

Feeding behaviour in ruminants: a consequence of interactions between a reward system and the regulation of metabolic homeostasis

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Abstract. Feeding behaviour, through both diet selection and food intake, is the predominant way that an animal attempts to fulfil its metabolic requirements and achieve homeostasis. In domestic herbivores across the wide range of production practices, voluntary feed intake is arguably the most important factor in animal production, and a better understanding of systems involved in intake regulation can have important practical implications in terms of performance, health and welfare. In this review, we provide a conceptual framework that highlights the critical involvement and interconnections of two major regulatory systems of feeding behaviour: the reward and the homeostatic systems. A review of the literature on ruminants and rodents provides evidence that feeding behaviour is not only shaped by homeostatic needs but also by hedonic and motivational incentives associated with foods through experiences and expectations of rewards. The different brain structures and neuronal/hormonal pathways involved in these two regulatory systems is evidence of their different influences on feeding behaviours that help explain deviation from behaviour based solely on satisfying nutritional needs, and offers opportunities to influence feeding motivation to meet applied goals in livestock production. This review further highlights the key contribution of experience in the short (behavioural learning) and long term (metabolic learning), including the critical role of fetal environment in shaping feeding behaviour both directly by food cue–consequence pairings and indirectly via modifications of metabolic functioning, with cascading effects on energy balance and body reserves and, consequently, on feeding motivation.

Additional keywords: diet selection, learning, metabolic hunger, neuroendocrine system.

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Introduction

Grazing animals face a world of change, where feed supply can vary enormously from season to season, and from patch to patch. Obtaining appropriate combinations of nutrients despite variability in supply is crucial for productivity and, indeed, survival. Given the variability in supply, both temporally and spatially, animals must regularly recalibrate their decisions and activities to the consequences of their actions.

Diet selectivity is one strategy animals use in an attempt to avoid deficiencies or toxicities. We tend to take for granted the phenomenon of animals showing selectivity, but underlying the exhibited behaviours is a complex set of interactions that are becoming better understood as the disciplines of nutrition, behaviour and brain sciences merge. New insights are emerging to show there is a ‘fuzzy line’ between nature and nurture, and that the experiences of animals modify behavioural responses, both in the short and long term, through neural and physiological effects on cells. The behavioural consequences of the

integration of complex signals is often loosely termed as ‘innate’ or ‘instinctive’, but a different term would be helpful to reiterate that the responses are not necessarily fixed traits, but a reflection of how an animal perceives and interprets its circumstances, and responds accordingly. A more useful terminology could be ‘adaptive behaviour’. As we discuss in this paper, feeding behaviours occur as a consequence of a myriad of signals that integrate the anticipated rewards from consuming a particular food and the metabolic state of the animal at the time. Furthermore, events during critical periods of time, especially during early-life development, can have long lasting effects on feeding behaviours.

In this paper, we present a framework that aims to show how a reward system and homeostatic regulation interact to influence feeding behaviour. We deliberately use the term ‘influence’ here, rather than ‘determine’, because any given factor arising at a point in time can be modified by other factors arising simultaneously or, interestingly, by events of

the past. That is, while any given feeding behaviour reflects the current motivation of an individual, that motivation is a consequence of the integration over time of many factors including sensorial, metabolic and physiological signals. Furthermore, individual animals may resolve the challenge of obtaining adequate nutrients in different ways from each other (Provenza *et al.* 2003), which may partly be due to different set-points in regulatory pathways. Hence, the same reward or metabolic signals may lead to a different magnitude of behavioural response between individuals, or perhaps even a different response altogether.

Throughout the paper, we will focus on voluntary-intake behaviour while considering the reward system that triggers feeding behaviour and the metabolic events, past and present, which shape the behaviour in the longer term. First, we present a conceptual framework to outline the main relationships that influence feeding behaviour. Then we elaborate on the concept of food rewards and discuss how the metabolic state of animals generates signals that are used to influence feeding behaviour. We make a point on satiety and interactions between the reward system and metabolic regulation and, finally, we outline implications to the ‘plasticity’ or adaptability of animals to respond to change and suggest areas requiring further research.

Conceptual framework linking feeding behaviour to signal integration

Eating behaviour begins before food is actually consumed. Recent biomedical research in mammals on the factors affecting food intake, with an emphasis on consequences to weight control, provides useful insights into the complete process, from the initial decision to acquire food, to ingestion and the metabolic processing of nutrients (Berthoud 2002; Berthoud *et al.* 2011). The initiation phase is often overlooked in livestock research; this is the step when animals make a decision to seek food, which could be a general desire to acquire energy or a specific desire for a particular food (e.g. a salt supplement). The initiation phase involves a switch in behaviour, from one activity (or resting) to the act of sourcing and procuring food. The decision to procure food is based on the expected rewards from eating and especially on what is named ‘wanting’ in behavioural neurosciences (Berridge 1996). Interestingly, the initial decision to seek food is based on the expectation of the reward, rather than on the actual reward. The actual reward, if sufficiently positive, will reinforce the instigated feeding behaviour while a sufficiently negative outcome will diminish feeding behaviour, which will subsequently affect ‘liking’ and ‘wanting’. Hence, prior experiences are crucial to the initiation phase, because the strength of the expected reward is influenced by the outcomes of previous encounters with the food. Animals are effectively making a cost–benefit decision based on reward expectancy, which is studied in the new field of ‘neuroeconomics’ (Berthoud *et al.* 2011).

The appetitive phase is the next step, although, in livestock, research is often considered as the first because the initiation phase is overlooked. Here, animals receive information about one or several present feedstuffs on the basis of their sensory

perceptions of sight, smell and taste (notably taste (e.g. Ralphs *et al.* 1995; Ginane *et al.* 2011) and olfactory (Pain *et al.* 2005) cues can be very influential), and have the opportunity to make a choice. These pre-ingestive stimuli and the degree to which they are ‘liked’ then reinforce the motivation to consume each food or act to reduce the likelihood of this food being consumed, on the basis of previous experiences that allow animals to link the sensorial ‘cue’ to metabolic outcomes of consuming the food (Provenza 1995).

Once an animal has been sufficiently motivated to procure food, and assuming the food is available and pre-ingestive signals reinforce the desire to consume the food, then ingestive, digestive and absorptive processes commence. The arrival of nutrients and secondary compounds to cells in the body provides a means by which the animal is able to assess how well its nutritional needs are being met and whether satiety for energy or particular nutrients is reached. The interactions between signals that motivate animals to procure food and physiological signals that occur in response to consuming food are made possible by the integration of signals that emanate from both the internal and external milieu. This integration is a key step in constructing behavioural responses.

