Review

Understanding and manipulating diet choice in grazing animals

J. J. Villalba[A,C], *F. D. Provenza*[A], *F. Catanese*[B] *and R. A. Distel*[B]

[A]Department of Wildland Resources, Utah State University, Logan 84322-5230, USA.
[B]Departamento de Agronomia, Universidad Nacional del Sur, and CERZOS, CONICET,
 8000 Bahia Blanca, Argentina.
[C]Corresponding author. Email: juan.villalba@usu.edu

Abstract.   Conventional models of foraging, such as optimal foraging theory, generally take the univariate approach to explain the decisions of consumers on the basis of the intrinsic properties of foods, including nutrient concentration and abundance. However, the food environment is inherently diverse and, as a consequence, foraging decisions are influenced by the interactions among multiple food components and the forager. Foraging behaviour is affected by the consumer's past experiences with the biochemical context in which a food is ingested, including the kinds and amounts of nutrients and plant secondary compounds in a plant and its neighbours. In addition, past experiences with food have the potential to influence food preference and intake through a mechanism, namely, food hedonics, which is not entirely dependent on the classical homeostatic model of appetite control. Research on the impacts of experience with food context and its behavioural expression in natural settings should pioneer innovative management strategies aimed at modifying food intake and preference of herbivores to enhance their nutrition, health and welfare, as well as the health and integrity of the landscapes they inhabit.

Additional keywords: behaviour, context, nutrients, diversity, food preference.

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Introduction

From the advent of foraging theory, the intrinsic chemical or structural properties of a plant and its abundance in a community were considered consequential for predicting a herbivore's foraging decisions and ultimately foraging success. According to classical optimal foraging theory (OFT), animals are expected to maximise the long-term rate of energy intake (Stephens and Krebs 1986), and on the basis of estimated profitability (fitness gain per investment of time), a food is either always or never taken (but see Stephens 1985). Thus, partial preferences are not well explained by pioneering OFT models, an outcome of over-emphasising the intrinsic quantitative and qualitative properties of food. More recent models introduce the possibility of partial preferences, an outcome typically observed in generalist herbivores grazing diverse plant communities (Provenza 1996; Provenza and Villalba 2006). However, the mechanisms proposed for partial preferences still retain the elementary idea of single foods and their intrinsic properties as determinants of food choice and they give little credit for the ability of herbivores to learn, remember and discriminate among foods. Thus, partial preferences have been attributed to limited perception (Berec and Krivan 2000), inability to discriminate (Illius *et al*. 1999) or sort (Courant and Fortin 2010) among different plant species, attempts to meet nutritional needs (Westoby 1978), or to dilute intake of plant secondary metabolites (Freeland and Janzen 1974).

In addition to the intrinsic chemical properties of plants, classical optimal foraging models consider plant abundance, which influences the likelihood of plant encounter by a herbivore (Stephens and Krebs 1986). Forage abundance is also the basis for developing preference indices in rangeland and pasture settings (e.g. Loehle and Rittenhouse 1982). Similar to the approach taken with the intrinsic quality of a food item described above, this view does not consider (1) the biochemical (but see Atsatt and O'Dowd 1976; Milchunas and Noy-Meir 2002) or spatial (but see Barbosa *et al*. 2009) context where a plant is growing, that is, the nutrients and plant secondary metabolites present in the associated plant community, and (2) the past dietary experiences of the herbivore within such a context. Plants and their chemical constituents do not act in isolation in a herbivore's body (Villalba *et al*. 2002). On the contrary, they evolve into associative or antagonistic relationships that yield fitness benefits different from those observed when an animal consumes any one food in isolation (Tilman 1982). Such relationships interact with the consumer's physiology, providing compounded experiences which then modify future decisions made by herbivores foraging in diverse plant communities. These experiences begin *in utero* (e.g. Wiedmeier *et al*. 2012) and continue throughout the lifetime of the individual.

Different approaches have been taken to understand and express foraging decisions by herbivores. For instance, forage preference has been defined as 'what animals select given the minimum physical constraints' (Parsons *et al*. 1994*a*), whereas selection is defined as 'preference modified by environmental

circumstances' (Hodgson 1979). Thus, preference may be viewed as what an animal 'wants' to eat in an ideal situation, whereas selection encompasses what it ends up eating due to some type of biotic or abiotic constraint (Rutter 2006). In this review, we present evidence of the impact of food context and past dietary experiences on herbivores' foraging decisions. On the basis of this analysis, we propose that changes in appetite and preference in ruminants are influenced by the way in which these contexts are experienced. Management of food context and past experiences can modify food preference in herbivores and facilitate the expression of preference in feeding systems (e.g. Meuret and Provenza 2014a, 2014b). Research on the impacts of food context on preference should pioneer innovative management strategies aimed at modifying food intake and preference to enhance the nutrition, health and welfare of herbivores, as well as the health and integrity of the landscapes they inhabit.

