gain or milk production (Bayer and Waters-Bayer, 1998). Intake and nutritive value of poor quality forages can be improved by supplementation. Diets of ruminants’ are supplemented for three
reasons; i) for maximizing rate of growth or production, ii) to correct deficient dietary component/s and iii) to pay off insufficient or poor-quality pasture (Hinton, 2007). Supplements can have catalytic (mineral supplements), additive (concentrates added to provide more energy and protein to cover additional production requirement) or substitution (when large amount of concentrates replace the basal diet) effects (Bayer and Waters-Bayer, 1998). In general, supplementation seems to improve the overall DMI, but may have positive or negative effects on intake of the basal forage (Romney and Gill, 2000). This may happen due to associative effects of the diets. Associative effects occur when digestion or intake of one feed is dependent of the other (Niderkorn and Baumont, 2009).

Positive Effects
According to McDonald et al. (2002), the effect of adding a concentrate supplement to roughage on intake depends on the digestibility of that roughage; concentrate added to roughages of low digestibility stimulates the function of microorganisms in the rumen, reduces retention time and increases its intake and the concentrate is consumed in addition to the roughage. This increased intake of poor quality feed could be due to the supply of a limiting nutrient by the concentrate (Romney and Gill, 2000). For instance, supplementation of straw with protein can improve its digestibility and voluntary intake by providing nitrogen and stimulating growth of rumen microbes (Church and Santos, 1981).

Negative Effects
Negative associative effects occur when the intake of fibrous diet (basal diet) decreases due to the inclusion of large amounts of concentrates (substitution effect)- the degree which varies according to the quality (digestibility) of the basal diet as well as the quality of the concentrate (Bayer and Waters-Bayer, 1998; Romney and Gill, 2000). However, supplementation increases the intake of digestible nutrients on the expense of forages (Forbes, 2007a). There is a negative relationship between the level of concentrate supplementation and the rate of forage digestion in the rumen (Forbes, 2007a). This is more pronounced when supplements with high concentration of readily fermentable carbohydrates (RFC) are used than supplements with more slowly fermentable components (Romney and Gill, 2000). This reduction in forage intake due to the fermentation of large quantities of RFC is due to the reduction of ruminal pH, which in turn depresses the activity of cellulolytic microbes and then the digestibility of plant cell walls (Mould et al., 1983). This constraint can be alleviated by using concentrates that have slowly fermentable carbohydrates (cellulose) (example, sugar beet pulp) than those containing RFC like starch (example, barley) (Forbes, 2007a). The associative effects of supplementation forages with concentrates are widely reported, but the effects that could exist due to combination of different forages are rare. Niderkorn and Baumont (2009) had reviewed if associative effects may exist between forages on digestion and intake
and they identified three main situations in which this can happen. These are: i) increased intake when grass and legume are combined due to fast digestion, higher rate of particle breakdown and passage of the legume, ii) increased digestion when poor forage is supplemented with high nitrogen content due to stimulation of the microbial activity and iii) modification of rumen digestive processes (proteolysis and methane production) due to certain bioactive secondary metabolites like tannins, saponins or polyphenol oxidase of the association.

**Anti-Nutritional Factors**

Ant-nutritional factors are those substances that reduce nutrient utilization or feed intake in animals (D’Mello, 2000). They are resulted mainly from plant secondary metabolism, but also from plant primary metabolism some times, and mycotoxins- toxic secondary metabolites produced by fungi during crop development and/or storage (D’Mello, 2000). Anti-nutritional factors have diverse effects including reduction in DMI, limit DM digestibility, nutritional imbalance, impairing vital systems that result in abnormal reproduction, disturbance of endocrine or neurological functions, genetic aberrations, suppress immune function leading to disease and death (Allen and Segarra, 2001). However, the effect may depend on the type, concentration, and associative effects with other diet components, especially in the case of plant secondary and primary metabolites, and in most cases their positive effects outweighs their negative effects.

**Animal Factors**

**Physiological Status of the Animal**

An animal’s physiological status affects its energy requirements and hence intake (Romney and Gill, 2000). If there is an increased need of energy or protein or both ruminants certainly increase their feed intake (Preston and Leng, 1987). In ruminants feed intake is high in; i) young growing and older animals that need to restore their depleted body tissue, ii) pregnant animals during the last trimester of pregnancy, iii) lactating animals and iv) heavily working animal (Preston and Leng, 1987).

