

13 Foraging in Domestic Herbivores: Linking the Internal and External Milieux

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Introduction

Food and sex are basic for life, but of the two, food comes first. Without adequate nutrition, animals do not reproduce. Selecting the right diet, then, is the foundation for the survival of individuals who ensure the persistence of species. During the several million years a species exists, biophysical and social environments change tremendously. How do the individuals who create the populations that make up a species cope with such dynamism and complexity?

Consider the following challenge. Imagine an animal foraging in an environment with 25–50 plant species. These plants differ in their concentrations of energy, protein, minerals and vitamins. They all contain toxins of one sort or another, but at the appropriate dose, many of these toxins have medicinal benefits. Envision further that how much of any one food an animal can eat depends on the other foods it selects because at the biochemical level, nutrients and toxins interact one with another – nutrients with nutrients, nutrients with toxins and toxins with toxins (Provenza *et al.*, 2003a). These challenges are further amplified because cells, organs, individuals, and social and biophysical environments change constantly. Now imagine that 3–7 foods will make up the bulk of the diet at any point in time. Which plants should an animal choose? Clearly, given 25–50 species and their interactions, there are a great many pos-

sibilities to mix and match different plant species.

Certainly the foods an animal can eat and the possibilities to live in an environment are influenced by how the animal is built (its morphology) and how it functions (its physiology) – the expression of its genome. Morphology and physiology affect the need for nutrients, the ability to cope with toxins and the value of medicines, thereby creating the bounds within which animals can use different foods and habitats. But genes do not operate in isolation. They are expressed, beginning at conception, through the interplay with the social and biophysical environments where an individual is reared (Lewontin, 2000; Moore, 2002). Learning itself is a genetically expressed trait, a kind of fixed plasticity, that much like evolution is continually shaped by the environment (Skinner, 1984). Thus, learning in concert with the genome influences the combinations of plants an animal will eat.

Animals function and maintain well-being within the internal milieu through behavioural interactions with the external milieu. These interactions are complex. They involve an ongoing dynamic influenced by history, necessity and chance such that at any time an animal's foraging behaviour is a function (i) of its evolutionary history, genetically expressed, in concert with its uniquely individualistic history of the social and biophysical environments where it was conceived and reared; (ii) of necessity

due to its current nutritional, toxicological and medicinal state relative to the biochemical characteristics of foods it can potentially consume at any moment; and (iii) of chance occurrences that involve gene expression and environmental variability (Lewontin, 2000; Moore, 2002). Unfortunately, we rarely stop to consider that the events we observe are processes, rather than snapshots in time, that reflect this ongoing dynamic influenced by history, necessity and chance.

Behaviour by Consequences

While difficult to realize fully and embrace graciously, the only constant in life is change. Things never were the way they were and they never will be again. To survive in a world where the internal and external milieux change constantly requires that individuals experience the consequences of their behaviours. That necessitates ceaseless monitoring by cells and organs and ongoing changes in behaviour in ways that integrate basic metabolic processes with the experiences of pleasure and pain, drives and motivation, emotions and feelings (Damasio, 2003). Monitoring is essential because behaviours at all levels – cells and organs to social and biophysical environments – alter ‘landscapes’ at every level as they unfold. At all these levels, behaviour is a function of the consequences that ensue from behaviours and which in turn change the likelihood of future behaviours.

Consequences that *increase* the likelihood of behaviours recurring are called reinforcement, and they can be either positive (positive reinforcement) or negative (negative reinforcement). Creatures seek *positive reinforcers*. When a hungry animal searches for a particular nutritious food, or a thirsty animal walks to water, or a hot animal seeks shade, they do so because food, water and shade are positive reinforcers – they are things the body wants. Conversely, animals avoid *negative reinforcers*. When a hungry animal searches for a nutritious food, or a thirsty animal walks to water, or a hot animal seeks shade, they also do so to get relief from aversive stimuli – lack of food, water and shade.

Consequences that *decrease* the likelihood of behaviours recurring are called *punishment*, and they are based on either presentation of an aversive stimulus (positive punishment) or the removal of a positive stimulus (negative punishment). *Positive punishment* results from presenting an aversive stimulus. For example, when livestock experience toxicosis after eating a plant, they stop eating the plant. *Negative punishment* results from the removal of a positive reinforcer. For instance, when an animal eats a plant that was once nutritious but is no longer so, the animal decreases its rate of responding (eating the plant) because a positive reinforcer (nutrients) has been removed.

Behaviour by consequences and foraging

In the case of foraging, behaviour by consequences (preference) is manifest as the interrelationship between a food’s flavour (behaviour) and its postingestive feedback (consequences) (Provenza, 1995a; Fig. 13.1). Flavour is the integration of odour, taste and texture with postingestive feedback from cells and organs in response to concentrations of biochemicals in foods. The senses of smell, taste and sight enable animals to discriminate among foods and provide pleasant sensations – liking for a food’s flavour – associated with eating. Post-ingestive feedback calibrates sensory experiences – like or dislike – according to a food’s utility to the body. Thus, flavour–feedback interactions emanate from an animal’s physiological state and a food’s chemical characteristics, and feedback affects liking for flavour (palatability) as a function of need and past experience with a food.

Feedback from the ‘body’ to the ‘senses’ is critical for health and well-being. Bodies are integrated societies of cells. They interact one with another and with the external environment through feedback mediated by nerves, neurotransmitters and hormones. In the case of flavour–feedback interactions, nerves for taste converge with nerves from the body in the brainstem and from there they synapse and relay to the limbic system and the cortex (Provenza, 1995a). Feedback from the body to

