2010

Links Between Ruminants' Food Preference and Their Welfare

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Animal (2010), **4:7**, pp 1240–1247 © The Animal Consortium 2010
doi:10.1017/S1751731110000467

Links between ruminants' food preference and their welfare

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(Received 26 August 2009; Accepted 4 February 2010; First published online 10 March 2010)

Nutrition is an important aspect of welfare, and in most recommendations for the welfare of animals adequate nutrition is a primary requirement. However, in intensive livestock production systems the decision for adequate nutrition is made based on traditional paradigms of feeding monotonous rations or plant monocultures, frequently with excesses or imbalances of nutrients relative to the individuals' physiology, which can compromise welfare. Individual ruminants can better meet their needs for nutrients and regulate their intake of secondary compounds when offered a variety of foods than when constrained to a single food, even if the food is nutritionally balanced. The concept of food variety is central because monotonous flavors and feeds and excess nutrients all cause animals to satiate, which in turn causes animals to eat a variety of foods. When offered a variety of foods, satiety for single foods stimulates the selection of a diverse diet and thus food intake, but when restricted to a monotonous diet satiety is aversive and limits food intake. Moreover, if a monotonous diet is aversive to animals then this could be stressful, even if monotony implies consuming a balanced diet. A diverse diet may also increase resistance to disease in ruminants, by allowing consumption of small amounts of compounds with antimicrobial/antiparasitic effects and immunity-enhancing properties. Herbivores also experience the benefits of ingesting compounds with medicinal (i.e. antiparasitic) benefits and they learn to prefer foods containing such compounds as their preferences are associatively conditioned by the food's homeostatic utility to the body. Such learned patterns of behavior begin in utero *and feeding experiences early in life cause changes – neurological, morphological and physiological – in animals, which influence on their subsequent behavior and welfare. Such experiences with the environment enable animals to adapt to local diets and stressors and reduce the levels of fear. Finally, feeding behavior in farm animals could be an aid in the early detection and mitigation of pain or sickness, and as such become an important tool in the identification of welfare and health of animals before the appearance of clinical signs. Management strategies in ruminant production systems could benefit by allowing animals to manifest their feeding preferences, thereby acknowledging the animals' role as active players in feeding systems, instead of regarding them as passive entities that just respond to prescriptions and formulations.*

Keywords: foraging, well-being, food selection, early experience, nutrients

Implications

Nutrition is an important aspect of welfare. However, in intensive livestock production systems animals receive monotonous rations or plant monocultures, frequently with excesses or imbalances of nutrients which compromise welfare. Exploring the feeding behavior of ruminants when offered a variety of feeds has the potential to improve their health and well-being by reducing levels of stress and fear and providing early detection of pain and illness. Management strategies in ruminant production systems should benefit by acknowledging the animals' role as active players in feeding systems and by incorporating feeding behavior as a measure on how well homeostasis is achieved.

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Introduction

Nutrition is an important aspect of welfare, and in most recommendations for the welfare of animals adequate nutrition is a primary requirement (FAWC, 1993; Kyriazakis and Savory, 1997). Under-nutrition not only impairs the biological functioning of animals, it also leads to hunger, which is a noxious experience (Mellor and Stafford, 2004). But what is adequate nutrition? What is the standard for adequate animal nutrition and consequently adequate animal welfare? Is feeding a diet that meets nutritional needs sufficient? Intensive livestock feeding systems commonly provide uniformly formulated foods based upon table values of nutrient requirements. If all nutrient requirements are met for the 'average' member of the herd, then it follows that adequate nutrition is achieved. Nevertheless, individuals

within a herd vary substantially in their intake and preferences for feeds, needs for nutrients and tolerance of excesses of nutrients in their diets.