**Pregnancy**

In pregnant animals, intake is increased at the early stages of pregnancy due to additional demand of nutrients for feotal development, but reduced at the later stages because of the reduction of the volume abdominal cavity by the expansion of the uterus (McDonald et al., 2002). This reduction in volume of the abdominal cavity can be exacerbated by abdominal fat (Forbes, 2007a). In sheep, it has been noted increased intake during mid pregnancy in single-bearing ewes, but not twin bearing; reduced intake in fat ewes at late pregnancy, the reduction in intake of standard feed become great in ewes that have been fed
at a high level or on good-quality silage during mid-pregnancy compared with that of ewes on poor silage (Forbes, 2007a).

**Lactation**

Milk production calls for additional nutrients and lactating animals increase their intake usually to a level that satisfies their requirement without use of their body reserves if provided with good quality food free choice (Forbes, 2007a). In lactating cows, nutrient requirement for lactation can account up to five times of their maintenance requirement and intake is usually higher than during pregnancy in comparison with non-lactating cattle (Forbes, 2007a). It has been long reported that, lactating cows can consume 35% more feed, on a live-weight basis, than their non-pregnant and non-lactating counterparts (Hunte and Siebert, 1986). The increase in intake following calving is due to clearance of the fetus and fetal fluid, which can occupy about 70 liter in parturient Holstein Friesian cow, that increase the volume of the digestive tract, especially the rumen (Forbes, 2007a).

**Growth and Age**

Intake in growing animals could be high due to the need for body tissue synthesis. Growing animals can only attained their potential growth rate in the presence of sufficient and high quality foods (Forbes, 2007a). A study by Hunte and Siebert (1986) showed that, as age and live-weight of steers increase, feed intake per unit body weight was declined, the rate of decline being significantly ($p < 0.05$) greater on good-quality diet compared to a poor-quality diet. The effect of compensatory growth on feed intake has variably reported. Higher DMI in restricted (compensating) than non-restricted zebu bulls (Ehoche et al., 1992) and steers (Rayan et al., 1993) was reported. On the contrary, lower feed intake in restricted animal, than non-restricted (control), in steers (Coleman and Evans, 1986) and in Sudanese female Goats (Yagoub and Babiker, 2009) was reported. The variations in the results may be related to type of animal, type and composition of feed, duration of restriction period and environmental factors.

**Animal Genotype and Size**

Under the same nutritional and environmental conditions, potential intake of a given animal is determined by its genetics (Preston and Leng, 1987). Hunte and Siebert (1986) reported, the intake of Herefords (Bos taurus) and Brahmans (Bos indicus) was similar on low quality diet while on high quality diet the former ate significantly ($P < 0.05$) than the later. Larger animals consume greater quantities of food; however, the relationship is not isometric but scales allometrically with body mass, and intake is commonly expressed on the basis of metabolic body weight, or live weight ($LW^{0.75}$)(Romney and Gill, 2000).

**Environmental Factors**
**Environmental temperature**

Both high (heat stress) and low (cold stress) environmental temperatures can affect intake in farm animals. Heat stressed animals reduce their feed intake in order to reduce increased heat production associated with feed consumption (Morrison, 1983). Heat stress is caused due to decreased heat transfer of the animal to its environment, which in turn is caused by high air temperature and humidity, low air movement and thermal radiation load, however, air temperature is usually the primary cause of heat stress while the other factors intensify the stress (Morrison, 1983). Hence, only the effect of ambient temperature will be discussed. Kadzerea et al. (2002), on their review, on the effect of high environmental temperatures on lactating cows, they found food intake in high yielding lactating cows starts to decline at the ambient temperatures of 25–26°C. When ambient temperature exceeds 30°C food intake drops more rapidly and when reached 40°C intake can be reduced up to 40%. A decrease in feed intake of 3-4 kg/day in mid-lactating dairy cows as a result of thermal stress was also reported (Grant and Albright, 1995). In fact, high ambient temperature can influence the performance of the animal besides its effect on DM intake.

According to Morrison (1983), heat stress affects animal performance by reducing feed intake, because animals having difficulty in losing heat decrease their intake in order to avoid the increased heat production associated with feeding. Marai et al. (2007) reviewed the effect of heat stress on physiological traits of sheep. They summarized, exposure of sheep to heat stress can result in a series of drastic changes in the biological functions, including a decrease in feed intake efficiency and utilization, disturbances in water, protein, energy and mineral balances, enzymatic reactions, hormonal secretions and blood metabolites, which all impaired production and reproduction traits of sheep. Furthermore, a recent study by Obitsu et al. (2011), on the impact of high ambient temperature on urea-nitrogen production in lactating dairy cows, a decreased DM intake and milk yield was reported (Table 1).