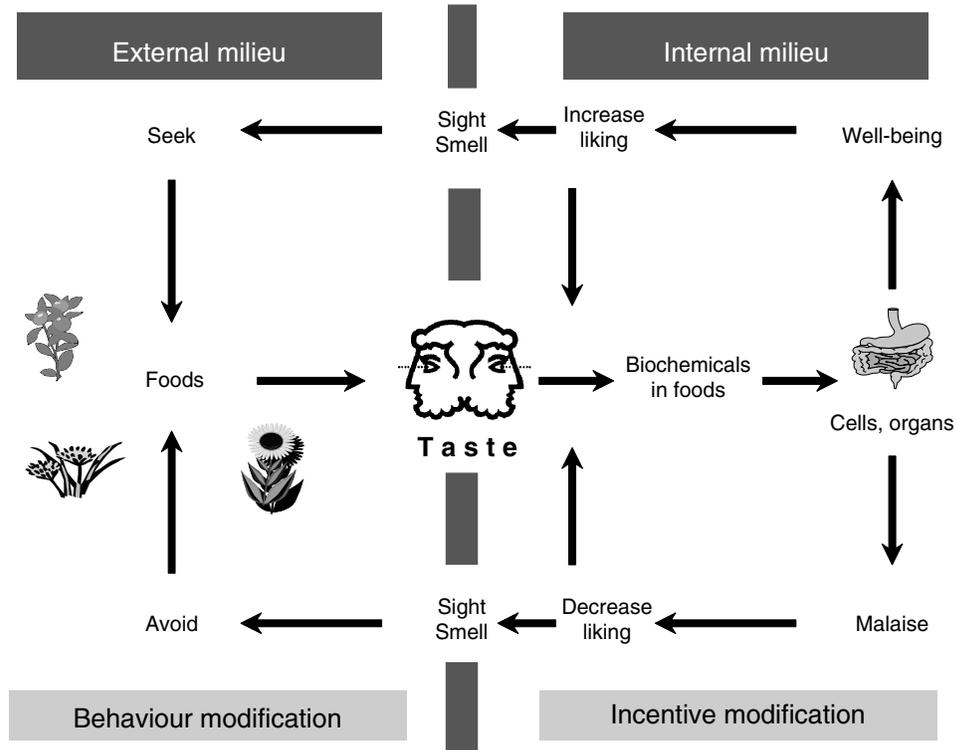


Fig. 13.1. Food intake, food preferences and palatability all result from the interrelationship between a food's flavour and its post-ingestive consequences. The integration of the internal (cells and organs) and external (foods) milieus occurs through two interrelated systems: affective (implicit or associative) and cognitive (explicit or declarative). Taste plays a critical role in both systems, and receptors for taste are situated at the junction between the internal and external milieus, like a Janus head – the Roman god of beginnings – placed at the gateway to the body, with one face looking outward and the other looking inward. The affective system integrates the *taste* of food with *post-ingestive feedback* from cells and organs in response to levels of ingested substances: nutrients, toxins, medicines. This system causes changes in the intake of food items that depends on whether the effect on the internal milieu is aversive or positive. The net result is *incentive modification* due to changes in well-being. 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 milieu 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 milieus and given that nutrients at too high levels are toxic, toxins at appropriate levels may be therapeutic and medicines in suitable doses can ameliorate excessive intakes of nutrients or toxins.

the palate is how societies of cells and organs influence certain foods, and how much of those foods are eaten by an animal. Feedback also influences the senses – smell, taste, touch – that are the interfaces between the internal milieu of the body and the external milieu where animals learn to forage.

Looking for spinoza: experiencing the consequences of behaviours

While much research has related physiology and behaviour, there has been virtually no work to understand how livestock actually experience the consequences of their behaviours, e.g.

increased well-being following a nutrient boost or illness following toxicosis. Our mechanical notions of animals have inhibited us from exploring the issues Damasio (2003) raises in *Looking for Spinoza: Joy, Sorrow, and the Feeling Brain*. Damasio argues that body mapping of life-sustaining processes by the central nervous system is linked to well-being and feelings in animals. At the most fundamental levels, this involves metabolic regulation, basic reflexes and immune responses. At somewhat higher levels, organisms experience the consequences of their behaviours on the internal milieu as a continuum from pain (aversive) to pleasure (positive). At yet higher levels, drives and motivations (incentives) emanating from the consequences of past behaviours influence the likelihood of future behaviours. And at the highest levels, the experience of emotions and ultimately feelings arises from different degrees of well-being emanating from ongoing interactions among cells, organs, individuals, and social and biophysical environments (Fig. 13.2).

The notion that animals experience and respond to different physiological states by altering their ingestive behaviour has not been widely accepted historically or in the present time. Hence, we know little about the processes that enable animals to ingest appropriate amounts of nutrients, toxins and medicines (Provenza, 1995a). Consider, however, that feedback provides detailed mapping simultaneously about the current states of the living cells throughout the body because every region of the body contains nerves that provide information to the central nervous system (Damasio, 2003). The signalling is complex. It is not a matter of 'zeros' or 'ones' indicating, for example, that a living cell is on or off. The signals are highly variegated and related to well-being at the cellular level. Among other functions – including feedback reflecting pH, oxygen and carbon dioxide in the vicinity of a cell as well as internally generated compounds signalling distress, disease and pleasure – they can indicate the concentrations of nutrients or toxins in the internal (gut) and external (skin) milieu, and thus indicate to the brain what the gut or skin is experiencing at any given moment. In addition, the central nervous system is also directly informed about variations in the concentrations of a myriad of chemical

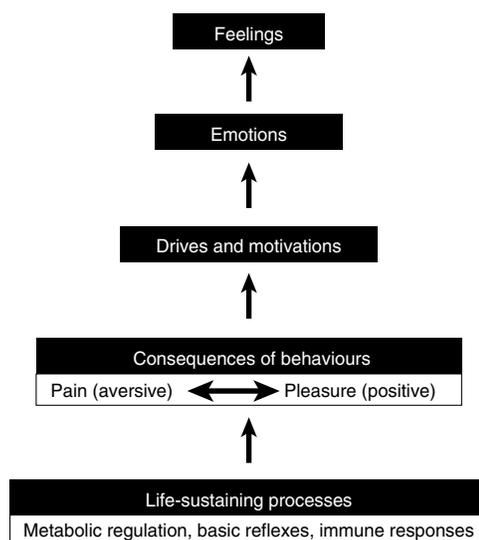


Fig. 13.2. Foraging behaviour is a function of its consequences, and ingesting foods results in postingestive consequences that affect the kinds and likelihoods of future foraging behaviours. Animals likely experience the consequences of their behaviours, for instance well-being following a nutrient boost or illness following nutrient excesses or toxicosis, through body mapping by the central nervous system that links life-sustaining processes to feelings (Damasio, 2003). Nerve endings in every region of the internal milieu provide detailed mapping simultaneously of the current state of cells that feedback to the central nervous system. At the most fundamental levels, this involves metabolic regulation, basic reflexes and immune responses. At somewhat higher levels, organisms experience the consequences of their behaviours as a continuum from pain (aversive) to pleasure (positive). At yet higher levels, drives and motivations (incentives) emanate from the consequences of past behaviours that influence the likelihood of future behaviours. At the highest levels, the experience of emotions and ultimately feelings arise from different degrees of well-being emanating from ongoing interactions among cells, organs, individuals, and social and biophysical environments.

molecules in the bloodstream via non-neural routes.