Differences in food intake and nutrient requirements depend on an animal's past experiences as well as on variations in how animals are built morphologically and how they function physiologically (Provenza *et al*., 2003). For instance, variation in dental arcade causes individual sheep and goat to forage with different efficiencies (Gordon *et al*., 1996). Differences in organ mass and how animals metabolize macronutrients affect foraging (Konarzewski and Diamond, 1994). Sheep and cattle of uniform age, sex and breed vary in their preferences for foods. Some animals prefer foods high in energy, whereas others prefer foods of medium or even low energy, and given a choice, individuals vary their diets from day to day (Provenza *et al*., 1996; Early and Provenza, 1998; Scott and Provenza, 1998 and 1999; Atwood *et al*., 2001a). Doses of sodium propionate that condition preferences in some lambs, condition aversions in others (Villalba and Provenza, 1996), and there are clear differences in the susceptibility to acidosis in feedlot cattle (Bevans *et al*., 2005). Thus, what traditionally has been considered, normal foraging behavior and adequate nutrition for the 'average' animal may not be so for specific individuals.

An alternative for prescribing adequate amounts and proportions of nutrients is allowing the animals to select from an array of feeds as a function of their physiological needs. When offered a diversity of feeds, individuals may be better able to select nutrients according to their specific needs and consequently achieve an adequate state of nutrition and well-being (Manteca *et al*., 2008). Allowing animals to choose from various alternatives is one of the primary techniques for assessing animal welfare (Fraser and Broom, 1997). Since the domestication of herbivores from 8500 to 11 000 years ago, animals met their nutrient requirements and avoided toxicosis in complex and diverse feeding environments, long before the emergence of the field of ruminant nutrition (Provenza, 1991; Villalba and Provenza, 2009). The reason for this is that herbivores are able to achieve homeostasis by modifying their feeding behavior (Villalba and Provenza, 2007).

Behavior by consequences and homeostatic regulation

Food preference (behavior) in herbivores develops because of the dynamic interplay between flavor and *post-ingestive* feedback (consequences), which is determined by an animal's physiological condition and a plant's chemical characteristics (Provenza, 1996; Provenza and Villalba, 2006). Taste, as well as smell and sight, are labels which animals use for discriminating among foods. *Post-ingestive* feedback calibrates a food's flavor with its homeostatic utility (consequences). If a particular food provides chemicals, which are required by an animal at a certain point in space and time, then preference for that food will increase. In contrast, if a food supplies chemicals which provide negative effects to the body or compounds which are not needed in that particular point in space and time (e.g. excess nutrients), preference for the food will decline, although selection becomes less efficient in complex feeding environments (Duncan *et al*., 2007). On this basis, herbivores preferentially ingest foods high in nutrients (Kyriazakis and Oldham, 1993; Villalba and Provenza, 1997a) and low in toxins (Provenza *et al*., 1990), but they avoid specific nutrients when needs are met (Villalba and Provenza, 1999) and they eat toxins when toxins provide medicinal (e.g. antiparasitic) effects (Lisonbee *et al*., 2009; Villalba *et al*., 2009a). Thus, the process of food selection in herbivores can be interpreted as the search for chemicals in the environment that restore homeostasis allowing animals to stay well (Villalba and Provenza, 2007).

Varied diets and animal welfare

Generalist herbivores achieve homeostasis by consuming a diverse diet. This is in part because of the fact that no one plant species can provide for all of the animals' nutrient demands (Westoby, 1978), and because generalist herbivores are unable to detoxify large amounts of chemically similar plant secondary metabolites (Freeland and Janzen, 1974). Yet, herbivores consume a diversity of foods even when nutritional needs can be met with single foods or when toxins are not a concern (e.g. Wilmshurst *et al*., 1995; Provenza *et al*., 1996). Other reasons for varied diets are sampling to update the information about available foods (Westoby, 1974) and increases in hedonics associated with switching to alternative foods (Rolls *et al*., 1983). It has also been argued that the preference for variety may result from aversions to any food eaten too frequently or in excess (Provenza, 1996). The process of ingesting a food causes animals to satiate on that food, and the satiety hypothesis attributes decreases in food preference because of transient food aversions caused by flavors, nutrients and toxins interacting along with the concentration gradients (Provenza, 1996).

Gustatory, olfactory and visual neurons stop responding to the taste, odor and sight of a particular food eaten to satiety, yet they continue to respond to other foods (Critchley and Rolls, 1996). Preference for a specific food declines when the food is eaten repeatedly, presumably because the taste of food consumed to satiety becomes less pleasurable (Swithers and Hall, 1994). Aversions become pronounced when foods contain high concentration of toxins or nutrients or nutrient imbalances. Thus, although undue restrictions of nutrients are recognized as important adverse influences on animal welfare (Ewing *et al*., 1999), excesses of nutrients and nutrient imbalances are also stressful and compromise animal well-being.