Reward regulation of food intake

As outlined in Fig. 1 and discussed in more detail in the section ‘Homeostatic regulation of feeding behaviour’, diverse metabolites inform the animal about its metabolic state and are directly involved in the regulation of food intake, via homeostatic regulation, which includes hunger and satiety. In addition, a large body of research over the past three decades indicates that there is a second system of intake regulation, closely related and connected to the homeostatic system (Berthoud 2007); the ‘reward system’ (Berridge 1996). As procurement of food is vital, the reward system has likely evolved to ensure that individuals will be sufficiently motivated to perform adequate behaviours in an attempt to guarantee ingestion of beneficial foods from a sparse and hostile environment (Berthoud *et al.* 2011). The consumption of beneficial foods is rewarded by pleasurable feedbacks (Provenza 1995) that, in turn, maintain or increase the animal’s motivation to seek the food.

The identification of the reward system as a component of food regulation has been elucidated from a large body of experiments, although mainly conducted in rodent species, many of which have aimed to understand apparent flaws in the regulation of feeding behaviour in humans that lead to health concerns such as obesity and eating disorders (Peciña and Smith 2010; Berthoud *et al.* 2011; Volkow *et al.* 2011). While our focus is on ruminant feeding behaviour, knowledge acquired from other species on the reward system and its interactions with the homeostatic system provides interesting new perspectives that may be equally relevant to understanding ruminant feeding behaviour, with potential consequences to production, health and welfare. However, we acknowledge that further research is needed to test the emerging hypotheses with ruminants.

As defined by Berridge and collaborators, food reward is a complex process that contains the following three distinguishable psychological and functional components:

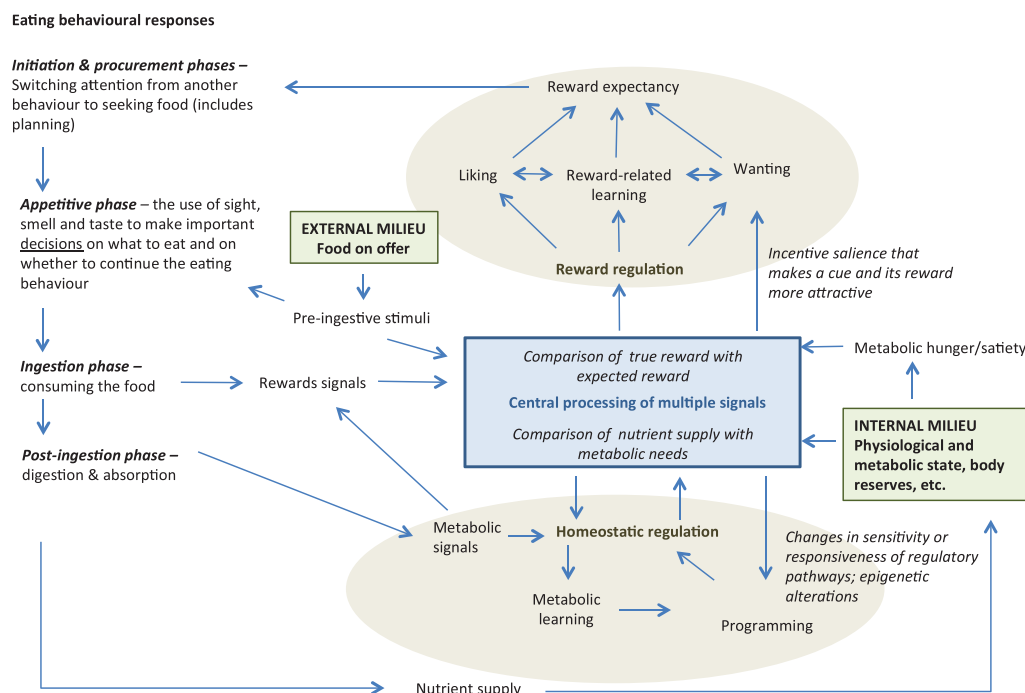


Fig. 1. A conceptual framework showing the relationships between reward regulation, homeostatic regulation and feeding behaviours, including the procurement and ingestion of food.

‘wanting’ (incentive motivation), ‘liking’ (hedonic impact) and learning (associations, representations and predictions) (Berridge 1996; Berridge and Robinson 1998; Berridge and Kringelbach 2008). ‘Wanting’ corresponds to the motivational value of food for which the animal is willing to work, and it can be linked to appetite or incentive salience. ‘Liking’ corresponds to the sensorial pleasantness of food, and it can be linked to affect (i.e. feeling or emotion) and palatability (which itself is influenced by post-ingestive consequences (Provenza 1995)). Finally, learning allows a stimulus that may initially be neutral in its effect to become a cue that acts as a predictor of reward and, therefore, as an incentive stimulus to orientate further behaviours based on past experience (Flagel *et al.* 2011). The ‘wanting’ and ‘liking’ components of the reward system involve different brain substrates and neurochemical pathways. The incentive component (‘wanting’) involves mainly dopaminergic pathways and the hedonic component (‘liking’) involves opioid and cannabinoid pathways (Berridge 1996, 2009; Pénicaud *et al.* 2012). Particular brain manipulations and behavioural tests to identify food ‘liking’ (affective taste reactivity or taste reactivity tests) or ‘wanting’ (instrumental behaviour) have shown that the two components can change in opposite directions, or independently depending on the type of behavioural tests (Berridge 1996).

The ‘wanting’ component

According to the incentive learning theory, the ‘wanting’ component allows the attribution of incentive value to rewarding stimuli. Dopamine has a key role by converting a behavioural event into neural circuits in which a stimulant acquires the ability to capture attention, elicit orientation and

approach, and instigate instrumental and cognitive strategies to want, seek and obtain the stimulant (Berridge 1996; Berridge and Robinson 1998). Therefore, dopamine is involved in the motivation to perform the behaviours necessary to procure and consume the food (Volkow *et al.* 2011), and specifically in the preparatory stages to obtain food (Berthoud *et al.* 2011), including a cost-benefit evaluation of the scheduled action (Salamone and Correa 2002). Experiments with rodents have indicated that the alteration of the dopaminergic function strongly affects ‘wanting’ but does not alter hedonic responses (‘liking’) (Berridge 1996; Berridge and Robinson 1998; Robinson *et al.* 2005). This has been interpreted as evidence that animals without dopamine are unable to use information about rewards to motivate and initiate goal-directed behaviours (Robinson *et al.* 2005), which can ultimately lead to death due to starvation in dopamine-deficient mice despite the presence of food (Szczycka *et al.* 2001). That is, only intact (control) animals ‘want’ the food even though both intact and modified animals ‘like’ it (Berridge 1996). Responses to addictive drugs, which exhibit many commonalities with food reward and addiction, are typically an example of irrational ‘wanting’ without ‘liking’ (Berridge and Kringelbach 2008).