Thus, feelings arise from collective representations of life in the process of being aligned for survival in a state of optimal performance. When bodily processes are engaged due to

internal and external stimuli and situations, the flow of the life process is made either more efficient, unimpeded and easier, or less so. The intensity of feelings depends upon the degree of corrections necessary when individuals experience negative states, and the level to which an animal is able to achieve positive states, both of which are directly related to sustaining life processes. Thus, to paraphrase Damasio (2003), the particular way a feeling is experienced depends on basic life-sustaining processes in multicellular organisms with central nervous systems; the current functioning – positive or negative – of life-sustaining processes; the corrective responses particular life states beget and the behaviours organisms exhibit given the presence of certain biophysical and social stimuli and situations; and the nature of the neural medium in which all of these structures and processes are mapped.

From Homeostasis to Homeodynamics

Homeostasis

Claude Bernard first introduced the notion that internal organs are protected by the constancy of the internal milieu. The need to maintain a hospitable environment where cells and organs can perform optimally was attributed to continuous engagement at all levels – cells, organs, individuals – in an active self-preservation (Bernard, 1957). Homeostasis is the tendency of an organism to maintain a uniform and beneficial physiological stability within and among its cells and organs, leading to organic equilibrium. The term ‘homeostatic regulation’ was created to describe physiological processes and mechanisms that keep the body ‘in balance’ (Cannon, 1966). Set points and thermostats, terms often used to portray homeostasis, connote regulation to maintain dynamic equilibrium, which implies a fixed point of balance around which a body oscillates.

These metaphors taken literally have led to static views of homeostasis and mechanical views of animals. With foraging behaviour, we observe animals selecting particular foods and habitats, and we assume their behaviours are

optimized by predetermined morphological structures and physiological processes. We consider their needs for different nutrients to be rigidly set, and we change physical environments to fit our perception of what we think animals require – we attempt to change the landscape to suit the animal – rather than changing the animal to suit the landscape. In the case of conservation biology, we strive to maintain ‘pristine’ environments we believe best meet the needs of animals. All of these notions, rooted in views of homeostasis tempered by rigid ideas of genes that affect feedbacks, set points and thermostats, have come to connote rigidity rather than fluidity. We do consider how history, necessity and chance interact to influence behaviour.

Homeodynamics

Ongoing regulation of the internal milieu requires ceaselessly engaging the external milieu, and both the internal and external milieus are best explained as strands in a web characterized by change. If we consider feedback among cells, organs, individuals, and social and biophysical environments, at all levels smaller-scale parts exist for and by means of larger-scale wholes, which in turn exist for and by means of smaller-scale parts. This is the essence of the holon, which is an autonomous entity when viewed from the perspective of its constituent subsystems, such as an animal from the viewpoint of a cell or an organ. The same holon, viewed from a larger scale, is merely a part of a larger system, such as an animal within a social group or an ecosystem. Interrelationships among holons make identity at any scale real and meaningful, as it is identity that makes the ongoing interrelationships possible. Interactions within and among holons – behaviour by consequences – involve the ongoing exchange of energy and matter at all levels from cells and organs to individuals and biophysical environments. While we often view these interactions in linear, hierarchical ways, in reality there is no one central controlling force, but only a large number of holons, all interacting and adapting to one another and to their local environments. Ultimately, kaleidoscopic patterns emerge from

ongoing interactions among all of the parts (Provenza *et al.*, 1998).

As in quantum physics, the critical attribute of any holon – an elementary particle, an individual, a social group – is the fact that the dynamics of its behaviour cannot be defined with certainty because the holon is inseparable from its history (Provenza *et al.*, 1999). An individual animal's behaviour reflects its evolutionary history (gene-expressed morphology and physiology), its cultural history (experiences of the social and biophysical environments where an individual is conceived, born and reared) and its ongoing interactions with those environments. This does not mean behaviours occur in an arbitrary fashion. It means only that the behaviour of any organism is determined by connections to a larger historical whole. Because we do not know all of these connections precisely, and because their interrelationships lead to emergent properties, the classical notion of cause and effect must be supplemented with notions of self-organization (Provenza and Cincotta, 1993; Provenza *et al.*, 1998).

Ultimately, each individual's behaviour is unique, and behavioural processes can be understood only in a dynamic context, in terms of movement, interaction and transformation. Thus, animals are not machines – set points never are – and feedback changes animal behaviour from conception to the death of the individual and among individuals across generations. For these reasons, Rose (1998) coined the term homeodynamics, as opposed to homeostasis, to connote ongoing adjustments to ever-changing internal and external milieux, rather than to oscillations about some fixed point of balance.

Thus, behaviour emerges from the functioning of holons and the integrity of the holon is the variable that is maintained (Maturana and Varela, 1980; Provenza *et al.*, 1998). Deviations in the internal milieu promote behavioural responses intended to maintain the holon's functioning and well-being. Behavioural regulation is maintained via the functioning of feedback loops involving circular arrangements of interconnected holons. Feedback influences behaviour through actual, not expected, performance, and it involves more than the linear cause-and-effect links between

inputs and outputs, such as temperature control by a thermostat (Capra, 1996). The inherent non-linear nature of interconnected loops, which involves thresholds and varying degrees of temporal delays between behaviour and consequences (Glass and MacKey, 1988), creates multiple arrays and levels of complexity that increase the flexibility and adaptability of responses to environmental challenges.

Flavour-Feedback Associations: Linking State and Substance

The amount of food eaten and preferences for foods are typically thought to be influenced by palatability. But what is palatability? It is a narrowly defined term with many meanings. *Webster's* defines palatable as pleasant or acceptable to the taste and hence fit to be eaten or drunk. Animal scientists usually explain palatability as the hedonic liking or affective responses from eating that depend on a food's flavour and texture, or the relish an animal shows when consuming a food or ration. Conversely, plant scientists describe palatability as attributes of plants that alter preference such as chemical composition, growth stage and associated plants. Thus, all popular definitions focus on either a food's flavour or its physical and chemical characteristics.

Historically, researchers thought palatability depended on the species of animals, and they attempted to rank food preferences based on their presumed palatabilities. Nutritionists understood that intake regulation involved feedback from receptors – chemoreceptors, osmoreceptors, mechanoreceptors – in the body (Van Soest, 1982). They also came to appreciate the fact that different concentrations of compounds used to assess the preferences of cattle, sheep and goats for sweet, sour, salty and bitter affect more than just taste – they have postingestive effects (Grovm, 1988). Even so, palatability remained a mystery, and its relationship to intake and preference unknown (Aronld and Dudzinski, 1978; Grovm, 1988), largely because we did not appreciate the complex interrelationships among taste, smell, sight and the postingestive effects of foods, as well as their relationship to

past experiences with foods. In essence, we did not consider history, individuality or feedback.