**Table 1: Effect of Ambient Temperature on Lactation Performance Holstein Dairy Cows (Obitsu et al., 2011)**

<table>
<thead>
<tr>
<th>Variables</th>
<th>18°C</th>
<th>20°C</th>
<th>SEM*</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter intake (kg/day)</td>
<td>24.6</td>
<td>19.5</td>
<td>1.16</td>
<td>0.054</td>
</tr>
<tr>
<td>Water intake (liter/day)</td>
<td>96.9</td>
<td>4.78</td>
<td>4.78</td>
<td>0.367</td>
</tr>
<tr>
<td>Milk yield (kg/day)</td>
<td>43.2</td>
<td>1.75</td>
<td>1.75</td>
<td>0.052</td>
</tr>
<tr>
<td><strong>Milk composition (%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fat</td>
<td>3.95</td>
<td>4.06</td>
<td>0.066</td>
<td>0.295</td>
</tr>
<tr>
<td>Protein</td>
<td>3.10</td>
<td>2.86</td>
<td>0.059</td>
<td>0.065</td>
</tr>
<tr>
<td>Lactose</td>
<td>4.63</td>
<td>4.67</td>
<td>0.033</td>
<td>0.510</td>
</tr>
<tr>
<td>Body weight (kg)</td>
<td>601</td>
<td>568</td>
<td>8.7</td>
<td>0.076</td>
</tr>
</tbody>
</table>

*SEM, standard error of means

Cold usually increases intake by stimulating appetite, which in turn is induced by the increased metabolic demands of the animal (Young, 1983). However, very low temperature causes hypothermia and the
animal failed to produce metabolic heat and, if the situation continues in this way may occur (Young, 1983). Intake by cattle may not be greatly affected when the environmental temperature reaches up to -16°C (Forbes, 2007a). In sheep it has been reported, the increased secretion of thyroxin hormone because of reduced environmental temperature might increase intake (Forbes, 2007a).

In general, if body temperature rises above thermo-neutral zone, animals reduce their intake in attempt to avoid extra body temperature resulted from activities of feeding, digestion, absorption and metabolism, while intake may be increased if body temperature is below the hermoneutral zone, in an effort to produce heat from the mention activities (Forbes, 2007a).

**Housing**

Provision of shade in hot climates increases intake (Forbes, 2007a) by reducing the impact of heat stress. The impact of heat stress is more severe in the tropical than the temperate region and provision of shade have more advantage. As it is expected, heat stress may vary from time to time (within a day, among days, months, season and years) according to climatic weather variations and hence its effect. A study by Muller and Botha (1994) over three summer seasons showed that cows provided with shade had higher feed intake than no-shade cows over two summers. Intake in both shed and non-shade cow was significantly higher in nighttime feeding period than daytime feeding period (Table 2).

**Table 2:** Day, night and total daily feed intake (mean ±SD) of Dutch type Friesian cows during 3 consecutive summer seasons experimental periods (Muller and Botha, 1994)

<table>
<thead>
<tr>
<th>Experimental Period</th>
<th>Feed Intake (kg dm/cow/day)</th>
<th>Shade</th>
<th>No Shade</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day time feeding period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(06:00-15:00)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1984/85</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1984/86</td>
<td>9.98±1.08</td>
<td>9.23±1.31</td>
<td>p&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>1986/87</td>
<td>9.91±0.75</td>
<td>9.90±0.85</td>
<td>p&gt;0.05</td>
<td></td>
</tr>
<tr>
<td>Night time feeding period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(16:30-05:00)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1984/85</td>
<td>10.90±0.87</td>
<td>10.67±0.86</td>
<td>p&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>1984/86</td>
<td>12.20±0.68</td>
<td>12.32±0.47</td>
<td>p&gt;0.05</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1984/85</td>
<td>20.20±1.49</td>
<td>19.88±1.50</td>
<td>p&lt;0.05</td>
<td></td>
</tr>
<tr>
<td>1984/86</td>
<td>20.88±1.82</td>
<td>19.90±1.75</td>
<td>p&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>1986/87</td>
<td>22.20±1.15</td>
<td>22.20±106</td>
<td>p&gt;0.05</td>
<td></td>
</tr>
</tbody>
</table>

The type of house may also have an effect on efficiency of obviating heat stress. Koknaroglu et al. (2008) conducted an experiment to investigate the effect of different housing systems (open lots, confinement and open lots with access to an overhead shelter) on feed intake of steers. They found steers in open lots
with access to an overhead shelter had higher daily DMI, daily gain and feed efficiency and were 38 kg heavier than stress kept in confinement (Table 3).