Ruminants can encounter pasture forages excessive in concentrations of protein, which degrades rapidly in the rumen, and so far as 73% of the ingested nitrogen may be excreted (Van Vuuren and Meijas, 1987). Excessive nitrogen concentrations can lead to ammonia build-up in the blood resulting in loss of appetite, infertility and death (Lobley and Milano, 1997). Likewise, feedlot rations with high concentrations of grain produce acidosis with negative effects on intake and animal health (Huber, 1976). Lambs prefer flavored-straw paired with low-to-moderate doses of energy

(e.g. the volatile fatty acids propionate or acetate) or nitrogen (urea and casein) delivered to the rumen, which do not cause satiety. However, at higher doses of energy or nitrogen, they become averse to that flavored straw (Villalba and Provenza, 1996, 1997a and 1997b).

Aversions also result when foods are deficient in nutrients and they occur even when a food is nutritionally adequate because satiety and surfeit are on a continuum from mild to stronger food aversions. Sensory-specific satiety refers to the decrease in preference for the taste of food as it is consumed too frequently or in excess (Rolls *et al*., 1981; Rolls, 1986). For instance, cows and sheep were fed with the same foods but with distinctive flavors one day (e.g. coconut) prefer a different flavor (e.g. maple) the next day (Early and Provenza, 1998; Scott and Provenza, 1998; Atwood *et al*., 2001a). The reward experienced by the hedonic value of a specific food (i.e. 'liking'), involves different neurotransmitter systems than the reward experienced by its nutrient value (i.e. 'wanting', Berridge and Robinson, 1998). This hedonic value is important in influencing food choice, and may play a role in animal welfare. A decrease in liking because of repeated sensory stimulation by a single food may stimulate animals in the search for food diversity. Likewise, sensory-specific satiety seems to be a reflection of both a reduction in liking and in wanting, (Balleine and Dickinson, 1998) which primes animals to search for alternative food sources.

In summary, animals experience flavor-nutrient toxin-specific satieties, satiety to single foods is mildly to strongly aversive, and that causes them to eat a variety of foods (Provenza, 1996; Provenza *et al*., 2003). Thus, monotonous diets typically used in intensive livestock feeding systems such as total-mixed rations (TMRs) or monocultures – even when nutritionally balanced – have the potential to cause aversions and consequently be stressful, which could depress intake and negatively impact animal welfare. There is evidence that psychological stress affects eating patterns in humans, with shifts in preferences toward more palatable foods of higher energy density (Oliver and Wardle, 1999; Lim *et al*., 2009), suggesting a variety of foods may help people to cope with the stress. In contrast, restriction of variety *per se* may be stressful. Rats exposed to attractive, but inaccessible food cues manifest higher levels of stress as measured by concentration of corticosterone (Polivy *et al*., 2008). Generalist herbivores evolved eating a variety of foods in diverse landscapes and this scenario is typically not replicated in confinement or at pasture. Needs of individuals differ because of environment and physiological state. The nutrient content of plants also varies during the growing season. Allowing animals to select their own diet may improve their productivity and well-being as single foods and monotonous rations may not completely meet the needs of individuals within the herd on a daily basis, and may even provide excesses of nutrients (Manteca *et al*., 2008). Beef calves offered a mixed ration of rolled barley, rolled corn, corn silage and alfalfa hay, or a choice among these foods offered individually manifest differences in intake and performance (Atwood *et al*., 2001b). During the trial, no two animals consistently chose the same ingredients, and none of them selected a diet of similar composition to the nutritionally balanced mixed ration, yet animals offered the choice that had similar protein : energy ratios. On average, as animals offered the mixed-ration and they gained weight at a similar rate and gain per unit food consumed (Atwood *et al*., 2001b). When grain and silage were offered as a choice to feedlot cattle, they consistently chose lower ratios of grain to silage (75% to 80% grain) than those offered to controls in a TMR (85% to 90% grain), but they had significantly lower dry matter intake, and higher overall feed efficiency than animals given the TMR (Zobel *et al*., 2006).