Behavioural regulation in the internal milieu

To maintain fluidity and well-being while foraging, cells and organs must integrate neural and hormonal signals corresponding with specific internal states, and animals must then associate changes in well-being with ingesting specific substances (Figs 13.1 and 13.2). The exchange of information between the internal and external milieux is processed through two interrelated systems: affective (implicit or associative) and cognitive (explicit or declarative). Taste plays a critical role in both systems. The affective system integrates the *taste* of food with *postingestive feedback* from cells and organs in response to levels of ingested substances – nutrients, toxins, medicines. This system causes changes in the intake of food items that depend on whether the effect on the internal milieu is aversive or positive. The net result is *incentive modification* due to changes in well-being. 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 milieu 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 milieux and given that nutrients at too high levels are toxic, toxins at appropriate levels may be therapeutic and medicines in suitable doses can ameliorate excessive intakes of nutrients or toxins.

Affective (non-cognitive) changes in palatability through flavour–feedback interactions occur automatically. Animals do not need to think about, or even remember, the feedback event, just as none of us need to consider which enzymes to release to digest the foods we eat. Even when animals are anaesthetized, postingestive 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.*, 1994a). Thus, feedback changes palatability without a bit of thought, and often in spite of rationality. For instance, people often acquire strong aversions to foods eaten just prior to becoming nauseated even when they know that the flu or seasickness – rather than the food – was responsible for the nausea.

Historically, few believed that cells and organs could influence the palate to select foods that meet their needs – that bodies have nutritional wisdom. In part, we assumed nutritional wisdom was not possible because it involved more cognitive, rational, analytical thought. We did not appreciate that the wisdom of the body depends strongly on non-cognitive, intuitive, synthetic processes mediated by cells and organs in response to nutrients, toxins and medicines (Provenza, 1995a, 1996). In considering the origins of human behaviour as well, we typically emphasize the cognitive, rational and analytical aspects, but the non-cognitive, intuitive and synthetic facets of ‘thinking’ most strongly influence our behaviours, and this occurs without a bit of ‘thought’ (Gladwell, 2005).

Feedback increases preference for substances that enhance well-being

Combinations of nutrients in appropriate doses enhance well-being. For example, livestock benefit from maintaining a balance of energy and protein in their diets and by discriminating specific flavours and nutrient-specific feedbacks. Lambs fed diets low in energy and protein prefer flavoured low-quality foods previously paired with intraruminal infusions of energy (starch, propionate, acetate) or nitrogen (urea, casein, gluten) (Villalba and Provenza, 1996, 1997a,b,c). Given preloads of energy or nitrogen, lambs prefer flavours previously paired with nitrogen or energy, respectively, during the ensuing meals (Villalba and Provenza, 1999). Thus, animals maintain a balance of energy to protein that meets their nutritional needs, and in the process, they recognize different internal states and discriminate among different nutrients (Egan, 1980; Wang and Provenza, 1996).

People learn to take aspirin for headaches, antacids for stomachaches and ibuprofen to relieve pain, and we obtain prescriptions from doctors for medications. Many of the drugs we use come from plants in nature. But what about other animals; can they too learn to write prescriptions from nature's pharmacy? While little is known about the abilities of animals to self-medicate, and many of the observations are anecdotal and equivocal (Clayton and Wolfe, 1993; Lozano, 1998; Houston *et al.*, 2001), there is evidence of self-medication in animals (Engel, 2002). Sheep ingest 'medicines' such as polyethylene glycol (PEG), a substance that attenuates the aversive effects of tannins, when they eat foods high in tannins, and they titrate the dose of PEG according to the amount of tannin in their diet (Provenza *et al.*, 2000). They discriminate the medicinal benefits of PEG from non-medicinal substances by selectively ingesting PEG after eating a meal high in tannins (Villalba and Provenza, 2001). They also forage in locations where PEG is present, rather than where it is absent, when offered nutritious foods high in tannins in different locations (Villalba and Provenza, 2002). Likewise, cattle foraging on endophyte-infected tall fescue high in alkaloids readily use lick tanks that contain FEB-200 (Altec™), but they ignore lick tanks [Q1] without FEB-200 (Cathy Bandyk, personal communication). FEB-200 contains the cell walls of yeast, which adsorb the alkaloids in tall fescue, thus acting as a medicine that enhances consumption of tall fescue by cattle. Sheep fed acid-producing substrates such as grains subsequently ingest foods and solutions that contain sodium bicarbonate, which attenuates acidosis (Phy and Provenza, 1998). In the most elaborate studies to date, sheep learned to selectively ingest three medicines – sodium bentonite, polyethylene glycol, dicalcium phosphate – that lead to recovery from illness due to eating too high amounts of grain, tannins and oxalic acid, respectively (Villalba *et al.*, 2005a). This first demonstration of multiple malaise–medicine associations supports the notion that herbivores can learn to self-medicate.

Animals may also learn to overcome internal parasite burdens by eating foods high in tannins and nutrients (Hutchings *et al.*, 2003). Livestock feeding on plants with tannins show lower nematode burdens, lower faecal egg

counts and higher body gains than those eating similar plants without tannins (Athanasiadou *et al.*, 2000; Coop and Kyriazakis, 2001; Min and Hart, 2003). Tannins also increase the supply of bypass protein (Reed, 1995; Foley *et al.*, 1999), which enhances immune responses to intestinal parasites (Min and Hart, 2003). Sheep with parasite infections also ingest needed nutrients (Hutchings *et al.*, 2003), thereby better coping with the nutrient drain and correcting the infection through increased immunity (Min and Hart, 2003). Finally, sheep with high parasite loads avoid parasite-rich pastures, even though those pastures offer higher nutrient rewards, to a greater extent than sheep with lower levels of parasite infection (Hutchings *et al.*, 2002).

Feedback decreases preference for substances that diminish well-being

Deficits or excesses of nutrients or toxins cause cells and organs to deviate from well-being and self-preservation. In this case, behaviours are geared towards limiting intakes of particular foods. Feedback from foods inadequate in nutrients decreases intake and preference. For example, sheep are reluctant to eat poorly nutritious foods such as straw; their intake and preference for straw increase only with feedback from more nutritious food (Greenhalgh and Reid, 1971) or starch (Villalba and Provenza, 1997a, 2000a) infused into the rumen immediately after a meal of straw. Animals detect and respond to an amino acid deficit within minutes of eating a diet low in an amino acid (Hao *et al.*, 2005). Preruminant and ruminant lambs become averse to diets deficient in specific amino acids and they readily sample other foods that may help them correct the deficiency (Rogers and Egan, 1975; Egan and Rogers, 1978). Finally, exposure even to a nutritionally balanced food for as little as a day can decrease preference for that food, and the decrease in preference is much more pronounced when the food is low in fermentable protein relative to energy (Early and Provenza, 1998).