Table 3: Dry matter intake (mean ±SE) and performance of steers feed for 158 days (Koknaroglu et al., 2008)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Open lot</th>
<th>Shelter</th>
<th>Confinement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial weight (kg)</td>
<td>299±0.08</td>
<td>299±0.08</td>
<td>299±0.07</td>
</tr>
<tr>
<td>Final weight (kg)</td>
<td>495±5.67&lt;sup&gt;a&lt;/sup&gt;</td>
<td>517±5.67&lt;sup&gt;a&lt;/sup&gt;</td>
<td>479±4.91&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Days on feed</td>
<td>158</td>
<td>158</td>
<td>158</td>
</tr>
<tr>
<td>Daily DMI (kg/day)</td>
<td>7.17±0.18&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.38±0.21&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.69±0.21&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Average daily gain (kg/day)</td>
<td>1.24±0.04&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.37±0.04&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.13±0.03&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Feed efficiency (kg feed/kg gain)</td>
<td>5.80±0.14&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>5.38±0.14&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.96±0.12&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Disease

Diseased animals reduce their intake and this is one of the first sign of many diseases (Forbes, 2007a). Infection with gastrointestinal nematodes and trematodes reduces feed intake, the degree of reduction depending on the severity of infection, up to 20% or more in moderate and heavy to less obvious with lighter infection (Parkins and Holmes, 1989). Parasites could affect feed intake and animal performance by reducing rumen pH, depressing rumen motility, changing the level of hormones (Example, gastrin) and impairing feed digestion, energy and nitrogen utilization (Parkins and Holmes, 1989). Continuous stimulation of receptors in the gastrointestinal tract wall by parasites could be the reason for a primary feed intake depression in sheep infested with helminthes (Forbes, 2007a).

Availability of Water

Water is the most important nutrient; its intake usually is about twice the weight of DM consumed and by the virtue of its involvement in the processes of food nutrients digestion and metabolism, both the amount and time of water intake are closely related to food intake (Forbes, 2007a). Sundram et al. (1998) conducted an experiment to analyze the effect of water restriction on daily feed and water intakes in artificially exercised Merino ewes. The animals were subjected to three groups; group 1 (G1), Group 2 (G2) and group 3 (G3) provided water unrestricted, for 1 hour+20 minutes and 1 hour respectively, immediately after exercised outdoors for 1 hour using circular machine at a rate of 5km/h for 1 h/day. G3 ewes had significantly lower (p<0.05) total daily water intake (TDW) than G1 and G2 ewes and this was about 60% of the TDWI of G1. Feed intake was also significantly lower (p<0.05) in G3 ewes than those of G1 and G2 (Table 4).
Table 4: Feed, water intake and gain (mean ±SE) of merino sheep during the experiment (Sundram et al., 1998)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed intake (g/head/day)</td>
<td>Group1</td>
</tr>
<tr>
<td></td>
<td>1,608±68</td>
</tr>
<tr>
<td></td>
<td>Group2</td>
</tr>
<tr>
<td></td>
<td>1,546±55</td>
</tr>
<tr>
<td></td>
<td>Group3</td>
</tr>
<tr>
<td></td>
<td>1,067±50</td>
</tr>
<tr>
<td>Total water intake (ml/day/head)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3,611±192</td>
</tr>
<tr>
<td></td>
<td>3,265±137</td>
</tr>
<tr>
<td></td>
<td>2,068±124</td>
</tr>
<tr>
<td>Water intake (60 minutes post exercise ml/head/day)</td>
<td>244±93</td>
</tr>
<tr>
<td></td>
<td>1,810±82</td>
</tr>
<tr>
<td></td>
<td>2,068±124</td>
</tr>
<tr>
<td>Gain (kg) (day 1 to day 12)</td>
<td>4.0±1.76</td>
</tr>
<tr>
<td></td>
<td>2.5±1.44</td>
</tr>
<tr>
<td></td>
<td>1.0±1.32</td>
</tr>
</tbody>
</table>

Group 1= water available for ad libitum; Group 2= water available for 1 hour+20 minutes; Group 3= water available for 1 hour; SEM=standard error of means, Means in the same row with different superscripts differ (p<0.05)