The ‘liking’ component

If ‘wanting’ can be related to the disposition to eat, ‘liking’ relates to the sensory pleasure of actually eating. The hedonic properties of food appear to be mainly related to changes in the opioid, cannabinoid and GABA systems (Berridge 2009). Indeed, opioid agonists increase the hedonic value of foods making them more pleasurable and palatable (Peciña and Smith 2010). Inversely, the administration of opioid

antagonists decreased the hedonic properties of sucrose solutions in the rat, as evidenced by the taste reactivity test (Parker *et al.* 1992). These modifications in pleasantness did not appear to be accompanied by a lessened ability to discriminate between foods (O'Hare *et al.* 1997). Similarly, the acquisition of a conditioned taste preference (Yu *et al.* 1999) or place preference (Delamater *et al.* 2000) was not affected by an opioid antagonist. Myers and Sclafani (2003) reported that after intragastric infusions of glucose, rats increased preference for a flavour paired with the glucose infusion (i.e. a conditioned stimulus), regardless of whether it was sweet, bitter or sour; however, this was accompanied by an increase in palatability (as assessed by taste reactivity tests) only when the taste of the conditioned stimulus was sweet. This suggests that under the conditioning procedure, the 'liking' component would not necessarily be affected, especially for flavours that appear inherently disliked, but that the increase in preference for flavours paired with a positive nutritional outcome (e.g. glucose infusion) would primarily be due to animals wanting it more, without necessarily liking it more (Myers and Sclafani 2003).

The learning component

Learning can be defined as a special type of plasticity that involves internal representations of new information obtained from the current external and internal environments (Dukas 2013). Learning allows animals to better exploit environmental features by continuously adjusting activity on the basis of the mobilisation of accumulated experience. In the domain of food reward, the learning component is essential because it ensures the attribution of incentive value to initially neutral stimuli (food stimuli, places) and the reinforcement of already salient ones (Berridge 1996), thereby allowing the animal to anticipate the likely reward for any possible action (Hyman *et al.* 2006), to develop motivation for reward-related cues, and then to make appropriate decisions. This attribution of incentive value is based on associational processes within reinforcement learning (Sutton and Barto 1998; Montague *et al.* 2004), one form of which is food aversion or preference conditioning.

In reward learning, dopamine pathways have been implicated as playing a role in the development of incentive salience and motivation ('wanting'). The attribution of incentive salience to stimuli makes it more difficult for the animal to resist such cues (Flagel *et al.* 2010) and shapes its determination to obtain the associated reward. This is why, once learnt, a certain feeding behaviour can be strongly enacted thereafter, until other events trigger new learning. Furthermore, dopamine responsiveness appears to encode discrepancy between rewards gained from an action and those predicted, which constitutes the 'reward prediction error' (Flagel *et al.* 2011) that shapes future behaviour so as to maximise rewards (Hyman *et al.* 2006). That is, if the expected reward from consuming a particular food is not received, an animal can recalibrate its expectations on the basis of the actual outcomes – especially with repeated occurrences – and thus changes its feeding behaviour. Several studies also suggest a role for ghrelin in feeding behaviour, via an alteration of brain functions in areas involved in both

reward and incentive motivation, and in learning and memory (Skibicka and Dickson 2011), thus providing a link between homeostatic and reward regulations.

Even though the different components of the food reward that influence motivational 'wanting' and hedonic 'liking' are dissociable in the brain and can fluctuate independently (Peciña and Smith 2010), in practical terms 'wanting' and 'liking' are closely related because animals tend to want food the more it is liked (Peciña and Smith 2010). These two components ('wanting' and 'liking') act in concert to modulate feeding behaviour, such that the most highly nutritious foods often possess a high hedonic value, while toxic elements are associated with low hedonic value. Indeed, from an evolutionary standpoint, this favours the possibility that foods rich in nutrients be considered as potent rewards that promote eating and trigger learned associations between the stimulus and the reward (Volkow *et al.* 2011). Furthermore, both motivational and hedonic values are modulated by physiological hunger and satiety, or by pairings between sensorial characteristics and post-ingestive feedbacks (Provenza 1995; Berridge 1996; Peciña and Smith 2010), which contribute to variability in food preferences. This complexity and variability over time, of 'wanting', 'liking' and body needs (i.e. metabolic requirements) may explain why few experiments with animals other than rodents or primates have attempted to disentangle their respective influences on feeding behaviour. In ruminants, this complexity is greater by rumen digestive processes that can modify ingested nutrients and compounds and delay nutrient absorption through retention of digesta in the reticulo-rumen, thereby altering the reward properties of a food.

Reward regulation of food intake in ruminants

In ruminants, there is no study, to our knowledge, that has aimed to assess the respective influence of 'liking' and 'wanting' components of food reward in the regulation of feeding behaviour. Some authors have investigated the opioid network, but have assessed the effects of injection of agonists or antagonists of opioid receptors on total intake or preference, which confounds 'liking' and 'wanting' components. Nevertheless, from these studies it has been shown that injections of an opiate antagonist generally decreased intake in the short term (few hours) in both sheep (Baile *et al.* 1981; Alavi *et al.* 1991; Obese *et al.* 2007) and cattle (Burgwald-Balstad *et al.* 1995; Montoro *et al.* 2012). Further, the capacity of the opiate antagonist to reduce intake was lower in lean than in obese sheep (Alavi *et al.* 1993) and in fasted than in satiated animals, suggesting that the greater the degree of negative energy balance, the greater the opiate drive for hunger (Alavi *et al.* 1991). Concerning dietary preference, injection of an opioid antagonist prevented calves from expressing preferences between a sweetened and a plain (unsweetened) starter feed, suggesting that in cattle, as in other species, the opioid system controls short-term feed intake by modulating the oro-sensorial response to feed consumption (Montoro *et al.* 2012). These results, even if not able to distinguish between hedonic and motivational components of feeding behaviour, underlie the fact that sensorial characteristics of foods are important for ruminants as in most other animals (Favreau-Peigné *et al.* 2013).