Intake and preference also decline when nutrients exceed needs. For instance, when

needs for NaCl are met, and lambs are fed flavoured straw previously associated with intraruminal infusions of NaCl, they avoid the flavoured straw because their needs for salt are met (Villalba and Provenza, 1996). Likewise, sheep avoid sulphur when their requirements for sulphur are met (Hills *et al.*, 1999), and cattle stop eating bones when their blood Pi (inorganic phosphate) levels are within normal or excessive ranges (Denton *et al.*, 1986; Blair-West *et al.*, 1992). The same is true with excesses of energy or protein. Lambs prefer a flavour of straw paired with low to moderate doses of energy (propionate, acetate) or nitrogen (urea, casein), but at higher levels of energy or nitrogen, they become averse to that flavour of straw (Villalba and Provenza, 1996, 1997a,b). Dairy cows fed high levels of protein in the barn subsequently avoid eating plants with higher nitrogen concentrations when given choices while they are foraging on pasture (Emmik and F.D. Provenza, [Q2] unpublished data).

Finally, excesses of toxins in foods cause food avoidance because they move the body away from normal functioning. Goats limit intakes of otherwise nutritious foods too high in tannins or lithium chloride (Provenza *et al.*, 1990). Oral gavage of toxins causes dose-dependent decreases in intake of toxin-containing foods (Wang and Provenza, 1997; Dziba and Provenza, 2005). Limits on intake are set by the rates at which toxins can be eliminated from the body (Foley and McArthur, 1994). At critical thresholds, toxins satiate the detoxification capabilities of herbivores (Provenza *et al.*, 2003a). At these levels, animals quit feeding, and resume eating only after toxin concentrations in the body decline due to detoxification and elimination (Pfister *et al.*, 1997; Dziba and Provenza, 2005; Dziba *et al.*, 2005). These processes cause cyclic patterns of intakes of particular foods with peak intakes at the lowest concentration of toxins in the body (Pfister *et al.*, 1997; Foley *et al.*, 1999).

Behavioural regulation when substances interact

Despite the diversity of chemicals herbivores ingest, most studies focus only on single compounds. Nevertheless, biochemical diversity is

essential for homeodynamics and all biochemical interactions depend on dosages (Provenza *et al.*, 2003a). For instance, tannins at high levels adversely affect animals, but sufficient protein can mitigate the effects of excess tannins; conversely, tannins in moderate amounts are beneficial as they reduce nitrogen loss in the rumen by decreasing the breakdown of protein into ammonia, thus increasing the 'bypass value' of proteins and amino acids, especially sulphur-containing amino acids such as methionine and cystine (Reed, 1995). Tannins eaten in modest amounts also decrease internal parasites (Min and Hart, 2003; Hutchings *et al.*, 2003).

Nutrient–nutrient interactions

When different nutrients interact, behavioural responses depend on the specific characteristics of the interaction. For instance, preference increases for diets with appropriate ratios of energy and protein, whereas preference decreases with an excess of either (Kyriazakis and Oldham, 1997; Villalba and Provenza, 1997c). Asynchronous releases of by-products of energy and nitrogen metabolisms cause a build-up of organic acids and ammonia that diminishes food preference (Cooper *et al.*, 1995; Francis, 2003). Balancing the supply of fermentable carbohydrates and nitrogen optimizes microbial protein synthesis and maximizes retention of rumen-degradable nitrogen (Sinclair *et al.*, 1993). Conversely, when the rate of ammonia formation exceeds the rate of carbohydrate fermentation, nitrogen is used inefficiently by microbes, and much nitrogen is lost in urine (Russell *et al.*, 1992). Excessive nitrogen/energy ratios cause ammonia toxicity (Lobley and Milano, 1997), whereas excessive energy relative to nitrogen produces acidosis (Francis, 2003). Supplements high in starch depress the intake of fibrous foods (Mertens and Loften, 1980).

Toxin–toxin interactions

All plants contain toxins, including the vegetables we grow in our gardens, the grasses and forbs we plant in pastures and the plants that

grow naturally on rangelands. None the less, herbivores seldom consume enough toxins to be poisoned because they regulate their intake of toxins. While we know little about this topic, we do know that interactions among toxins can cause aversions or preferences, depending on the specific characteristic of the interaction (Provenza *et al.*, 2003a). Ingesting foods with a variety of different toxins, which act upon different organs and detoxification pathways, is likely to be less harmful than a large dose of any one toxin (Freeland and Janzen, 1974). Indeed, sheep eat more when offered choices of foods with various toxins that affect different detoxification mechanisms, and thus are complementary (Burritt and Provenza, 2000; Villalba *et al.*, 2004). In contrast, when toxins impact the same detoxification pathway or are antagonistic, ingestion of toxins decreases (Burritt and Provenza, 2000). Interestingly, sheep and goats maintain high levels of intakes when they can select a variety of shrubs that contain different toxins, and the effect is far greater than that due to medicines such as PEG and activated charcoal; these medicines have a pronounced effect only when the number of shrubs in the diet is reduced to less than two or three (Rogosic *et al.*, 2005a,b).

Nutrient-toxin interactions

Rates of detoxification are influenced by the nutritional status of an animal. The general mechanism of detoxification involves converting more toxic lipophilic compounds to less toxic water-soluble compounds that can be excreted in the urine (Cheeke and Shull, 1985; Cheeke, 1998). Biotransformation of toxins is carried out largely in the liver and usually occurs in two steps. The first step (phase I) introduces a reactive group – such as OH, NH₂, COOH or SH – into the structure of the toxin; those interactions typically produce a less toxic compound. During the second step (phase II), the newly formed compound is conjugated with a small molecule such as glucuronic acid, amino acids (e.g. glycine), sulphates, acetates or methyl groups (Osweiler *et al.*, 1985). Importantly, these transformations require nutrients such as protein and

energy (Illius and Jessop, 1995, 1996). Thus, detoxification processes reduce the protein and energy that otherwise would be available for maintenance and production (Freeland and Janzen, 1974; Illius and Jessop, 1996).

When animals ingest adequate amounts of energy and protein, they can eat more foods that contain toxins. Lambs ingest more of the toxin LiCl as the energy content of their diet increases (Wang and Provenza, 1997). Likewise, sheep offered terpene-containing diets with increasing concentrations of energy or protein consume terpenes in a graded fashion with a positive relationship between energy and protein intake of foods with toxins (Villalba and Provenza, 2005). Supplemental energy and protein increase the ability of sheep and goats to eat foods that contain toxins such as terpenes (Banner *et al.*, 2000; Villalba *et al.*, 2002a), tannins (Villalba *et al.*, 2002b) and saponins (Williams *et al.*, 1992; Martinez *et al.*, 1993). In contrast, herbivores eat less food with toxins when levels of nutrients such as sodium are low (Freeland *et al.*, 1985; Freeland and Choquenot, 1990).