Regulation of Feed Intake

Animals eat to supply their tissues with nutrients required for the maintenance of physiological process, growth, milk production and work (Romney and Gill, 2000). However, it is unlikely that feeds contain the nutrients in the same ratio as required by the animals (Romney and Gill, 2000; Forbes, 2007a) and hence they try to take the amount they require from different sources. While trying to meet the requirement of one nutrient it may result in a deficiency or excess of another nutrient (Romney and Gill, 2000). For example, if the protein content is too low relative to energy, the animal is in a dilemma whether to increase its intake to satisfy its protein requirement that results in excess energy intake, or to reduce its intake to avoid over consumption of energy, but reduced quantity and/or quality of products due to lack of dietary protein (Forbes, 2007a). However, if animals get the amount of nutrients that satisfy their requirements in their diet, their intake will be optimum (Forbes, 2000). Moreover, all dietary components can be toxic when they are in excess of the requirement, while deficiency of an essential nutrient can bring food aversion (Forbes and Provenza, 2000). For example, a deficiency of any of the essential minerals results in reduced food intake, while an excess of many of the minerals has toxic effects, including reduced intake (Forbes, 2007a). Therefore, it is logical that animals have the tendency to insure this optimum intake, by avoiding both under feeding and excessive intake of nutrients via some regulation mechanism.

Theories of Feed Intake Regulation

Physical Regulation of Intake

According to Forbes (1996), the supports of ‘physical’ theory had developed it based on the observation of the positive relationship of forage intake and rate or extent of digestion in the rumen. DMI can be reduced due to restricted flow of digesta, along the GIT, that can result in distention of one or more segments of the GIT (Allen, 1996). And anything that causes sufficient destination of the reticulo-rumen or any other compartment of the digestive tract may stimulate stretch sensors (mechano-receptors) found in the tract wall, which transmit a message to central nervous system resulting in cessation of feeding.
(Dougherty and Collins, 2003; Tahir, 2008). This distension or fill is an intuitive feedback in ruminants (Fisher, 2002). Physical fill can be described on the basis of three main aspects: the reticulorumen volume which is mostly related to the animal’s characteristics, the rate of digestion of feed and the rate of passage (rumen emptying) (Tahir, 2008).

**Rumen Capacity and Intake**

Intake is not only affected by the digestibility (the rate and extent of degradation) and passage rate, but also by the capacity of the digestive tract, especially the rumen (Forbes, 2007a), and physical capacity of the rumen (rumen size) and feed intake are positively correlated (Tahir, 2008). Despite the fact that the rumen has a large capacity to accommodate forage feeds, the slow rate of digestion of forage feeds means that rumen capacity can be limiting to intake (Forbes, 2000). Therefore, factors, which reduce the volume of the rumen, can bring reduction in intake (Table 5).

**Table 5:** Factors Affecting the Capacity of the Rumen and Hence Intake

<table>
<thead>
<tr>
<th>Factor</th>
<th>Effect</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fat (abdominal)</td>
<td>Decrease</td>
<td>McDonald <em>et al.</em>, 2002; Forbes, 2007a</td>
</tr>
<tr>
<td>Pregnancy</td>
<td>Decrease (especially late pregnancy)</td>
<td>McDonald <em>et al.</em>, 2002; Forbes, 2007a</td>
</tr>
<tr>
<td>NDF content</td>
<td>Decrease</td>
<td>McDonald <em>et al.</em>, 2002; Van Soest, 1994</td>
</tr>
<tr>
<td>Inert fill</td>
<td>Decrease, but results are inconsistent</td>
<td>Reviewed by; Allen, 1996; Forbes, 2007a</td>
</tr>
</tbody>
</table>

**Rate of Digestion and Passage (Rumen Emptying)**

Rate of digestion of a feed and its digestibility are closely related (McDonald *et al.*, 2002). The process of digestion is time dependent and rate of digestion relative to rate of passage determines the amount of nutrient extracted from the diet and become available for absorption (Huhtanen *et al.*, 2008). The gross energy of forages and cereal grains per unit of DM is almost comparable, but the energy value of the former is low and largely variable than the later, because of high cell wall content of forages and limited digestibility of this fiber by the rumen microbes (Ralph *et al.*, 2004). For cell walls, the rate of digestion in relation to passage is very slow compared with cell solubles, which explains the larger variability in cell wall digestibility (Huhtanen *et al.*, 2008).