Role of experience with post-ingestive feedback on herbivores' foraging decisions

Past experiences have life-long influences on behaviour (Provenza 1995a, 1995b, 1996). Animals experience and respond to different physiological states by altering their ingestive behaviour through affective (implicit or associative) and cognitive (explicit or declarative) processes (Provenza and Villalba 2006). On one hand, affective processes involve the non-cognitive (i.e. non-cortical) integration of the taste of food with post-ingestive feedback from cells and organs in response to levels of ingested chemicals. This integration causes changes in the liking for and intake of food items that depend on whether the effect on the internal environment is aversive or positive (Provenza 1995a). The net result is incentive modification. On the other hand, the cognitive system integrates the odour and sight of food with its taste. Animals use the senses of smell and sight to differentiate among foods, and to select or avoid foods whose effect on the internal environment is either positive or aversive. The net result is behaviour modification. Together, affective and cognitive processes enable animals to maintain fluidity, given ongoing changes in the internal and external environment (Provenza and Villalba 2006). Affective (non-cognitive) changes in palatability through flavour–feedback interactions occur automatically. The cortex is not directly involved in these processes. Even when animals are anesthetised, post-ingestive feedback still changes palatability. When sheep eat a nutritious food and then receive a toxin dose during deep anaesthesia, they become averse to the food because the negative feedback from the toxin occurs even when animals are deeply asleep (Provenza *et al.* 1994).

Livestock benefit from maintaining a balance of energy and protein in their diets by discriminating specific flavours and nutrient-specific feedbacks. Lambs fed diets low in energy or protein prefer flavoured low-quality foods previously paired with intra-ruminal infusions of energy (starch, propionate, acetate) or nitrogen (urea, casein, gluten) (Villalba and Provenza 1996, 1997a, 1997b, 1997c). Given pre-loads of energy or nitrogen, lambs prefer flavours previously paired with nitrogen or energy, respectively, during the ensuing meals (Villalba and Provenza 1999a). Thus, animals maintain

a balance of energy to protein that meets their nutritional needs, and in the process, they recognise different internal states and discriminate among different nutrients (Egan 1980; Wang and Provenza 1996). Sheep also learn to discriminate among minerals such as phosphorus, calcium and sodium and they learn to select the flavoured 'food' previously paired with recovery from deficiencies of each of these minerals (Villalba *et al.* 2008). In addition to learning preferences for nutritious foods, herbivores learn to prefer medicinally beneficial foods, as post-ingestive feedback from medicines provides positive post-ingestive experiences to sick animals (Villalba *et al.* 2006a; Villalba and Landau 2012). These studies have shown that herbivores can discriminate among many different internal states and that they learn to ingest foods that ameliorate nutrient deficits and that rectify illness.

Role of temporal sequence and chemical context on herbivores' foraging decisions

Temporal sequence and preference

Associations between the orosensorial properties (taste, smell, irritation) of foods and their specific post-ingestive consequences are not perfect, especially the greater the time delay between consumption of food and post-ingestive consequences (Yearsley *et al.* 2006). This is because when two or more foods are ingested in close temporal association (i.e. within 1–2 h), part of the post-ingestive effects of any one food are attributed to the rest of the foods consumed in the same feeding bout (Duncan and Young 2002; Yearsley *et al.* 2006; Duncan *et al.* 2007). Thus, when palatable and unpalatable foods are ingested in close temporal association, herbivores are more likely to transfer at least part of the rewarding post-ingestive properties of the palatable food to the unpalatable ones.

Studies in psychobiology show that preference depends on the temporal context. The phenomenon of intake 'induction' or 'facilitation' involves augmented consumption of a food in the first part of a meal sequence when the food consumed in the ensuing part of the meal is more palatable (Flaherty and Grigson 1988; Weatherly *et al.* 2005). Such an induction effect is seen when sheep first eat a poorly nutritious food (oat hay) followed by small amounts of concentrate (soya bean meal, ground corn) relative to controls not provided with concentrate during conditioning sessions (Freidin *et al.* 2011, 2012). The reverse temporal arrangement (eating a palatable food followed by a non-nutritive food) may also influence preference. For example, rats acquire preferences for non-nutritive solutions consumed shortly after glucose ingestion (Boakes and Lubart 1988). In contrast, simultaneous availability of a poorly nutritious food (oat hay) and a concentrate food (sunflower meal and corn grain) did not change preference for or intake of the former food by sheep (Catanese *et al.* 2010) due to a simultaneous negative contrast effect (Catanese *et al.* 2011). Collectively, these studies suggest that when animals consume a diverse diet, temporal context plays a role in the way they value specific dietary components and that can be used to increase intake of various mixtures of forages on pastures and rangelands (Meuret and Provenza 2014a, 2014b).