Ingesting specific toxins also influences selection of nutrients by animals, presumably behaviour aimed at correcting the disturbed internal state. Lambs infused with terpenes, nitrates, tannins or lithium chloride select diets with higher protein/energy ratios than animals that do not receive those toxins. In contrast, following infusions of cyanide, lambs prefer foods with lower protein/energy ratios than controls (Villalba *et al.*, 2002c). In every case, the needs for nutrients increase, but the preferred protein/energy ratio depends on the specific toxin involved. Thus, there is not likely to be a set proportion of protein/energy needed to counterbalance a toxin challenge. Rather, these proportions vary on a toxin-by-toxin basis depending on physiological state. Many toxins promote formation of organic acids that disrupt acid/base status, which has led to the proposal that metabolic acidosis is a common effect of absorbed toxins (Foley *et al.*, 1995). The selective effects of different toxins on preferred protein/energy ratios discussed above suggest that toxins cause other physiological effects in addition to acidosis, and that herbivores can discriminate among

the postingestive effects of different toxins (Provenza, 1996; Villalba *et al.*, 2005a). Thus, toxins impose different metabolic costs and consequences that modify homeodynamic behaviour.

Finally, feeding decisions depend on an animal's capacity to detoxify plant toxins. Thus, an herbivore that can detoxify a toxin more quickly should be able to eat more. The aforementioned findings are consistent with this thesis, but they do not provide direct tests, which have been difficult because we generally do not know the specific mechanisms the body uses to detoxify toxins. Recently, more direct tests have been conducted with brushtail possums (Marsh *et al.*, 2005). Possums supplemented with glycine metabolize benzoic acid faster and in response eat more; animals detoxify benzoic acid primarily by conjugating it with glycine to form benzoyl glycine (hippuric acid). Moreover, when given a choice, possums select a diet containing both benzoate and glycine over diets with a high concentration of just one of these supplements. The ability of possums to regulate intake of benzoate and glycine when these compounds are offered separately or mixed together suggests they experience excesses of amino acid or benzoate and modify their feeding behaviour accordingly.

Integrating the Internal and External Milieux

Maintaining fluidity while foraging can be viewed as an ongoing series of bifurcations, or choices, in the face of varying degrees of uncertainty. Behaviour at bifurcations is influenced by history, necessity and chance, all of which influence the relationship – preference to aversion – between the internal and the external milieux. These interactions begin *in utero* and continue through life. Thus, more static views of organisms as machines, of innate appetites and of 'wisdom of the body' originally developed by Bernard, Cannon and Richter must be expanded to include homeodynamic notions of behaviour as multifaceted, flexible and organic (Schulkin, 2001; Provenza *et al.*, 2003a).

Learned responses and multiple flavour–feedback associations

Given the dynamic nature of foods and landscapes, common sense suggests that nature did not confer specific recognition, through the senses of smell and taste, of every nutrient (Provenza and Balph, 1990; Schulkin, 2001). It is not enough for animals to have specific and static preferences for 'nutritious' foods, or even to possess an odour–taste system organized to discriminate nutrients from toxins. Such organization would not be sensitive enough to ongoing changes in the internal and external milieux. To maintain well-being throughout the life of the individual and the species, these systems must be plastic (Scott, 1990) and sensitive to ongoing interactions among cells and organs in play with ever-changing social and biophysical environments (Provenza, 1995a). Thus, beyond the ability to sense by odour or taste specific nutrients such as sodium (Richter, 1976), animals evolved mechanisms that enabled them to learn about interactions among nutrients, toxins and medicines.

The plasticity of flavour–feedback associations provides a mechanism for generating, through experience, limitless and very specific flavour–feedback associations. For example, sheep can discriminate among three flavours associated with rumen infusions of three different nutrients – starch (flavour 1), casein (flavour 2) and water (flavour 3) (Villalba and Provenza, 1999), and among three flavours associated with NaCl (flavour 1), NaH₂PO₄ (flavour 2) and water (flavour 3) (Villalba *et al.*, 2005c). Furthermore, the ability to learn multiple associations suggests that animals learn to seek or avoid substances that rectify deviations in their internal milieux. Indeed, experienced animals increase their preference for a buffer, PEG or dicalcium phosphate when challenged, respectively, with excessive amounts of grain, tannins or oxalates (Villalba *et al.*, 2005a). Buffers, PEG and dicalcium phosphate attenuate, respectively, malaise due to over-ingesting grain, tannins and oxalates.

The ability to learn preferences does not negate the possibility of more 'hard-wired' appetites that act in concert with learning. For instance, animals recognize and consume more salt when deficient, and they also learn to

associate various flavours with intragastrically (untasted) administered sodium (Hill and Mistretta, 1990; Villalba and Provenza, 1996). The preference for bones, typically observed when animals experience deficits of phosphorous, occurs automatically (Blair-West *et al.*, 1992). However, animals experiencing phosphorus deficiencies can also learn to eat new forms of the element (Reynolds *et al.*, 1953). These learned responses are influenced by the postingestive effects of phosphorus (Blair-West *et al.*, 1992; Villalba *et al.*, 2005c). Likewise, recognizing and rejecting amino acid-deficient diets occurs through a general control system, triggered by accumulation of amino acid-depleted transfer RNA in cells of the anterior piriform cortex in the brain. This internal nutrient sensor involved in maintaining amino acid homeodynamics appears to be conserved across evolution from single-cell organisms to mammals (Hao *et al.*, 2005). Animals use flavour cues to develop aversions or preferences for diets that induce or restore amino acid imbalances, but only after they have experienced the postingestive effects of those diets (Gietzen, 1993).

The ability to learn multiple flavour–nutrient feedback associations, as well as to select different proportions of protein and energy to ameliorate the effects of different toxins (Villalba *et al.*, 2002c) or a parasite load (Kyriazakis *et al.*, 1994), suggests that animals experience multiple internal states as opposed to general states of need (nutrients) or malaise (toxins). This is consistent with findings that feedback from every region of the body provides detailed mapping simultaneously as to the current state of the living cells in particular regions because every region of the body contains nerve endings that provide feedback to the central nervous system (Damasio, 2003). Thus, well is not well is not well, and sick is not sick is not sick. Animals discriminate among multiple internal states.