Ruminants are unable to meet their energy demands if fed on diets having high cell wall-contents that limit them from consuming sufficient amount (Jung and Allen, 1995). Cell walls are mainly composed of carbohydrate polymers (cellulose and hemicelluloses), but also lignin and other organic substances (proteins, pectic substances or cutin) and silica are found. The cell wall content of feeds is highly related to their organic matter digestibility (Giger-Reverdin, 1995). The neutral detergent residue, called neutral detergent fiber (NDF) of Van Soest may contain almost all of the hemicelluloses, cellulose and lignin, at least for forages (Giger-Reverdin, 1995). The NDF content can greatly affect the rumen volume (Van...
Soest, 1994) and hence affect intake due to its contribution to the rumen fill and this filing effects is related to its more slowly fermentation and passage along the reticulo-rumen relative to non-fiber contents of feeds (Jung and Allen, 1995). The quantity and digestibility NDF are important parameters of forage quality and both can greatly varies, depending on species, maturity, and growing environment (Oba and Allen, 1999).

Forage NDF varies widely in its degradability (Oba and Allen, 1999), and feeds with the same NDF content but different in NDF digestibility (NDFD) can have different DMI and resulted in different animal performance (Example, Dado and Allen, 1996; Kendall et al., 2009). Dado and Allen (1996) fed alfalfa silages with similar NDF (40%) and CP, but different in NDF in vitro digestibility contents (40% Vs 45%) to lactating dairy cows. They found significant increases in DMI (19.4kg/day Vs 20.4kg/day) and milk yield (36.3kg/day Vs 38.2kg/day) for 40% and 45% digestible NDF respectively. Hoffman and Bauman (2003) also reported that DMI, NDF intake and milk yield in mid lactating dairy cows was increased, as NDFD content of the experimental diets increased (Table 6). In general, feed intake in ruminants consuming fibrous forage is primarily determined by the level of rumen fill, which in turn is directly related to the rate of digestion and passage of fibrous particles from the rumen (Van Soest, 1994).

Table 6: Dry matter intake, NDF intake and milk yield of early-mid lactating dairy cows fed diets containing different levels of NDFD (Hoffman and Bauman, 2003)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Dietary NDF, % of NDF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>45%</td>
</tr>
<tr>
<td>Dry matter intake (kg/day)</td>
<td>20.5</td>
</tr>
<tr>
<td>NDF intake (kg/day)</td>
<td>8.5</td>
</tr>
<tr>
<td>Milk yield (kg/day)</td>
<td>33.5</td>
</tr>
</tbody>
</table>

Metabolic Regulation of Intake

Metabolic control of feed intake occurs due to concentrations of nutrients, metabolites or hormones that can signal the nervous system to cause the animal to start or to stop feeding (McDonald et al., 2002). The theory of metabolic regulation of intake states that some factors related the metabolism of the feed like the concentrations and flows of nutrients and energy, including VFA produced via fermentation in the rumen controls feed intake in ruminants (Illius and Jessop, 1996) through sending their feedback to the brain (Fisher, 2002). Intake is influenced primarily by hunger, which is distressing, and by satiety, which is generally pleasurable (Forbes, 2007a). Intake can be regulated at short-term and long-term, the former being associated with the activities of digestion, absorption and metabolism of nutrients along the alimentary canal (i.e. initiation and cession of individual meals) while the later is associated with maintenance of relatively constant body weight over long period of time (i.e. long-term energy balance) (McDonald et al., 2002). However, the distinction between the short and long terms of intake regulation...
does not apply an absolute biological difference because the long-term factors can only influence intake by changing the size and/or timing of meals (Forbes and Barrio, 1992).

**Short-Term Intake Regulation**

**Effect of Volatile Fatty Acids**

Feed carbohydrates consumed by ruminants are fermented by microorganisms into VFA and sometimes into lactic acid (Faverdin, 1999; Dijkstra et al., 2012). The ingested carbohydrates (i.e. soluble sugars, starch, hemicellulose and cellulose) fermented to VFA mainly in the reticulo-rumen but too little in the omasum and large intestine and such produced VFA can represent 50–75% of the ruminant’s energy supply (Faverdin, 1999). Sometimes glucose can be produced in the intestine if starch is escaped from the action of microbes in the rumen (Faverdin, 1999), but gulucose is not the main energy-yielding substrate in ruminants (Forbes, 2007a). As does glucose for monogastric animals, VFA are the main energy carrying molecules in the blood stream of ruminants (Tahir, 2008) and are metabolized rapidly as they pass along the rumen wall (Faverdin, 1999). Acetic and butyric acids changed into ketonic and acetate in the blood, whereas propionic acid is almost totally converted into lactate first in the ruminal epithelium and later into glucose in the liver (Faverdin, 1999).