Temporal sequence and food quality also influence preference for plant secondary compound-containing foods. Sheep learned

to eat a low-quality food with tannins and a high-quality food in two different temporal arrangements (Villalba *et al.* 2006*b*). In one case, sheep were fed the high-quality food for 12 days, followed by food with tannins for 12 days, such that their synergistic effects were dissociated temporally. In the other case, sheep were fed both foods simultaneously for 12 days so their effects were associated within the same meal. Subsequently, all sheep could forage at locations containing either both foods, only the high-quality food, or only the food with tannins. Sheep that initially ate both foods in a meal always ate more food with tannins than did those that initially experienced the foods in two distinct feeding periods, even when the high-quality food was available *ad libitum*. As the high-quality food decreased in abundance, lambs that learned to mix both foods foraged more opportunistically and remained longer at locations with both foods or with just the food with tannins. Even when both groups spent about the same amount of time at locations with both foods, lambs that initially ate both foods in a meal ate more food with tannins and thus consumed more food. Similar effects of experience increasing food intake were observed with sheep that had experience mixing two nutritious foods with three other foods that contained either tannins, terpenes or oxalates; they ate considerably more of the three foods containing the secondary compounds than did sheep that had experience eating only the two nutritious foods (Villalba *et al.* 2004). Likewise, heifers that grazed in a sequence of either alfalfa or birdsfoot trefoil first and then tall fescue spent considerably more time foraging on tall fescue than did heifers that grazed in the reverse sequence (Lyman *et al.* 2011). Sheep also eat more food with terpenes when they first eat food with tannins than when they ingest the reverse sequence (Mote *et al.* 2008).

Chemical context and preference

Interactions among foods (associative effects), commonly observed in ruminant nutrition studies, may enhance or reduce digestibility (Van Soest 1994). Sheep and goats eating mixed diets on rangeland display daily intakes much greater (two times greater) than reference intake values obtained with animals fed single forages of similar nutritive value in confinement (Agreil and Meuret 2004; Meuret and Provenza 2014*a*). By consuming a mixed diet, a forager obtains a more beneficial mixture of nutrients (Westoby 1978) that can dilute or inactivate secondary compounds (Freeland and Janzen 1974; Catanese *et al.* 2014), thus allowing for greater growth and reproduction (Rapport 1980; Pennings *et al.* 1993). For example, lambs fed a basal diet of endophyte-infected tall fescue (containing alkaloids) supplemented with either alfalfa (containing saponins) or birdsfoot trefoil (containing tannins) ate more (total dry matter and nutrients) than did lambs fed only endophyte-infected tall fescue and the forage with tannins had a greater effect than the food with saponins (Owens *et al.* 2012*a*, 2012*b*).

In ecological theory, contextual relationships among foods are categorised as complementary, antagonistic or substitutable, when combinations of foods exceed, reduce or maintain, respectively, the fitness benefit of consuming any one food in isolation (Tilman 1982). In support of this, sheep that learn to mix their diets with foods containing different secondary compounds, such as tannins, terpenes and oxalates, eat much more than do sheep that lack that experience (Villalba *et al.* 2004). Likewise, preference for foods high in secondary compounds is affected by the nutritional state of an animal. For instance, in one study, a group of lambs first ate a low-quality food containing tannins while on a basal diet low in nutrients, and then several weeks later they ate the same low-quality food containing terpenes while on a basal diet adequate in nutrients; conversely, another group of lambs first ate food with terpenes and then ate food with tannins under the same regime described above (Baraza *et al.* 2005). When offered a choice between the two foods, lambs consumed more of the food, either tannin or terpene, they ate while on the basal diet high in nutritional quality.

The aforementioned findings showed that the temporal context in which foods of different chemical characteristics are eaten affects ruminants' orosensorial and post-ingestive experiences with food, which in turn influence appetite and food preferences. They also indicated that the relationships created among foods ingested within a meal are more important than the individual foods that comprise the meal (Meuret and Provenza 2014*a*, 2015).

Role of incentive value and satiety on herbivores' foraging decisions

Incentive value and post-ingestive feedback

Animals conditioned with foods that lead to rewarding post-ingestive experiences develop a preference for the taste of foods associated with such experience, and preference persists even during extinction tests after the cessation of the post-ingestive event (Mehiel 1991). For instance, sheep that eat low-quality flavored foods paired with intraruminal infusions of starch develop strong food preferences for those foods, which persist for many months during extinction tests (Villalba and Provenza 1997*a*).

Post-ingestive feedback from starch also plays a key role in modulating rates of food intake in sheep. Rates of intake of a low-quality food (wheat straw) were low and variable when no starch was infused into the rumen. However, sheep that received intraruminal infusions of starch consumed more straw, at greater intake rates, and took more and larger bites than did control lambs that received intraruminal infusions of the vehicle; these preferences persisted for months (Villalba and Provenza 2000). Thus, post-ingestive effects from starch modulated the rate of straw consumption and enhanced the motivation to eat (Villalba and Provenza 2000).