Considering the three components of reward regulation, the one that has received most attention is learning, i.e. the ability to associate foods (discriminated and identified by their pre-ingestive characteristics) with the digestive and metabolic consequences experienced after ingestion (post-ingestive consequences, Provenza and Balph 1987; Provenza 1995), and to use this knowledge to shape future behaviours. Since the initial works of Zahorik and Houpt (1981), and then of Provenza and collaborators from the 1980s onwards (Thorhallsdottir *et al.* 1987; Provenza and Balph 1988), a large body of research has compiled strong evidence of the learning abilities in domestic ruminants on the basis of post-ingestive consequences (negative or positive). Hence, ruminants have been shown to develop aversions for foods associated with gastro-intestinal malaise due to administration of emetic substances (du Toit *et al.* 1991), to plant secondary compounds (Provenza *et al.* 1990; Kyriazakis *et al.* 1997; Duncan *et al.* 2000), to excess of nutrients (Ralphs *et al.* 1995) or even to excessive ruminal fill (Baumont *et al.* 2007; Villalba *et al.* 2009). Conversely, they have developed preferences for foods associated with energetic rewards (e.g. glucose, Burritt and Provenza 1992), protein rewards (e.g. casein, Arsenos and Kyriazakis 1999; Ginane *et al.* 2009), mineral rewards (e.g. phosphorus, Villalba *et al.* 2006) and, as recently found, vitamin E (D Amanoel, DT Thomas, D Blache, JTB Milton, MG Wilmot, DK Revell, HC Norman, unpubl. data) (for a general review see Provenza and Villalba 2006). The learning component is closely linked with the other two reward components because it ensures the attribution of incentive value to initially neutral stimuli ('wanting') and calibrates the palatability of foods according to post-ingestive consequences ('liking'). In return, the hedonic value of a food maintains a direct role in the learning process and the establishment of subsequent preferences in ruminants; the strength of the learned preference or aversion increases when the taste or flavour of a food is initially appreciated or not, respectively (Favreau *et al.* 2010a, 2010b). Thus, if a 'liked' food is also 'wanted', the preference is reinforced and learning is facilitated. However, when 'liking' and 'wanting' are inconsistent, the strength of the association is lowered and learning impaired. Burritt and Provenza (1996) reported that sheep had more difficulty in associating a negative consequence with a familiar and safe food than with a new food; this highlights the importance of the relationship

between what an animal expects and what it experiences in determining behavioural decisions, at least in the short term, and the importance of past experiences influencing these responses. The interplay between 'liking' and 'wanting' may help explain why animals appear to show inconsistent behaviours to the same food over time and, indeed, why different individuals may show different behaviours to the same food at any given point in time (Table 1).

Support for the relationships in Table 1 was shown in a recent experiment where grazing sheep were offered a mixture of forage shrubs and moved to a new plot every day (Revell *et al.* 2013). The shrubs were all novel to the animals at the start of the experiment. When the animals were first presented with the plants (over Weeks 1–4), they readily consumed some species, removing most of the edible biomass from each plant, but selected other shrub species to a lesser extent. As there had been no prior opportunity for the animals to learn about the consequences of consuming the different plants, the initial intake pattern was likely a reflection of how much they 'liked' the different plant species. Over Weeks 4–8, the initially preferred plants remained highly sought after (Scenario A in Table 1), some of the initially avoided plants became more readily consumed (Scenario C), whereas others remained less preferred (Scenario D). Scenario B (i.e. a decline in preference value) was not observed, presumably because no plant that was initially 'liked' generated negative metabolic signals post-ingestion, to alter its acceptability by the sheep.

Behaviours based on hedonism and post-ingestive consequences may appear logical and consistent with what we, humans, feel about foods and how our intake patterns can change, but we believe that, in ruminants too, feeding behaviour is not only shaped by homeostatic needs but also by sensorial characteristics of foods and rewards associated to their consumption. Improving our understanding of the relationships existing between these determinants and how we can influence them by altering the feedstuffs or plants we offer to livestock represents an opportunity to improve animal welfare, health and performance.

Homeostatic regulation of feeding behaviour

Food intake is related to the nutritional requirements of the animal and this relationship is based on the concentration of

Table 1. Summary of interactions between the hedonic (reward) and metabolic homeostatic systems on short- and long-term feeding behaviours

Scenario	Hedonic system	Post-ingestive reward	Likely behaviour in short term	Changes in hedonic and motivational drivers	Likely behaviour in longer term
A	'Likes'	Positive	Ready consumption of the food	Increased 'wanting' and 'liking'	Consistently high preference value – ready consumption of the food
B	'Likes'	Negative	Ready consumption of the food	Decreased 'wanting' and 'liking'	Decline in preference and possible decline in intake
C	'Dislikes'	Positive	Avoidance of the food	Increased 'wanting' No change in 'liking'	Changing preferences, from low to medium. Possible increase in intake but may be limited by a persistent dislike
D	'Dislikes'	Negative	Avoidance of the food	Decreased 'wanting' and 'liking'	Consistently low preference value – avoidance of the food

peripheral signals (nutrients, metabolites, hormones or peptides) that reflect both the short–mid-term energy balance and nutritional status, and the long-term energy stores (adiposity). Some of these peripheral signals are now recognised to gain access to the brain and induce neuro-endocrine responses that regulate food intake (orexigenic and anorexigenic systems) and energy expenditure, and thus energy balance (homeostatic regulation). Our framework on the regulation of feed intake (Fig. 1) includes peripheral signals that vary depending on food intake and physiological state, and the concept that pathways involving these peripheral signals are centrally integrated to influence food intake in concert with the reward system.