Learning multiple flavour–feedback associations within and among meals

If palatability is more than a matter of taste, and it is, then how does the body discriminate among different foods, based on specific

flavour–feedback interactions, within and among meals? There is some debate concerning how ruminants learn multiple flavour–feedback associations within a meal (Provenza *et al.*, 1998; Duncan and Young, 2002). This debate has arisen in part due to a lack of knowledge of the interactions – from conception until death – among history, necessity and chance in the ongoing evolution of flavour–feedback associations. Here, we discuss separately, for the sake of simplicity, several factors that enable multiple flavour–feedback associations. However, just as a river is in all places simultaneously – at the source, along the course, in the ocean and in the atmosphere – so too these behaviours reflect past and ongoing experiences that are at the same time uniquely individualistic, cultural and environmental. The uniqueness of these interactions makes each individual different. The plasticity of these processes lets animals adapt to ever-changing environments, and enables people to use behaviour to transform systems (Provenza, 2003a).

Historically, we believed that ruminants could not associate a food's flavour with its postingestive consequences for two reasons: (i) the presumed long delays between food ingestion and postingestive consequences; and (ii) the complexity of making multiple flavour–feedback associations within and among meals. More recent research shows ruminants can learn with delays between food ingestion and consequences of up to 8 h for toxins (Burritt and Provenza, 1991) and up to 1 h for calories (Villalba *et al.*, 1999). In many cases, feedback from nutrients and toxins occurs within minutes as opposed to hours. Moreover, the lack of feedback from less nutritious food influences behaviour as much as rapid feedback from nutritious foods because the greater the delay between food ingestion and consequences, the less likely a food is to be nutritious and preferred (Provenza *et al.*, 1992). We are also learning how multiple flavour–feedback associations mediated by cells and organs help the body assess which foods provide which benefits as enteric (gut) and central (brain) nervous systems interact with one another to integrate a food's flavour with its postingestive effects (Provenza, 1995a,b; Provenza *et al.*, 1998; Fig. 13.3).

These interactions begin early in life, and because nervous systems have long memories, flavour–feedback interactions do not have to be relearned each time an animal eats a food, any more than a human has to relearn when different garden vegetables are ripe. Flavour–feedback relationships merely need to be updated as flavours and feedbacks change.

Familiar–novel dichotomy

Pasture and rangeland researchers, as well as nutritionists and ecologists, typically consider foraging only in terms of how plant structural and nutritional characteristics influence nutrient intake. The social environment, if it is considered at all, is typically viewed as a ‘nuisance variable’ that may modify processes that are physically and chemically driven. This has been an unfortunate oversight. The social environment influences selection of foods and habitats (Provenza and Balph, 1988; Howery *et al.*, 1996, 1998; Mosley, 1999), and creates patterns of behaviour that make sense only in light of social history and culture (Provenza, 2003a,b; Provenza *et al.*, 2003a).

Social organization creates culture, the knowledge and habits acquired by ancestors and passed from one generation to the next about how to survive in an environment (De Waal, 2001). Cultures develop when learned practices contribute to the group’s success in solving problems. Cultures evolve as individuals in groups discover new ways of behaving, as with finding new foods or habitats and better ways to use them (Skinner, 1981). Accordingly, interactions with the mother and peers markedly influence what a young animal prefers to eat and where it prefers to live (Provenza, 1994, 1995a); an individual reared in shrub-dominated deserts of Utah will behave differently – and is morphologically and physiologically different – from one reared on grass in the bayous of Louisiana (Distel and Provenza, 1991; Distel *et al.*, 1994, 1996; Wiedmeier *et al.*, 2002).

Socializing enhances learning efficiency because each animal no longer has to discover everything through trial and error. When sheep and goats must learn to drink from a water device that requires pressing a lever, it

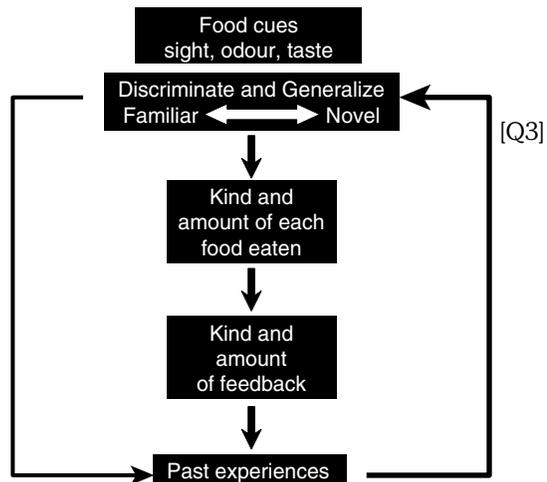


Fig. 13.3. Animals use food cues – sight, odour, taste – to discriminate and generalize among different foods based on the dichotomy between the familiar and the unfamiliar, which ranges along a continuum influenced by the degree of similarity between past and ongoing experiences. That dichotomy affects the kinds and amounts of foods eaten, which in turn impacts the kinds and amounts of feedback an animal experiences. These interactions begin *in utero* and continue throughout life, and because nervous systems have long memories, flavour–feedback interactions do not have to be relearned each time an animal eats a food. They merely need to be updated as flavours and feedbacks change in response to an animal’s physiological conditions, a food’s chemical characteristics and the biochemical characteristics of other foods in the diet. Collectively, these updates can be viewed as an ongoing series of bifurcations, or choices, influenced by history, necessity and chance. When nutritional state is adequate, familiarity breeds content, novelty breeds contempt and animals are neophobic – they are more cautious of novel foods. Conversely, as nutritional state becomes inadequate, familiarity breeds contempt, novelty breeds content and animals become neophilic – they sample novel foods more readily.

takes only one individual to learn how to do it, and in no time all the others are drinking. Thus, when an individual discovers how to use a new resource, the group benefits, but discovering new resources is not inevitable (Provenza, 2003a). For example, goats browsing blackbrush-dominated rangelands experience

energy and protein deficiencies. Of 18 different groups of goats foraging on six separate blackbrush pastures during three different winters, goats in only one group discovered that the interior chambers of woodrat houses provide a good source of supplemental nitrogen, and they performed much better than their counterparts. One goat likely learned the value of eating woodrat houses, and the other goats learned from it. Animals have similar difficulties learning through trial and error about the medicinal effects of substances, especially if behaviour and consequences (flavour-feedback) are not contingent (paired consistently) and contiguous (paired closely in time), as illustrated in studies that either did or did not closely pair medicine (flavour) and benefit (feedback) (Provenza *et al.*, 2000; Villalba and Provenza, 2001; Huffman and Hirata, 2004; Villalba *et al.*, 2005a). In all of these cases, social models increase the efficiency of learning over trial-and-error learning by individuals. When a mother's behaviour (eat or avoid) is subsequently reinforced by postingestive feedback (positive or negative), her offspring respond strongly (eat or avoid) to a food (Provenza *et al.*, 1993b). Such knowledge then becomes a part of the culture, wherein young animals learn from their ancestors through their mothers.