There may be other reasons besides flavors, nutrients and toxins for herbivores to display varied diets. Sheep, cattle and goats show a consistent diurnal pattern of food selection, with a strong preference for legumes in the morning, and an increased preference for grass over the course of the day (reviewed by Rutter, 2006; Hill *et al*., 2009). One explanation for this pattern of behavior has been attributed to a predator avoidance strategy aimed at reducing food consumption at night. Such a strategy involves eating a bulky feed rich in fiber with a low rate of passage (i.e. grass) in the evening, helping to maintain rumen fill and reducing the need to eat to maintain rumen fill at night (Rutter, 2006). Sheep appear to target fiber in the evening (Dumont *et al*., 1995), and restricting the allowance of roughage in cattle significantly increases the development and frequency of oral stereotypies (Redbo and Nordbald, 1997). It has also been argued that deviations from the animal's optimal supply of fiber generate discomfort, which the animal tends to minimize to improve well-being (Forbes, 2003). It has also been proposed that ruminants will choose a diet associated with the maintenance of optimal conditions in the rumen (Cooper *et al*., 1996). Thus, availability of roughage (and other feeds) at certain points in space and time may allow animals to express their foraging preferences, to minimize the discomfort and enhance their welfare.

Foraging behavior, plant secondary compounds and animal health

Plants provide herbivores with an array of chemicals with the potential to improve health and well-being. For instance, phytochemicals – known as secondary compounds – which protect plants from consumers and pests adversely affect cellular and metabolic processes in herbivores (Rosenthal and Janzen, 1979; Cozier *et al*., 2006), but at low doses and in appropriate mixtures, they can have beneficial effects on animal nutrition and health (Lozano, 1998; Engel, 2002). For instance, eating plants high in tannins is a way for herbivores to reduce internal parasites (Min and Hart, 2003) and tannins alleviate bloat by binding to proteins in the rumen (Waghorn, 1990). By making plant protein unavailable for digestion and absorption until it reaches the more acidic abomasum, tannins also enhance the nutrition by providing high-quality protein to the small intestines (Barry *et al*., 2001). Plant-derived alkaloids, terpenes and phenolics also have antiparasitic properties

(Kayser *et al*., 2003; Hocquemiller *et al*., 1991), and sesquiterpene lactones have anti-tumorigenic, anti-amebic, anti-bacterial, anti-fungal and cardiotonic properties (Picman, 1986; Robles *et al*., 1995; Huffman *et al*., 1998). Some complex carbohydrates (i.e. galactomannans, glucans and arabinogalactans) and flavonoids stimulate macrophage function and have immunomodulatory properties (Tizard *et al*., 1989; Middleton *et al*., 2000; Schepetkin and Quinn, 2006). The biochemical diversity of plants thus offers animals the opportunity to enhance their health and well-being, provided such diversity is present in their diets. For instance, of the 192 recognized plant food species routinely consumed by Mahale chimpanzees in Africa, many have ethnomedicinal uses (Huffman *et al*., 1998). Eating diverse diets thus provides herbivores all the advantages of bioactive compounds such as anti-parasitic agents and immunomodulators on a daily basis with health-maintenance effects.

Herbivores exposed to varied diets may also learn about the benefits of specific plant secondary compounds for alleviating certain maladies. In their quest for substances in the environment, which contribute to homeostasis, animals may experience the medicinal properties of specific foods. For instance, wild chimpanzees suffering from parasite-related diseases with overt signs and symptoms of sickness consume the bitter pith of the anti-parasitic plant *Vernonia amygdalina*, even when they have available *ad libitum* species of much higher nutritive value (Huffman and Seifu, 1989; Huffman, 2003). Consistent with this observation, sheep also increase intake and preference for tannin-containing foods when they are infected with endoparasites relative to when parasitic loads are not present (Lisonbee *et al*., 2009; Villalba *et al*., 2009a). Other studies suggest livestock self-medicate by grazing specific medicinal plants when ill (Grade *et al*., 2007 and 2009).