In reviewing the peripheral signals that may be involved in the regulation of food intake, we report the variation of different nutrients, metabolites and hormones that arise from nutritionally or physiologically induced variations in food intake in ruminants (Table 2). Among the many factors that have been studied to link peripheral signals and food intake, we use food deprivation and early lactation as examples to discuss how the concentration of metabolites in plasma and neural-fluid compartments can influence feeding behaviour. Food deprivation or fasting have been extensively used to identify short- (days) and medium-term (weeks) signals influencing energy balance (Chilliard *et al.* 1998) and the available data may help identify hunger signals (orexigenic signals). Briefly, food deprivation leads to (i) increases in plasma non-esterified fatty acids (NEFA) arising from fat mobilisation, pre-prandial β -hydroxybutyrate arising from hepatic ketogenesis, and also ghrelin and growth hormone, and (ii) decreases in plasma insulin, leptin and metabolite concentrations resulting from food digestion (i.e. acetate, total amino acids and urea). Peculiarities in the concentration of peripheral signals in underfed ruminants lie in that glucose concentration is not modified or only slightly decreased due to its metabolic (hepatic neoglucogenesis from NEFA) rather than digestive origin, because a major portion of ingested carbohydrates is degraded to volatile fatty acids in the rumen. Moreover, the concentration of triglycerides decreased in underfed ruminants, contrary to what is observed in monogastric animals, due to the low recycling in the liver of plasma NEFA (mobilised from adipose tissue) as triglycerides-rich lipoproteins (Bonnet *et al.* 2000, 2004).

The periparturient period in dairy ruminants is another well-characterised metabolic state associated with a decrease in food intake. In this case, reduced food intake occurs as a consequence of reduced digestive-tract capacity, changes in hormones and metabolites associated with the onset of lactation, and changes in body energy stores and energy balance (Bell and Bauman 1997; Chilliard 1999). Secretion of numerous hormones varies during lactation to re-orient metabolic flows (telephoresis) to ensure priority of lactation. During early lactation, plasma concentration of growth hormone increases together with a decrease in insulin, which favours nutrient partitioning to the mammary gland. The plasma concentration of telephoretic hormones can be modified by other hormones, peptides or nutrients, such as adipokines and gut peptides (incretins; Relling and Reynolds 2007). Many of these hormones or metabolites are involved in both central

Table 2. Variation in concentration of nutrients, metabolites, hormones and peptides in the plasma and the cerebrospinal fluid (CSF) from underfed and periparturient ruminants

–, +, =, a decrease, increase or no change, respectively; n.d., not determined

	Underfed ruminants		Periparturient ruminants	
	Plasma	CSF	Plasma	CSF
Glucose	= ^A or – ^B	– ^A	– ^C	– ^C
Acetate	– ^{A,D,E}	n.d.	+ ^C	n.d.
Urea	– ^{D,E} or = ^A	= ^A	+ ^C	+ ^C
β -hydroxybutyrate	+ ^{D,E} or + ^A	= ^A	+ ^C	+ ^C
Lactate	= ^{D,E}	= ^A	– ^C	– ^C
NEFA	+ ^{A,B,D,E,F}	= ^A	+ ^C	= ^C
Total amino acids	= ^A	– ^A	= ^C	– ^C
Leucine, isoleucine	+ ^A	= ^A	= ^C	+ ^C
Arginine, lysine	+ ^A	= ^A	= ^C	= ^C
Carnosine, tryptophan	– ^A	= ^A	= ^C	= ^C
Serine, threonine, tyrosine	= ^A	– ^A	= ^C	= ^C
1- and 3-methylhistidine	+ ^A	+ ^A	= ^C	= ^C
Glutamine	= ^A	= ^A	– ^C	– ^C
Glycine	= ^A	= ^A	+ ^C	+ ^C
Citruline	= ^A	= ^A	= ^C	+ ^C
α -aminobutyric acid	= ^A	= ^A	+ ^C	+ ^C
Insulin	– ^{B,D,E}	– ^J	– ^K	n.d.
Leptin	– ^{G,H}	n.d.	– ^C	– ^{C,L}
Acylated ghrelin	+ ^{B,F}	n.d.	= ^C	= ^C
GH	+ ^{B,I}	n.d.	+ ^K	n.d.
Resistin	n.d.	n.d.	– ^C	= ^C

^AData from lactating (87–96 DIM) cows underfed (–50% intake = –235% energy balance) during 9 days (Laeger *et al.* 2012).

^BData from steers underfed (80% MER) during 21 days (Wertz-Lutz *et al.* 2008).

^CData from periparturient (–20 days versus +40 days postpartum) lactating cows (Laeger *et al.* 2013).

^DData from dry non-pregnant ewes underfed (20% of maintenance energy requirement, MER) during 7 days (Bocquier *et al.* 1998).

^EData from dry non-pregnant cows underfed (20% MER) during 7 days (Delavaud *et al.* 2002).

^FData from heifers underfed (50% MER) during 8 weeks (Field *et al.* 2013).

^GData from dry non-pregnant ewes underfed (20% of maintenance energy requirement, MER) during 7 days (Bonnet *et al.* 2000).

^HData from dry non-pregnant cows underfed (20% MER) during 7 days (Bonnet *et al.* 2004).

^IData reviewed by Chilliard *et al.* (2000).

^JData from adult male sheep underfed (–70% of intake) during 8 weeks (Rhind *et al.* 2000).

^KData reviewed by Chilliard (1999).

^LData reviewed by Chilliard *et al.* (2005).

control of feed intake and regulation of adipose tissue, providing a mechanism to link feed intake and tissue metabolism. For example, peptides secreted by the small intestine during the digestive process may stimulate insulin secretion by the pancreas, decrease food intake through hypothalamic receptors (e.g. glucagon-like peptide 1) and affect adipose tissue metabolism, at least in monogastric animals. Also, the release of the anorexigenic leptin is positively correlated with both the energy ingested daily in the short term, and the degree of adiposity and plane of nutrition in the long term (Chilliard *et al.* 2005). In the dairy goat, leptin

concentration decreases during early lactation, and this persists throughout lactation despite a positive energy balance (Bonnet *et al.* 2005). The prolonged hypoleptinemia may increase the metabolic efficiency of the dairy female and allow the recovery of adipose tissue (Chilliard *et al.* 2005). Inversely, the peptide ghrelin secreted by cells of the abomasum is an endogenous ligand for the receptors of growth hormone secretagogues and acts as an orexigenic signal. Acute injection of ghrelin in beef cattle has tended to increase food intake in the following hours (Wertz-Lutz *et al.* 2006), although during long-term infusion of ghrelin in lactating cows, there was a decrease in body condition score and an increase in plasma NEFA concentration (Roche *et al.* 2008a). Leptin, ghrelin, insulin, specific amino acids and fatty acids are among the peripheral signals that are likely to enable ruminants to sense the short-medium-term energy balance (nutritional status) and long-term energy stores. They play a key role in the neural control of energy homeostasis in monogastrics (Berthoud *et al.* 2011; Volkow *et al.* 2011; Moullé *et al.* 2014) as well as in ruminants (Roche *et al.* 2008b; Allen and Bradford 2012).