Rates of food intake during meals are also influenced by an animal's physiological condition and nutritional composition of food. When lambs' need for either protein or energy is high, the nutritional composition of the food (i.e. a food high in energy or protein) overrides structure (ground, low intake rates; pellets, higher intake rates) in determining lamb's preferences (Villalba and Provenza 1999*b*) and affects where lambs go to forage (Scott and Provenza 2000). Fasting increases rates of food intake (Newman *et al.* 1994), but non-fasted lambs can show greater rates of intake than fasted lambs when the food on offer provides the nutrient that non-fasted lambs need, so as to balance their diet. For instance, non-fasted lambs fed a nitrogen-rich basal diet

had higher rates of intake of an energy-rich food (barley) than did fasted lambs fed a basal diet high in grain (Villalba and Provenza 1999*b*). Thus, rates of food intake and preference for food and foraging location can be modified by animals' experiences with the contextual properties of foods. This suggests that the food context can influence intake rate and food use to an extent that cannot be predicted solely by the chemical or structural properties of a single food. For instance, intake or intake rate may not be predicted solely by food properties that lead to substantial fill effects due to high concentrations of fibre (Allen 1996), or by the animal's physiological state due to activation of the satiety cascade during the onset of a meal (Blundell 1991). In summary, context impacts orosensorial and post-ingestive experiences in ruminants, which affect the expression of at least some of the components of food reward (i.e. liking, wanting; see below), ultimately influencing appetite and food preferences.

The satiety hypothesis

In contrast to the incentive value emerging from flavour–feedback associations with infusions of calories, sheep develop aversions to the flavours of foods paired with excesses or imbalances of nutrients (Villalba and Provenza 1997*b*, 1997*c*). The satiety hypothesis attributes changes in preference to transient food aversions due to the integration within the body of flavours, nutrients and secondary compounds as they interact along concentration gradients (Provenza 1996). Cyclic patterns of intake of different foods arise from eating any food or combination of foods too often or in too large amounts, and the less adequate the diet is relative to an animal's needs, the greater and more persistent the aversion (Early and Provenza 1998). Hence, transient food aversions cause animals to eat a variety of foods and to forage in a variety of places (Provenza 1996; Bailey and Provenza 2008).

No forage can provide the balance of nutrients or secondary compounds found by eating a variety of forages (Freeland and Janzen 1974; Westoby 1978). Thus, by consuming a mixed diet, a forager obtains a more beneficial mixture of nutrients, allowing for greater growth and reproduction (Westoby 1978; Provenza *et al.* 2007). In contrast, animals faced with consuming only one unbalanced food, or unbalanced foods of the same type, may quit eating as they satisfy their requirements for the nutrient in highest concentration, but are ultimately unable to satisfy their requirements for other nutrients occurring in lower concentrations (for examples, see Provenza and Villalba 2006), a phenomenon known as incidental restriction (Raubenheimer 1992). Alternatively, the animal may continue foraging to satisfy requirements, a compensation that will inevitably lead to overconsumption of the nutrient occurring in highest concentration (for examples, see Provenza and Villalba 2006), a phenomenon known as incidental augmentation (Raubenheimer 1992). This response may lead to extra energy costs to metabolise the excess of ingested nutrients, with a concomitant decrease in productivity (Soder *et al.* 2007), which ultimately leads to a reduced intake relative to animals exposed to a combination of foods that enables each animal to meet its nutritional needs (Provenza *et al.* 2003).

When sheep have a choice of adjacent monocultures of ryegrass and clover, they prefer clover (70%), and they achieve daily intakes similar to those of sheep grazing pure clover, even though animals given a choice are including 30% grass in their diet, which offers considerably lower intake rates than does clover (Chapman *et al.* 2007). Some have suggested that there is a boost in intake when grass is included in the diet, presumably because grass allows animals to overcome a nutritional constraint to eating pure clover (Cosgrove *et al.* 2001; Champion *et al.* 2004). This constraint may involve the rate of release of ammonia from the soluble protein fraction of the forage, and subsequent uptake in the blood, which causes a decrease in preference for clover and an increase in preference for grass. By mixing grass with clover, the animal is able to increase the duration of the meal, potentially reflecting a 'better' dietary balance of energy to soluble protein that controls the rate of accumulation of ammonia in rumen fluid and blood, which is known to diminish food intake (Hill *et al.* 2009). Similarly, sheep showed partial preference for ryegrass (82%) when offered free choice with barley (Catanese *et al.* 2009*a*), although digestible dry matter intake and nitrogen retention were similar to those of sheep fed ryegrass only. The fact that sheep consumed almost exclusively ryegrass in the morning and then increased their consumption of barley in the afternoon suggests that they developed a transient food aversion to ryegrass as consumption of this forage progressed throughout the day. Such imbalances may underlie the development of stress responses in ruminants. For instance, exposure to monotonous rations increases the concentration of blood cortisol in sheep, relative to animals offered a choice of foods of contrasting chemical compositions (Villalba *et al.* 2012; Catanese *et al.* 2012, 2013).