Foraging behavior and experience with food

Past experiences *in utero* and early in life have life-long influences on behavior, but we seldom notice because we know or remember so little about the history of any animal. Experiences with food have life-long influences on diet, health and disease in humans and herbivores by causing neurological, morphological and physiological changes, which influence on foraging behavior (Provenza and Balph, 1990; Distel *et al*., 1994 and 1996). By interacting with the genome during growth and development, social and biophysical environments influence gene expression and behavioral responses (LeDoux, 2002; Fish *et al*., 2004; Meaney, 2009). Each individual emerges from the ongoing interplay between its genes and social and the biophysical environments, and much of this dialog occurs during development *in utero* and early in life. An important form of this interaction, termed predictive adaptive responses, refers to responses that are (i) induced by the environment early in life, (ii) cause changes neurologically, morphologically and physiologically, and (iii) confer survival advantages when the environment of rearing matches the environment where a young animal then lives (Gluckman *et al*., 2005). Predictive adaptive responses act through developmental plasticity early in life to modify the phenotype so it matches the environment of rearing, which is expected to be inhabited later in life. This will be so (i) if the behavior of mother is appropriate for the *post-weaning* environment and (ii) if that environment does not change too drastically during the life of the offspring.

Given the importance of experience on animal physiology and behavior, it follows that it may also have an impact on the welfare of animals. For instance, exposure to novelty (i.e. lack of experience) is one of the most potent experimental conditions to cause negative emotions of fear and anxiety (Boissy, 1998). This is probably why animals typically sample novel foods cautiously, a phenomenon known as food neophobia (Chapple and Lynch, 1986). Excessive fearfulness can cause chronic stress and reduce productivity and therefore reducing the level of fearfulness has advantages for both animal welfare and production (Jones, 1997). Selecting less fearful livestock improves maternal behavior and animal survival (Kilgour and Szantar-Coddington, 1997). Fearfulness may also affect feeding behavior and the acceptance of new foods, and three lines of evidence suggest such a relationship in ruminants. First, the neural substrate responsible for the fear response is also involved in diet selection. Neuronal networks in the amygdala and the hippocampus are involved in both fear and diet selection responses (Bechara *et al*., 1995). Second, when sheep are placed in a new environment likely to elicit a stress response, they show a greater reluctance to eat novel foods compared with the same animals offered new food in a familiar environment (Burritt and Provenza, 1997). Finally, work with wild and farm animals shows environmental enrichment that allows animals to show more flexible foraging behavior decreases chronic stress (Carlstead and Shepherdson, 2000). A study carried out in our laboratory to determine whether there was a link between general fearfulness (as measured by the open field test) and stress-induced hyperthermia (SIH) and the readiness of sheep to eat new foods suggests that individuals less responsive to social isolation (lower number of bleats) may be less cautious at accepting novel foods than individuals more responsive to social isolation, but no correlation was found between SIH and food neophobia (Villalba *et al*., 2009b).

From a management and welfare perspective, it is important that animals readily accept new foods. Overcoming food neophobia by adding a familiar flavor to food (Launchbaugh *et al*., 1997) or ameliorating neophobia through repeated exposure to new foods, or exposing pregnant mothers (Nolte and Provenza, 1992a and 1992b), or individuals early in life (Distel *et al*., 1994 and 1996) are all ways to improve intake of novel foods and reduce fearfulness and stress within the herd.

Feeding behavior as criteria for measuring welfare

Feeding behavior may also represent an important tool for detecting pain or sickness in livestock, before overt symptoms are displayed. Early detection of pain, as well as its quantification could substantially contribute to its mitigation for improving the welfare of animals (Schwartzkopf-Genswein *et al*., 2009). For instance, self-selection of

analgesic drugs by animals considered to be in pain may be an important indication that they are in pain (Smith and Boyd, 1991). If the amount of analgesic consumed is proportional to the level of pain, then the amounts of analgesic selected could be used as an objective measurement of pain. There is some evidence that animals self-select their analgesics. Rats suffering from adjuvant-induced arthritis consumed more of an analgesic agent than control animals (Colpaert *et al*., 1980). Lame broiler chickens also learn to self-administer the analgesic carprofen in their feed and the amount of the analgesic consumed increased with the severity of lameness (Danbury *et al*., 2000).