Peripheral signals can be classified as anorexigenic or orexigenic if they fulfil key criteria (Roche *et al.* 2008b), such as their ability to reach neural tissues and affect voluntary feed intake when exogenously administered. To affect feeding control centres within the central nervous system, peripheral signals must pass from blood to neural tissues or their fluid spaces, which implies a transport across the blood-brain barrier or the blood-cerebrospinal fluid (CSF) barrier. Whether the peripheral signals presented above cross the barriers and whether the differences in plasma concentrations are also found in the CSF have been investigated in underfed ruminants (Rhind *et al.* 2000; Laeger *et al.* 2012) and in periparturient cows (Laeger *et al.* 2013; Table 2). Orexigenic signals in underfed and periparturient ruminants are decreased plasma and CSF concentrations of well known anorexigenic signals such as glucose and leptin, as well as insulin, serine, threonine and tyrosine. Indeed, intra-cerebroventricular injections of glucose (Seoane and Baile 1972), insulin (Foster *et al.* 1991) and leptin (Miller *et al.* 2002) in fed ruminants decreased food intake through central pathways (reviewed by Roche *et al.* 2008b), and serine, threonine and tyrosine are proposed to decrease food intake directly or indirectly as precursors of anorexigenic neurotransmitters (Laeger *et al.* 2012). Thus, the low concentration of glucose, serine, threonine, tyrosine, insulin and leptin in CSF may elicit hunger and favour increase in food intake in underfed and early lactating ruminants. The hypoleptinemia of lactation has been proposed to activate neuropeptide Y orexigenic pathways and attenuate anorexigenic melanocortin and cocaine- and amphetamine-regulated transcript (CART) pathways in the hypothalamus (Sorensen *et al.* 2002). At the other end of the control system, proposed anorexigenic signals are increased concentrations, both in plasma and CSF, of 1- and 3-methylhistidine (in underfed ruminants) and β -hydroxybutyrate, glycine, citrulline, α -aminobutyric acid, leucine and isoleucine (in early lactating cows). Whether these peptides and amino acids act on food intake by a direct effect on the brain, on the synthesis of neurotransmitters, or through an indirect effect by modulating plasma concentration of insulin

(Kuhara *et al.* 1991), or all of the above, remains to be studied. Altogether these data highlight that peripheral signals can be used as sensors of the energetic balance and body reserves in ruminants and, therefore, can be integrated by the brain to regulate feed (energy) intake and energy expenditure.

Interactions between homeostatic regulation, hunger, satiety and the reward system

As we have seen in previous sections, both homeostatic and reward regulatory systems act on feeding behaviour. Food deprivation and peripheral homeostatic regulators of energy balance (leptin, insulin, orexin, ghrelin or peptide YY) modulate the rewarding attributes of food cues (see Lattemann 2008 for review; Skibicka and Dickson 2011), due to an overlap between neurocircuitries (Volkow *et al.* 2011). For example, in rodents, injections of the orexigenic signal ghrelin in normal animals increased consumption of a rewarding diet or of saccharin solution over regular chow or water, while they failed to do so in rats or mice insensitive to ghrelin (Disse *et al.* 2010; Egecioglu *et al.* 2010). Functionally, it appears that the increase or decrease in sensitivity of limbic brain regions (and specifically of dopamine neurons) to food stimuli by orexigenic (e.g. ghrelin) and anorexigenic (e.g. leptin) peripheral signals, respectively, links the reward and homeostatic regulatory systems (see Chuang *et al.* 2011; Berthoud *et al.* 2011; Skibicka *et al.* 2011; and Volkow *et al.* 2011, for reviews). Behaviourally speaking, this would result in a state where a hungry animal is more attentive to minor environmental cues indicating potential food rewards and assigns them higher incentive value. Thus, homeostatic and reward circuitry act in concert to promote an animal's motivation to engage in eating behaviours under conditions of deprivation and, once needs are satisfied, to stop the feeding behaviour permitting other critical behaviours (such as mating, social relations, resting) that, all together, ensure an individual's fitness.

Furthermore, at the scale of meal-eating or daily intake, changes in feeding motivation and decisions to start or stop eating rest on the processes of hunger and satiety, which are an integration of signals associated with (i) sensorial characteristics of the food, (ii) physical distension of the digestive tract after ingestion of food, and (iii) metabolic consequences of absorbing nutrients. As discussed in the previous section, 'Homeostatic regulation of feeding behaviour', products of digestion actively participate in regulating feed intake. During main meals, rapid fermentation of the soluble fraction of feeds increases the osmotic pressure and volatile fatty acid (VFA) concentration in rumen fluid (mainly acetic, propionic and butyric acids), and lowers pH (Rémond *et al.* 1995). These increases in VFA induce satiety, as shown in experiments where VFA infusion in the rumen decreased feed intake in the short-term (Faverdin *et al.* 1995). These signals are sensed by chemoreceptors present in the rumen wall and/or in the liver that enable the animal to avoid nutritional excess and disorders. This may explain the low duration of meal eating observed in sheep fed grass silage, for example, which contains large amounts of organic acids and ammonia, especially when the silage is poorly preserved

(Van Os *et al.* 1995). In such cases, satiation occurs before rumen fill reaches a maximum.

Physical satiety relies on stretch- and mechano-receptors in the rumen wall (Leek 1977) that detect digestive-tract distension. When experimentally stimulated by rumen filling with indigestible material, both cattle and sheep showed a decrease in total intake and an increase in the number of meals and in the time spent ruminating per unit of feed ingested (Baumont *et al.* 1990a, 1994; Favardin *et al.* 1995) in an attempt to increase the rate of digesta outflow and reduce rumen fill to its normal level. Rumen capacity can thus play an important role in intake regulation and may help explain variability between individuals in intake and food conversion efficiency, notably on poor-quality forages that cause a high level of gut fill.