Hedonics and orosensation

Current models of appetite control recognise the interaction of the hedonic aspects of food intake with episodic homeostatic mechanisms involved in satiation and satiety (Dalton and Finlayson 2013). The structure of the rewarding properties of foods probably consists of hedonic (liking) and motivational (wanting) subcomponents (Berridge 2007). Liking involves the subjective experience of pleasure created by the sensory perception of food, whereas wanting refers to the motivational attractor that elicits appetitive behaviours activated by cues signalling food. A third component 'reward learning' is involved in the linkage between liking and wanting responses across time as a function of the foods in the diet (reviewed by Dalton and Finlayson 2013). These different components of food reward are heavily involved in processes that govern food selection and intake, which can be somewhat independent of the animals' physiological needs (i.e. those responding to the conventional homeostatic model of appetite control; Blundell and Finlayson 2008). For instance, food liking and wanting in humans can override the inhibitory effects of satiety signals and actually increase food intake (Yeomans *et al.* 2001, 2005; see also papers in Blundell and Bellisle 2013).

The physiological mechanisms underlying liking involve endogenous opioids that mediate hedonic responses to food

consumption by stimulating well defined clusters of neurons in the central nervous system termed 'hedonic hotspots' (Berridge *et al.* 2009). Blockade of opioid receptors through the use of naloxone (an opioid receptor antagonist) substantially reduces preference in dairy cows for a palatable sweet food relative to control animals, suggesting that naloxone inhibits the sensorial pleasure elicited by feed consumption, thereby diminishing food preference and intake (Montoro *et al.* 2012).

The importance of orosensorial experiences is also manifest when a single food is eaten to satiety. In this case, liking for that food decreases to a greater extent than that for foods that have not been consumed. This phenomenon, termed sensory-specific satiety, involves both decreases in liking and wanting, and plays a key role in regulating food consumption in humans (Rolls *et al.* 1981; Sørensen *et al.* 2003) and other species (McSweeney and Swindell 1999), including ruminants (Early and Provenza 1998; Atwood *et al.* 2001; Villalba *et al.* 2011). For instance, lambs fed a basal ration in a choice of three different tastants (umami, sweet, bitter) ate more food with fewer peaks and nadirs of intake than did lambs fed the basal ration containing just one tastant (Villalba *et al.* 2011). Likewise, offering sheep the same pasture hay in different flavours stimulated intake of the hay (Distel *et al.* 2007).

A decrease in liking also has been observed for foods that share similar sensory characteristics with the ingested food, a phenomenon known as sensory-specific transfer effects. Sensory-specific transfer effects have important implications for the control of food intake when the availability of foods is not constrained and the sensory properties of foods are varied (Dalton and Finlayson 2013). Sensory-specific transfer effects account for the increased intake of foods of contrasting sensory properties, relative to ingesting a single food or foods of similar orosensorial properties. In a study with humans, liking and wanting of snacks of a similar taste were weaker than for snacks with dissimilar tastes (Griffioen-Roose *et al.* 2010). Orosensorial diversity thus reduces sensory-specific transfer effects and increases intake of foods, while foods of contrasting post-ingestive effects may lead to synergistic or positive associative effects within and among meals such that intake rate is maximised.

From the aforementioned analysis, we can depict scenarios where animals experience food contexts with similar or contrasting orosensorial and post-ingestive properties (Fig. 1). If foods are the same, or of similar chemical and orosensorial properties, then food reward will decline due to combined sensory-specific and nutrient-imbalance effects and, as a consequence, food intake and preference will be reduced. Orosensorial or post-ingestive diversity likely leads to greater preference and intake because of a reduction in sensory-specific satiety or sensory-specific transfer effects and an increase in associative effects, as the satiety hypothesis predicts (Provenza 1996). The greatest intake and preference for single food items is likely to be achieved when foods present contrasting sensorial and post-ingestive properties because the likelihood of reduced sensory-specific satiety and associative effects will be the greatest (Fig. 1). Sheep generalise aversions from one legume (sainfoin) to another (alfalfa) to a greater extent than to a grass (tall fescue) (Ginane and Dumont 2011). Thus, ruminants may categorise functional forage types and the more contrasting the orosensorial and post-ingestive properties within such food types, the greater the likelihood of reducing sensory-, nutrient-, and secondary compound-specific transfer effects.

Collectively, this discussion suggests that adjustments in hunger are linked to sensory-specific satiety and that some components of food reward may not be consistently downregulated by the physiological (i.e. homeostatic) consequences of food ingestion. On the contrary, some of the components of food reward may be largely independent of homoeostatic processes influencing food intake (Finlayson *et al.* 2008). For instance, calves fed different combinations of nutritionally complementary foods (alfalfa-grass hay and corn grain) in separate feed bunks over-ingested grain and thus failed to select a balanced diet (Catanese *et al.* 2009*b*). In contrast, calves offered four foods *ad libitum*, namely, rolled barley, rolled corn, corn silage and alfalfa hay, selected an adequate diet throughout a 2-month trial (Atwood *et al.* 2001).