According to Forbes (2007a), VFA can affect feed intake through their effect on: i) rumen pH; ii) the tonicity of the epithelial muscles and iii) metabolic state after absorption into the blood stream. The accumulation of VFA or lactic acids in the rumen can reduce the ruminal pH and if this lower pH persists for longer time, each day it affects feed intake, microbial metabolism and feed digestion, and has also been related to inflammation, diarrhea and milk fat depression (reviewed by Dijkstra et al., 2012). Reduced rumen pH can reduce NDFD (Forbes, 2007a) which could be associated to inhibition of fibrolytic bacteria at low pH. The reduction in the tonicity the epithelial muscle in the reticulo-rumen can slow down its motility resulting in decreased bouts of rumination and a decreased rate of passage of feed, which both in turn related to reticulo-rumen fill (Forbes, 2007a).

There are receptors in the reticulo-rumen, intestines and liver, which are sensitive chemicals including VFA (Forbes, 1996). However, the reticulo-rumen is the main sensitive area for metabolic regulation of feed intake (Tahir, 2008). The stimulation of these receptors sends feedback signals to the central nervous system and hence intake is regulated (Forbes, 2007a). This has been proved by the infusion of external acids to animals. In general, VFA depressed intake when infused directly in to the rumen, but did not when infused intravenously (Baile and Forbes, 1974) and intake is inversely related to the amount of VFA infused (Faverdin, 1999).
Effect of Proteins and Other Nutrients

Provision of digestible proteins can stimulate appetite in ruminants and by using proteins with different rumen degradability; it is possible to partition proteins between the microbes and the host itself (Faverdin, 1999). However, if there is excessive degradation of protein or non-protein nitrogen it will result in excessive ammonia production, high blood ammonia concentration and toxicity and under such conditions; the animal reduced its feed intake (Forbes, 2007b). Low protein can depress intake (Forbes, 2007b), but the balance of amino acids can also have an effect comparable to low content although this is not important for ruminants (Forbes, 2007a).

Moderate level addition of lipids to ruminant diets of (Example, cow), to increase energy density, can improve the energy status of cows, but it can also have negative effect on energy balance and reduces fertility (Sinclair and Garnsworthy, 2010). One reason for this reduction in fertility is decrease due to reduced DM intake (Allen, 2000). When minerals, vitamins or individual amino acids are consumed in excess to a level that can cause toxicity and illness, animals try to avoid this effect by reducing their daily intake, although this action reduces the supply of energy and proteins (Forbes, 2007a).

Regulatory Hormones

Cholecystokinin (CCK)

It is one of the many hormones secreted in the stomach and duodenum, its concentration increased rapidly during feeding and when the digesta pass along stomach and duodenum, and has satiety signal in most farm animals (Forbes, 2007a). In ruminants, it has a little effect, because of the delay between feeding and arrival of to the duodenal CCK-producing sites, however there are some evidences that supports high concentration of CCK can depress feed intake in ruminants (Forbes, 2007a). The effects of CCK on intake are complex because of its interaction with gastric distension and gut motility (Pittroff and Soca, 2006) and exogenous CCK may cause contractions of the digestive tract that activate mechanoreceptors (Forbes, 2007a).

Ghrelin

It is produced by the stomach wall and stimulates feeding by acting on the hypothalamus (Forbes, 2007a). Roche et al. (2008) reviewed the effect of ghrelin on feed intake of ruminants, and he found the experiments done on this area are few and there was inconsistency of reports, some reported no effect on intake following infusion of ghrelin, while other report there was increase in intake. However, regardless of this, ghrelin could act as a hunger hormone (Forbes, 2007a).
Long Term Feed Intake Regulation

Animals have the tendency to maintain more or less constant body weight for long periods, which is evidenced by their effort to retune back to their former weight after deviation from it by either under feeding or forced over feeding (McDonald et al., 2002). Metabolites in blood may have three fates; i) utilized by tissues ii) stored by tissues like adipose and muscle, or iii) excreted by the kidneys (Forbes, 2000). In the adult animal, large proportion of glucose and fatty acid absorbed, once maintenance requirements have been met, is stored in the adipose tissues (Forbes, 2000). The maintenance of relatively constant body weight over long period suggests the presence of a signal from the adipose tissues that alter feeding behavior of the animal in a manner to correct any change in body fat content, the mechanism which is called lipostatic regulation (McDonald et al., 2002; Forbes, 2000).