The sensorial attributes of foods that influence dietary decisions as discussed in the section 'Reward regulation of food intake', are also involved in the regulation of hunger and satiety. For example, they can at least partially override satiety signals due to rumen fill to maintain intake. This can be seen with satiated sheep consuming a substantial second meal following the presentation of new, palatable food (Baumont *et al.* 1990b). This second meal was then associated with an increase of ~10% in rumen fill compared with the daily maximum observed without this additional food source. In contrast, monotonous sensorial stimulation that occurs when there is no variety in food offerings can lead to satiety. This relates to the concept of 'sensory specific satiety', which assumes that the hedonic value of food sensory characteristics will decrease as it is consumed (Rolls 1986).

During a meal, all of the signals that contribute to the satiation process act simultaneously and probably additively, as indicated by the additive effects of an increase in rumen fill and acetate infusion (Adams and Forbes 1981). Different signals are integrated by the central nervous system and balanced with other stimuli to help ensure that the selected diet meets, as best as possible, the needs of the animal.

Developmental programming can reset the 'internal' state of an animal: long-term and possible trans-generational regulation of feed intake

As discussed in the 'Reward regulation of food intake' section, the regulation of the reward system is shaped by experiences that alter an animal's prediction of the magnitude of reward. We suggest that there is an analogous phenomenon associated with homeostatic regulation, whereby nutritional experiences can shape physiological and metabolic processes. This is often referred to as 'metabolic memory', or 'programming', although the latter term implies an element of certainty regarding the destiny of an animal, which overstates the reality. Nevertheless, events, or 'insults', during critical periods of growth and development may have lifelong impacts on offspring due to lasting alterations in structures and functions of tissues (e.g. kidney morphology in lambs born to ewes that consumed a high-salt diet during the last third of pregnancy (Tay *et al.* 2012), and in re-setting neuroendocrine systems and tissue growth (Cottrell and Ozanne 2008; Dulloo 2008; Chadwick *et al.* 2009a, 2009b; Symonds *et al.* 2009; Bonnet *et al.* 2010; Greenwood *et al.* 2010)). The concept of developmental programming, also termed 'fetal programming',

'the Barker hypothesis', 'the thrifty phenotype' or 'the developmental origin of health and disease', has generated studies in ruminants that provide some evidence that alterations in maternal and neonatal nutrition may alter the profile of peripheral signals and have 'carryover' effects on feed intake (Roche *et al.* 2008b). From a functional standpoint, these experiences are preparing the fetus for the environment where it will live. That is, prior events that influence metabolic responses can alter feeding behaviours in the longer term, which can have impacts on animal production. For example, lambs born from ewes that consumed the high-salt plant, saltbush (*Atriplex nummularia*), performed better when they grazed saltbush after weaning (Chadwick *et al.* 2009c).

Plasma concentrations of some orexigenic and anorexigenic peripheral signals can be modified by 'developmental programming'. For example, plasma concentrations of insulin and glucose in near-term ovine fetuses are decreased by maternal undernutrition (~50% level of controls, Ehrhardt *et al.* 2002; Yuen *et al.* 2002) and increased by maternal overfeeding (about +55% of controls, Muhlhauser *et al.* 2007) during late gestation. In the same studies, plasma concentration of leptin or leptin gene expression in adipose tissues were not modified, which indicates that secretion of leptin in sheep fetuses is relatively resistant to medium-term maternal undernutrition or overfeeding (McMillen *et al.* 2006; Forhead *et al.* 2008). However, fetal leptin synthesis by adipose tissue can be modified by profound and chronic variations in insulinaemia (Devaskar *et al.* 2002) which suggests that leptin may actually participate in the hormonal responses to changes in the intrauterine environment. To what extent exposure to variations in plasma concentrations of peripheral signals *in utero* results in the regulation of food intake and energy expenditure (homeostatic regulation) may be questioned because of the lack of the concept of 'appetite' in fetuses that normally received a near-continuous transplacental supply of nutrients. Nevertheless, variations in peripheral signals during late pregnancy may coincide with the maturation of the brain and the hypertrophic growth of tissues and may consequently 'program' the sensitivity and functioning of central feeding centres and peripheral tissues involved in the homeostatic regulation of offspring. Indeed, in ruminants (which differ from rodents in this respect), the hypothalamus-pituitary-adrenal axis and hypothalamus-adipose axes develop before birth and thus may be sensitive to intrauterine influences (Symonds *et al.* 2009; Breton 2013). At least in monogastric animals, leptin and insulin can be trophic factors during development that stimulate connectivity of appetite-regulating brain pathways (Spencer 2013). In support of the concept of fetal programming of food intake in ruminants, hyperphagia was reported for lambs born with low birthweight (as the result of maternal undernutrition; Greenwood *et al.* 1998), in 30-day-old lambs born from overfed ewes (Muhlhauser *et al.* 2006), and interestingly, in 6-year-old ewes born from underfed ewes (George *et al.* 2012). Fetal programming of food preferences for high-fat diet has also been suggested in young lambs born from underfed ewes (Nielsen *et al.* 2013).

The reported hyperphagia may result first from modifications in the fetal or post-natal hypothalamic appetite-regulating systems of the offspring. Indeed, maternal undernutrition

increases the mRNA abundance of the orexigenic neuropeptide Y (Warnes *et al.* 1998), increases histone acetylation and hypomethylation of the glucocorticoid receptor, and decreases the promoter methylation of the *POMC* gene (Begum *et al.* 2012) in the fetal sheep hypothalamus. Most of the recent attention in the area of developmental programming has focussed on changes to the epigenome, at least in monogastric animals, as it is the mechanism that allows cells to respond to changing environmental stimuli more quickly than is possible with changes to the genome itself. Changes to epigenome marks (e.g. histone modifications, microRNAs and methylation) may confer the ability of cells to 'memorise' encounters with their environment (Intine and Sarras 2012). The few epigenetic studies in ruminants suggest that differences in promoter methylation and acetylation of two major hypothalamic genes controlling food intake may have implications for feeding behaviour in adult sheep.

Second, the hyperphagia also may have been indirectly induced from peripheral signals that report the variations in adiposity and in the sensitivity of peripheral tissues to insulin or glucose. In sheep, maternal undernutrition during early pregnancy increases back fat thickness and leptinemia at 4 months of age and visceral adiposity at 6–12 months (for review, see Bonnet *et al.* 2010), as well as at 24 months (Nielsen *et al.* 2013). Moreover, maternal undernutrition during late pregnancy and maternal overfeeding throughout pregnancy decrease whole-body insulin sensitivity at 6 months of age in lambs (Khanal *et al.* 2014) and impair insulin muscle signalling at 24 months in sheep (Yan *et al.* 2011).