Integrating previous experience with foods into foraging models

As previously explained, learning is influenced not only by the intrinsic nutritional properties of food but also by the chemical and temporal context in which a food is ingested (e.g. Sclafani 1995). Thus, motivation to eat a food with limited nutritional

	O - Similar	O - Diverse
P-Similar	Low intake and preference	Enhanced intake and preference
P-Diverse	Enhanced intake and preference	Greatest intake and preference

Fig. 1. Four contrasting effects animals experience while foraging (O, orosensorial; P, post-ingestive). If foods are of similar orosensory and chemical properties (O-similar, P-similar), food reward will decline as sensory-specific and uniform (imbalanced) post-ingestive effects reduce preference and intake. Foods of similar orosensorial properties, but of different chemical composition (O-similar, P-diverse) or *vice versa* (O-diverse, P-similar), will enhance preference due to complementarities among nutrients, which reduce sensory-specific satiety effects. The greatest intake is expected in foods of contrasting and complimentary sensory and post-ingestive properties (O-diverse, P-diverse).

content should change if it was previously experienced in combination with foods of higher nutritional quality. Even though the latter has been corroborated in experimental settings (Villalba and Provenza 2000), foraging decisions in natural situations seem to be rather insensitive to the effects of previous learning with low-quality foods. For instance, sheep fed spotted knapweed (*Centaurea maculosa* Lam.) and high-energy liquid molasses showed greater intake of knapweed than did sheep not conditioned with molasses, but preference for knapweed during a subsequent field trial, in which other palatable grasses were available, was similar between the groups (Whitney and Olson 2007). The inability to extrapolate from pen trials to the field can be explained by the way studies focussed on food preference tests change diet selection. Free-choice tests between the same food offered in different flavours (e.g. Freidin *et al.* 2011), or a low-quality food and one or more higher-quality alternatives (e.g. Catanese *et al.* 2010), may not fully represent the types of foraging challenges animals face in nature. In free-choice tests, foods are commonly offered in small areas with unrestricted availability, whereas in nature, food choice involves plants of diverse nutritional composition, and variable temporal and spatial distributions (O'Reagain and Schwartz 1995). Herbivores are sensitive to these sources of variation (e.g. availability, composition and structure of pastures) and adapt their intake rate and diet selection according to optimisation rules that involve food quality and availability (Parsons *et al.* 1994*b*). Thus, preference for low-quality foods is affected by environmental attributes that integrate foraging decisions at different scales with previous experiences of foods.

What do foraging models predict about herbivores' behaviour when confronted with a low-quality food? One prediction of interest is that the inclusion of low-quality foods should be strongly dependent on the availability of higher-quality options, which implies a non-linear relationship between the availability of a high-quality food and acceptance of a low-quality food (Distel *et al.* 1995; Hirata *et al.* 2006). If nutritious plants are available (i.e. alternatives of higher dietary rank; Stephens and Krebs 1986), inclusion of lower-quality options in the diet may be minimal and delayed until availability of higher-quality foods declines, a prediction that has been demonstrated empirically (O'Reagain and Grau 1995). This has important implications for the positive experiences with a low-quality food during conditioning and their impact on preference for the low-quality food in a 'real life' scenario. Even when significant increases in preference for low-quality foods can be achieved through the use of a proper conditioning procedure, they cannot change the fact that these foods have properties (e.g. high fibre content, low protein concentration, plant secondary compounds) that reduce immediate rewards and, ultimately, animal fitness. Nonetheless, we can identify two scenarios in which the time and timing of an animal's experience with the low-quality food is consequential for understanding preference.

If previous positive experiences with a low-quality food do not lead to permanent morpho-physiological changes in the consumer, i.e. either because such experiences occurred in a relatively short temporal scale, or because they occurred later in life, then we predict that such experiences should have little impact on selection when availability of greater-quality alternatives is not restricted. This prediction was tested in a recent experiment in which sheep with contrasting previous experiences with a low-quality food were faced with choices in which access to a preferred food had variable levels of restriction, while access to the low-quality food was unrestricted (F Catanese, RA Distel, JJ Villalba, unpubl. data). When accessibility to the high-quality alternative was not constrained, all sheep fed almost exclusively on this food. However, when accessibility to the high-quality food was restricted, such that animals were required to walk a certain distance to consume limited amounts of the preferred food, sheep started to incorporate significant amounts of the low-quality alternative to their diets. However, sheep with a previous positive experience with the low-quality food, namely, the low-quality food was eaten in close temporal association with a high-quality food, showed a much greater increase in the use of the low-quality food than did sheep that lacked such previous positive experience. Likewise, Shaw *et al.* (2006) observed that when animal density was low and availability of preferred herbs and grasses was high, sheep familiar with eating *Artemisia tridentata* (a shrub high in terpenes) with grasses and herbs showed similar preference for the shrub as did sheep that lacked experience eating *A. tridentata*. However, as animal density increased and availability of grasses and herbs declined, sheep familiar with ingesting the shrub with the associated vegetation displayed a much greater preference for *A. tridentata* than did control animals. Sheep conditioned with intraruminal infusions of glucose while ingesting an alkaloid-containing plant (*Delphinium occidentale*) did not eat more *D. occidentale* than did control animals that lacked such experience. However, after desirable forages had been consumed, previously conditioned animals grazed more *D. occidentale* than did control animals (Ralphs 2005).