Pain not only may affect selection and intake of analgesics but feeding patterns. Monitoring feeding patterns is a useful tool for the early detection of sickness in livestock. For instance, pain associated with castration results in calves making fewer visits to the feeder while daily feeding duration does not differ from control animals (Schwartzkopf Genswein *et al*., 2009). Sick steers in feedlots, identified as having bovine respiratory disease, spend 30% less time feeding than healthy steers (Sowell *et al*., 1998).

Assessing the links between food choice and animal welfare

Our thesis is that food variety allows animals to express their foraging preferences, which in turn enhances their welfare. Behavioral measurements may represent an important tool to assess such an effect in livestock. For instance, it would be possible to explore the willingness or motivation of an animal to get access to multiple foods. Livestock are prepared to do extra work (i.e. pay a cost such as walking) to gain access to preferred foods (Dumont *et al*., 1998). Thus, it may be possible to quantify the motivation of animals (e.g. distance walked; number of lever-press responses) to obtain a diversity of feeds in their diets.

Lack of food alternatives could lead to frustration behavior which in extreme situations may develop into stereotypies (Broom, 1986). These stereotyped behaviors are persistent, recurrent actions (i.e. fence-pacing and head-weaving) which can be linked to types of automatism or repetitive comfort behaviors (Gregory, 2004). Compulsive water drinking can be a sign of frustration or anxiety (Gregory, 2004); a behavior which could also give insights into the welfare of animals fed monotonous diets. Increases in exploratory behavior (e.g. rooting in pigs) may also be indicative of the effects of stress caused by boredom (Van Roijen, 1991), and potentially food monotony. Play behavior (e.g. running) has also been suggested as a useful measure of how the welfare of ruminants is affected by feeding practices (e.g. milk allowance) (Krachun *et al*., 2010).

Physiological measurements such as estimation of corticotropic responses are useful in monitoring fear and stress in farm animals and may represent an important tool in the future for complementing behavioral parameters to improve the assessment of welfare in animals fed with different types of diets. The hypothalamic pituitary-adrenal (HPA) axis is activated during aversive situations. The level of cortisol in the blood increases in pigs, cattle and sheep when they were subjected to a painful procedure like castration (e.g. Coetzee *et al*., 2007). The HPA is also activated in animals separated from familiar peers, mixed with unknown animals, transported and restrained in a shoot (Boissy and Le Neindre, 1997). In addition, corticotropin-releasing hormone produced by the hypothalamus in response to a stress situation has a direct effect on reducing food intake (Matteri *et al*., 2000), suggesting a link between feeding behavior and activation of the HPA axis. The HPA axis is also activated during frustration and anxiety in mammals (Dantzer *et al*., 1980; Landgraf *et al*., 1999) and lack of food alternatives may lead to such states in herbivores. Glucocorticoid hormones can be measured in plasma, saliva, urine and feces (Berman *et al*., 1980). The compound 11,17-dioxoandrostanes, a group of cortisol metabolites, have been used with fecal sample to evaluate the adrenocortical activity (Fell and Shutt, 1986) and cortisol metabolites increase in cattle feces after transport and after adrenocorticotropin administration (Palme *et al*., 1999).

Conclusions

Ruminants are able to modify their foraging preferences as a function of the consequences they experience after food ingestion. This mechanism – behavior by consequences – suggests individuals are able to meet nutritional requirements and self-select certain medicines and analgesics if they are offered the opportunity to do so when offered a variety of foods. Understanding the feeding behavior of ruminants when offered food choices is necessary to be able to improve their health and well-being by reducing levels of stress and fear; it may as well lead to the early detection of illness. Thus, management strategies in ruminant production systems should benefit from allowing animals manifest their feeding preferences. This implies a paradigm shift in the way animals are fed, recognizing their role as active players in the feeding system, as opposed to passive entities just responding to prescriptions and ration formulations.

Acknowledgments

This effort was supported by grants from the Utah Agricultural Experiment Station. This paper is published with the approval of the Director, Utah Agricultural Experiment Station, and Utah State University, as journal paper number 8132.

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