Insulin

It is secreted by the b-cells of the pancreatic islets of Langerhans, and controls energy homeostasis by inhibiting of glucose synthesis in liver via its inhibition of the activities glucagon, and facilitating glucose utilization by peripheral tissues (Roche et al., 2008). In general, insulin may regulate long-term intake and weight in ruminants, however, its role in depression of intake in dairy cows at early lactation, when insulin concentration is low, is unlikely (Forbes, 2007a). The clearance effect of insulin on glucose may also play a role in short-term intake regulation because of its induction hypoglycaemia, which signals the animal to eat (Roche et al., 2008).

Leptin

It is secreted mainly by adipose tissues (Forbes, 2000; Roche et al., 2008), and its secretion is increased as adipocyte size increases (Forbes, 2000). Highly concentrated receptors for leptin are found in the hypothalamus (Pittroff and Soca, 2006). Its circulation in the bloodstream influences receptors in the brain (Forbes, 2000) and by this, it play a key role in the regulating of the intake and expenditure of energy by animals (Roche et al., 2008). Therefore, it is assumed that the concentration of leptin in the blood gives the animal information regarding to its nutritional condition and energy store. Through its interaction with the hormones insulin and neuropeptide Y, leptin it plays an important role in regulation of food intake in relation to fatness and metabolism (Forbes, 2003). It impart its action via its binding to the dorso- and ventromedial nuclei of the hypothalamus and to the acute nucleus, which are the areas of the brain involved in the control of hormone secretion and food intake (Forbes, 2007a).

Oxygen Efficiency Theory

According to Pittroff and Soca (2006), the central idea of the theory of oxygen efficiency (proposed by Ketelaars and Tolkaamp, 1996), is that animals regulate their feed intake in order to optimize a balance
between benefits (provision of nutrients) and costs (damaging by-products of metabolism or free radicals) of feed consumption. In other words intake is regulated to maximize the yield of net energy per liter of oxygen consumed (Fisher, 2002). In this theory, the physical fill has nothing with intake regulation it is simply considered as feeding behavior of the animal (Fisher, 2002) and this was so because the cost-benefit model was developed based on inappropriate experimental methods and interpretation (Forbes, 2007b). Monitoring of metabolizable energy intake and some quantification of free radicals (FR) as well as identification of the pathways through which information flows between the events occurring in the cells (FR formation) to integrating centers are its experimental challenges (Pittroff and Soca, 2006).

Integration of Signals in Feed Intake Regulation

The factors that control feed intake works in integrated way (Forbes, 1996) and the separate consideration of the physical and metabolic intake regulations is only for connivance, and the ruminant’s central nervous system (CNS) integrates the signals (Fisher, 2002). In general, a series of negative feedback signal emanated from the digestive tract, liver and other organ in response to the presence of nutrients controls intake, as well food’s particular sensory prosperities (appearance, flavour, texture), and its metabolic consequence already learned from its previous consumption will determine it is intake or refusal all being integrated by the CNS (Forbes, 2000). There is no single factor that could be considered as a sole regulator of intake, rather a combination of different mechanisms yet interacting with each other controls intake (Fisher, 2002). Therefore, ‘whole system can be viewed as a cascade’ (Figure 1) (Forbes, 2000). The CNS controls most of the activities of the animal including VFI, growth, fattening and reproduction (Forbes, 2007a). It has a role in maintaining homeostasis between nutrient intake and body reserves via integrating the information it receives and hence regulating energy intake and/or energy expenditure (Roche et al., 2008).

![Figure 1: Satiety ‘cascade’. Dotted arrows indicate flows of information to CNS as food goes from being identified in the environment to its nutrients being stored in the body (Forbes, 2000).](image-url)
Conclusion

Ruminants are able to utilize fibrous feeds that have no direct nutritional value for man and process them into human edible (milk and meat) and usable products (hide and skin). However, these fibrous feeds are not able to meet the nutrient requirements of ruminants in most cases and the animals try to obtain the nutrients they require by eating different feeds. This may result in deficiency or excess intake of one or more nutrients. However, ruminants regulate their intake using different mechanisms. Therefore, understanding of the factors affecting intake and the intake regulation mechanisms of ruminants is important for academic and practical purposes.

References

60. Tahir NT. 2008. Voluntary feed intake by dairy cattle; with special emphasis on the effects of interactions between fibre and starch quality in the diet. SLU, Rep No. 3. Available at: http://www.pub.epsilon.slu.se/3427/01/Tahir_N_081121.pdf