We can then identify a second scenario where experiences *in utero* and early in life cause a suite of neurological (e.g. LeDoux 2002; Doidge 2007), morphological (e.g. Schlichting and Pigliucci 1998) and physiological (e.g. Dufty *et al.* 2002) changes in consumers. By interacting with the genome during growth and development, social and biophysical environments influence gene expression and behavioural responses, as the emerging field of epigenetics is highlighting. Over generations, these interactions create animals locally adapted to landscapes (Provenza 2008). For instance, lambs exposed to a high sodium-containing shrub during uterine life grow faster and handle a salt load better than do lambs from mothers on pasture (Chadwick *et al.* 2009). Likewise, goats reared from 1 to 4 months of age with their mothers on blackbrush-dominated rangeland ate over 2.5 times more blackbrush than did goats naive to blackbrush, a shrub low in nutritional quality and rich in tannins (Distel and Provenza 1991). Rumen volume and ability to cope with tannins were higher for goats reared on blackbrush than for goats reared on a non-tanniferous diet. Sheep (Distel *et al.* 1994) and cattle (Wiedmeier *et al.* 2012) exposed early in life to low-quality foods display later in life an increased nitrogen retention and ability to digest fibre. Thus, the 'absolute fitness value' for a certain low-quality food may change as a function of an animal's early experiences with such food. In this scenario, we may expect an enhanced utilisation

of unpalatable foods, even when high-quality alternatives are highly available, because the ability of animals to use those forages has been enhanced by experiences during development *in utero* and early in life. For instance, goats with 4 months of experience consuming blackbrush (*Coleogyne ramosissima*) with mother early in life ate 30% more blackbrush than did inexperienced goats 9 months after weaning, even when allowed to choose between the poorly nutritious blackbrush and alfalfa pellets at any level of alfalfa-pellet availability, which ranged from 20% to 100% of *ad libitum*.

In summary, the experimental conditions imposed by traditional free-choice trials in confined conditions may not reveal how herbivores value a certain low-quality food on the basis of their previous experiences. This is because *ad libitum* availability of preferred foods in a choice 'hides' such valuation, as the costs of foraging on these resources are negligible. However, when conditions in natural environments change, such as when abundance of preferred alternatives declines and travelling and searching and handling costs increase, previous experiences eating low-quality foods by herbivores are revealed. These findings suggest that future management techniques should consider integrating preference conditioning procedures to improve experience with low-quality forages (i.e. incentive value of forages) and environmental conditions to encourage their use in natural situations.

Manipulating choice in grazing animals

The reviewed evidence on the impact of food context and past dietary experiences on herbivores' foraging decisions highlights (1) the importance of food diversity for selecting a diet that better meets individual nutritional requirements and avoids toxicity and/or metabolic disorders, and (2) the possibility to manipulate choice through past experiences with food context. A constraint for ruminants grazing multi-species pastures involves animals preferentially selecting one species over another, achieving an uneven use of the forages on offer. The question here is whether livestock that learn about contextual complementarities among forages will incorporate a higher proportion of less preferred forages into their diets, as some studies (Villalba *et al.* 2004) and experiences of ranchers (Provenza 2003) suggest?
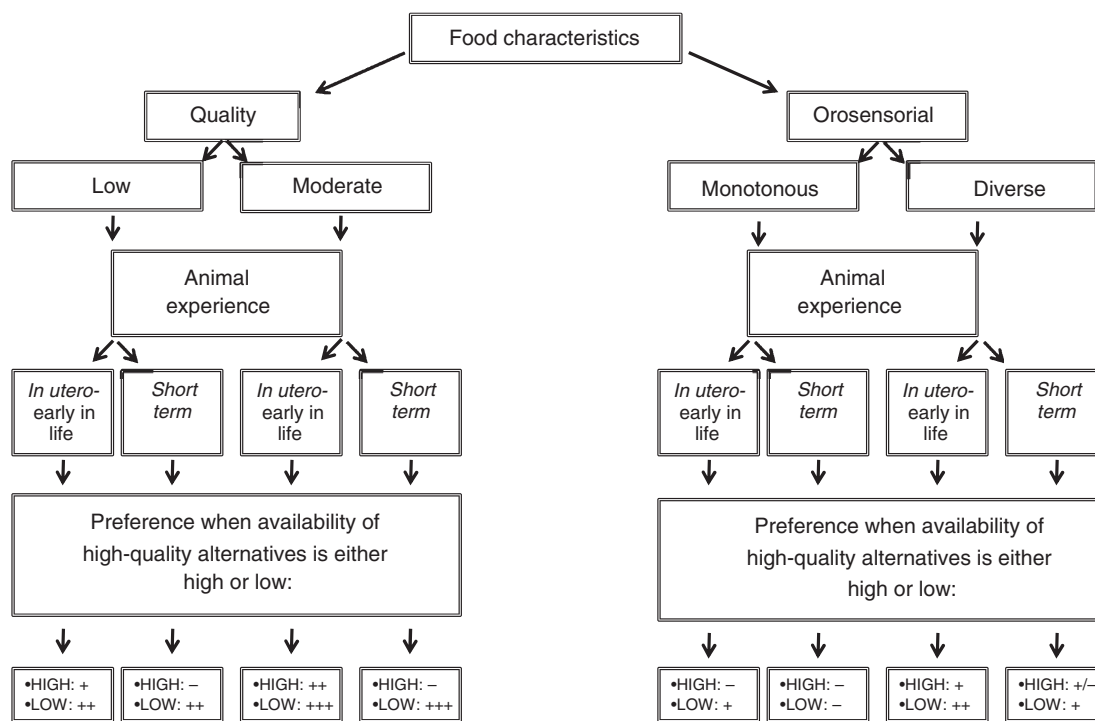