The interplay between the modified central pathways, altered adiposity, insulin-signalling and the perinatal environment and nutrition may contribute to short- and long-term changes in food intake, and thus suggests implications for the control of food intake in adulthood if we assume that mechanisms described in monogastric animals with high adiposity (Berthoud *et al.* 2011; Volkow *et al.* 2011) are conserved in ruminants (Nielsen *et al.* 2013). The few ruminant studies (e.g. McMillen *et al.* 2006) are, in general, consistent with those reported in monogastric animals (Breton 2013; Spencer 2013), but highlight that in ruminants, insulin and glucose rather than leptin seem to be involved in fetal programming of voluntary food intake and energy expenditure after birth.

Developmental programming has been reported in the first generation while programming of subsequent generations has received less attention, especially in ruminants. Transgenerational fetal programming in ruminants was proposed by Vonnahme *et al.* (2006) who managed two flocks differently over 6–8 generations, namely, either a sedentary lifestyle and adequate nutrition or nomadic lifestyle and limited nutrition. When ewes were underfed in early pregnancy, lambs born from sedentary ewes but not those born from nomadic ones exhibited increased appetite, adiposity, plasma glucose concentration and insulin resistance when they were subjected to *ad libitum* feeding during growth (Burt *et al.* 2007; Ford *et al.* 2007). Other evidence comes from identifying epigenetic processes that exert lasting and heritable controls over gene expression without altering the genetic code. These controls are mediated through DNA methylation,

acetylation, covalent histone methylation, non-coding RNA. Thus, modified acetylation or methylation in promoter region of *POMC* and glucocorticoid receptor genes in fetal hypothalamus born from underfed ewes (Begum *et al.* 2012) may influence food intake not only in the first generation but also in the following generations, but this remains to be investigated.

Implications to managing livestock to cope with change and capitalise on diversity

Domestic herbivores worldwide are confronted with a large range of production systems, from intensive feedlots with nutrient-dense, formulated diets to diverse rangeland conditions where variability in food availability and quality occurs both temporarily and spatially. Regardless of the system, dry matter intake is arguably the most important factor in ruminant animal production (Roche *et al.* 2008b). In intensive systems, key issues relating to feed intake notably include the following: the need to maintain high intake levels in high-producing animals such as dairy cows to minimise adverse health events at key times (e.g. in early lactation); minimising substitution with supplements to better utilise pasture; and avoiding neophobia to facilitate feeding transitions. Managing neophobia can also be important in low-input systems where animals may be fed low-palatability feeds due to scarcity of other forages, or where pasture species vary considerably over time and space. All these issues highlight the need to promote or maintain high motivation to consume foods varying in both sensorial and nutritional characteristics. Better understanding of the systems involved in the regulation of food intake will help identify ways to improve performance, health and welfare of livestock. This opens the way to interesting future research.

We have seen that feeding behaviour is not only shaped by homeostatic needs but also by sensorial characteristics of foods and rewards associated with their consumption. Consequently, considering the satisfaction of sensorial needs may help improve feeding motivation. Domestic grazing herbivores are generalists in that they select a high diversity of food items if they have opportunity to choose (Duncan *et al.* 2003) and have experience with the range of foods on offer. The observed stimulation of total intake when diversity is offered (Ginane *et al.* 2002), preference for places offering a diversity of flavours (Scott and Provenza 1998), or even higher cortisol concentrations in lambs receiving a monotonous diet than in counterparts receiving a diverse one (Villalba *et al.* 2012), can be seen as the expression of the interaction between the ruminant's need to satisfy sensorial requirements and to obtain a mix of nutrients to meet its metabolic requirements. As a consequence, offering diversity can increase feeding motivation, with possible consequences on intake, feeding efficiency and performance. Fynn (2012) reviewed the implications of functional resource heterogeneity in livestock production, and reported that capacity of grazing herbivores to manage temporal and spatial variation is advantageous and the greater the spatial heterogeneity of vegetation, the higher the survival rates of domestic (Scoones 1993) and wild (Walker *et al.* 1987) ungulates. Offering a diversity of foods increases the opportunity for animals to adjust intake in response to changes

in their own requirements, and allows individuals to each select a diet appropriate to its specific circumstances (Villalba *et al.* 2010).

It may appear challenging to manage animals in a way that capitalises on diversity when the feeding environment can be so variable (over space or in time). Providing animals with experience is particularly important to improve the acceptability of foods that are new or, initially, of low palatability. As discussed above, early life exposure, especially during key developmental 'windows' during gestation or early post-natal life, can have persistent effects. There is an opportunity for managers of livestock to capitalise on this phenomenon by ensuring, as much as possible, that food sources that an animal will likely encounter later in its life are offered to its dam during pregnancy and pre-weaning (e.g. see Petersen *et al.* 2014). Providing repeated opportunities, or 'lessons', is a way for animals to become familiar with foods and learn about, pre-ingestive sensory cues and post-ingestive consequences of consuming particular foods or plants. Where possible, using a familiar and 'liked' flavour may encourage animals to consume a novel food.

Beyond the nature of foods offered early in life to animals, the context in which first experiences occur may also be important. Thus, the circumstances that prevailed when an animal was previously presented with a feedstuff or a particular plant may influence its initial willingness to consume it during subsequent encounters. If an animal had a higher metabolic hunger when previously exposed to the food, it is more likely to 'like' it when it next encounters that food (see Villalba *et al.* 2015). Conversely, if a particular food was present as a small proportion of an abundant supply and the animal had a relatively low metabolic hunger at the time, the degree of motivation to subsequently consume the plant is likely to be low. In this case, a greater effort to entice the animal to consume the food may be needed, such as applying a higher grazing pressure or using experienced animals as 'peer trainers' (Thomas *et al.* 2009).

Feeding behaviours, from the motivation to procure food through to the metabolism of ingested nutrients, reflect a complex interaction between a reward-related learning and metabolic learning or programming. Much of the literature in the emerging disciplines of behavioural genetics, brain science and nutritional behaviours has been based on studies with monogastric animals (rodents or humans), but there is sufficient evidence with ruminants to indicate that the same principles should apply. Nevertheless, there is a great opportunity for knowledge of ruminant nutrition to be combined with insights in behavioural sciences to better understand the complex regulation of feeding behaviours to promote feeding practices that optimise performance, resource use and welfare of grazing livestock.

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