Fig. 2. Herbivores' preference for unpalatable plant species in a community as a function of their prior contextual experiences. Signs indicate the direction (+, increased; –, no change) and number of signs indicate the intensity of preference relative to inexperienced Controls. Experiences *in utero* and early in life have a stronger effect on preference than short-term experiences in adult animals due to potential epigenetic effects. Thus, experienced animals may show a greater preference for unpalatable plants than do inexperienced animals, even when the abundance of high-quality alternatives in the community is high (HIGH). When landscapes are invaded by unpalatable species, i.e. there is a low abundance of high-quality alternatives (LOW), experienced animals are expected to use those species to a greater extent than are inexperienced animals due to their prior positive contextual experiences with those unpalatable species. Contextual experiences with plants of moderate quality may lead to greater preferences than contextual experiences with plants of low quality due to the greater nutrient content of the former. Diverse orosensorial experiences are expected to increase preference relative to monotonous orosensorial experiences due to sensory-specific satiety effects. Preference for familiar flavours (experienced *in utero*, early in life, or in the short term) are predicted to be more pronounced when availability of high-quality alternatives is low.

Learning contextual complementarities among forages may increase dietary contribution of less preferred foods if they serve a positive post-ingestive function to the animal and/or if those less preferred foods provide some orosensorial properties that are different from the preferred foods. We propose that the inclusion of lower-quality foods into herbivore diets will depend on the relative quality of the food (e.g. moderate to low) and on the time and timing of contextual experiences with those foods (Fig. 2). Experiences *in utero* or early in life may cause permanent changes that make the food 'more nutritious' because animals may become more efficient at extracting nutrients from such foods than are inexperienced animals. In this scenario, preference for unpalatable foods may increase, even when higher-quality alternatives are present. In contrast, if the aforementioned epigenetic changes do not take place, we predict that positive contextual experiences will enhance the use of low-quality foods only when availability of greater-quality foods is restricted, because of increased handling and/or searching costs. Thus, preference for low-quality foods experienced in an appropriate nutritional context are predicted to be more pronounced as the availability of high-quality alternatives in the plant community declines due to reduced accessibility in space and time (Fig. 2), increased searching and handling costs, or greater competition among consumers. In relation to handling and searching costs, recent research and management recommendations for natural grasslands in southern Brazil stress the importance of the interaction between forage structure and quality on herbivores' foraging decisions. Cattle use tussocks (non-preferred) to gather high bite masses throughout the day, whereas they ingest higher-quality herbs and more palatable grasses in inter-tussock areas (preferred) to gather bites, even when smaller, of greater quality (Carvalho 2013). The greater-quality bites 'supplement' the lower-quality, but more readily accessible, bites to achieve an optimal diet. The same is true regarding synergies in time and space for pastures and rangelands in France (Meuret and Provenza 2014*a*, 2014*b*). In addition to the synergistic nutritional benefits of ingesting tussocks and herbs, contrasting orosensorial experiences and reduced sensory-specific transfer effects may contribute to the maintenance of high intake rates by cattle throughout the day. Diverse orosensorial experiences are expected to increase preference relative to monotonous orosensorial experiences due to sensory-specific satiety effects (Fig. 2).

Conclusions

Experience with diverse food contexts can modify food choice in herbivores. However, evidence of this effect in ruminants is limited to binary or trinary interactions among food items on pastures and controlled settings. More research is needed in natural settings and with a greater number of plant species. Psychobiological research with rats, ruminants and human beings all suggests that hedonic aspects of appetite control interact with homeostatic mechanisms involved in satiety. Evidence of hedonic shifts in ruminants warrants further exploration of the influence of food reward (orosensorial, post-ingestive) on appetite control and food preference in range and cultivated pastures. In addition, the fitness and reward values

of unpalatable foods may change as a function of the consumer experiences *in utero* and early in life to such foods. Finally, the experimental conditions imposed by free-choice trials in controlled settings may not always reveal how herbivores value a certain low-quality food on the basis of their previous experiences. *Ad libitum* availability of all foods in free-choice trials can 'hide' such valuation, because the cost for selecting any preferred food in this scenario is negligible. All of these variables – animal experience, food type, quality and quantity – give managers 'tools' to manipulate diet choice so as to achieve different patterns of use of plants in a community as a function of pre-determined objectives. More research on the impacts of food context on preference should pioneer innovative management strategies to achieve pre-established land-manipulation goals and/or enhance forage intake, productivity and animal welfare.

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