Critically, lessons learned early in life from a mother create a dichotomy between the familiar and the unfamiliar (novel) essential for survival. Of the many factors that interact during updates about foods in which an animal's past experiences with a food are integrated with new information about the food, none is more important than novelty (Provenza *et al.*, 1998). Novelty includes anything from a complete lack of acquaintance with the flavour of a food never before eaten, to a change in the flavour of a familiar food, to a novel food whose flavour is somewhat similar to a familiar food. The body evaluates new foods and flavours very carefully for their potential nutritional or toxicological effects.

While temporal contiguity – the proximity in time between a behaviour and its consequences – is of utmost importance in shaping behaviour, novelty even trumps temporal contiguity. For example, if an animal eats two foods in sequence, and then gets sick, the ani-

mal will strongly avoid the food eaten just prior to illness, unless the food eaten first was novel, in which case the animal will avoid the novel food (Provenza *et al.*, 1993a). Even more critically, novel foods are evaluated cautiously by the animal and the body (internal milieu) within a meal. Sheep eat small amounts of a novel food, and they acquire an aversion only to the novel food when toxicosis follows a meal of several familiar foods and a novel food (Burritt and Provenza, 1989, 1991). Conversely, when sheep eat the same low-energy food in two different flavours, one familiar and the other novel, and then receive intraruminal infusions of starch directly proportional to the amount of the novel food consumed, they form preferences for the novel flavour (Villalba and Provenza, 2000b).

Past experiences

Past experiences influence behaviour, as illustrated in studies of the effects of prior illness on preference. In one study, sheep first made averse to a particular food, and then allowed to eat the food until the aversion extinguished, avoided the food that made them ill in the past when toxicosis followed a meal of several foods (Burritt and Provenza, 1996). In another study, when toxicosis followed a meal of five foods, including one novel and one that made them ill in the past, sheep subsequently would not eat the novel food and markedly decreased their intake of the food that made them ill in the past; they did not avoid the other three familiar foods (Burritt and Provenza, 1991).

Experiences early in life have life-long influences on food intake and animal performance, as illustrated in a 3-year study where 32 beef cattle 5–8 years of age were fed ammoniated straw from December to May (Wiedmeier *et al.*, 2002). Although the cows were similar genetically and were fed the same diet, some cows performed poorly, while others maintained themselves. Researchers were baffled until they examined the dietary histories of the animals. Half of the cows were exposed to ammoniated straw with their mothers for 2 months early in life, while the other half had never seen straw. Throughout the study, the experienced cows had higher body weight and

condition, and for the first 2 years of the study, they also produced more milk and bred back sooner than cows with no exposure to straw, even though they had not seen straw for 5 years prior to the study.

Thus, past experiences have life-long influences on behaviour, but we seldom notice because we know or remember so little about the history of any animal. Nutrient-conditioned food preferences, which may have occurred as a result of brief exposure to a food 3–5 years previously, cause some animals (experienced) to readily eat a food other animals (naive) avoid (goats – Distel and Provenza, 1991; Distel *et al.*, 1994, 1996; sheep – Green *et al.*, 1984; cattle – Wiedmeier *et al.*, 2002). Likewise, food aversions often extinguish in the absence of toxicosis. However, if after an aversion has extinguished a sheep eats a meal of familiar foods, one of which previously made it ill, and then experiences toxicosis, the sheep will avoid the food that previously made it ill, not the other familiar foods (Burrill and Provenza, 1991, 1996). This point was highlighted when an adult ewe previously trained – conditioned with toxicosis – to avoid a tree (Russian Olive) began to eat the tree during meals 3 years later. When a meal of foods that included Russian Olive was followed by toxicosis, the ewe subsequently avoided the Russian Olive, the food that made her ill 3 years previously, not the other familiar foods eaten in that meal (F.D. Provenza, unpublished data). Without knowledge of the ewe's dietary history with Russian Olive, her behaviour would not have made sense.

[Q4]

Discriminating and generalizing based on past experiences

The familiar–novel dichotomy – the first line of defence for evaluating foods – also causes animals to discriminate and generalize based on their past experiences. For example, if the flavour of a familiar, nutritious substance such as molasses occurs in a novel food, the likelihood increases that animals will eat the food, provided they had positive experiences with molasses previously. Conversely, if the flavour of a familiar, toxic substance occurs in a novel food, the likelihood that the food will be eaten

decreases if the animals previously experienced toxicosis after eating that food.

The ability to discriminate and generalize based on past experience helps animals identify potentially toxic foods quickly. Animals generalize aversions from past experiences, thus reducing the risks associated with toxic novel foods or familiar foods whose flavours have changed. When lambs eat cinnamon-flavoured rice and then experience toxicosis, their preference for cinnamon-flavoured rice declines. When they are subsequently offered wheat, which they prefer, but with cinnamon flavour added, they refuse to eat the cinnamon-flavoured wheat. Thus, lambs generalize an aversion from rice to wheat based on a common flavour – cinnamon (Launchbaugh and Provenza, 1993).

Sheep and goats also generalize preferences. Lambs experienced in eating grains such as milo, barley and wheat, which are about 80% starch, subsequently prefer novel foods such as grape pomace with added starch (Villalba and Provenza, 2000c). Sheep and goats prefer hay sprayed with extracts of preferred high-grain concentrates (Dohi and Yamada, 1997), and sheep more readily eat novel foods such as rice bran when they have been sprayed with extracts from familiar grass (Tien *et al.*, 1999). Livestock also generalize preferences to weeds sprayed with molasses (Provenza, 2003a).

Sheep and goats discriminate among foods based on the concentration of the flavour, and they typically avoid flavour concentrations most different from what they have eaten in the past. For instance, when lambs familiar with unflavoured barley eat a meal of barley with a low and a high concentration of an added flavour and then receive a mild dose of toxin, they subsequently avoid the barley with the highest flavour concentration because it is most different from unflavoured barley (Launchbaugh *et al.*, 1993). The same is true for goats foraging on shrubs. Current season growth (CSG) and older growth (OG) twigs from the blackbrush shrub likely share a common flavour, but the flavour is much stronger in CSG. When goats first eat a meal of CSG and OG and then experience toxicosis, they subsequently avoid CSG because it is most different from the familiar food (Provenza *et al.*, 1994b).

Animals also discriminate based on changes in flavour. Lambs decrease intakes of a familiar food (rice) when rice contains a novel flavour (onion) (Provenza *et al.*, 1995). Similarly, sheep routinely fed elm from one location would not eat elm of the same species from another site, evidently because the smell and taste of elm differed between two locations (Provenza *et al.*, 1993b). By reducing their intakes of familiar foods with novel flavours animals reduce the likelihood of overingesting toxins.

Sheep generalize preferences based on the quantitative interrelationship between flavour and feedback. Lambs exposed to low or high concentrations of a flavour, and then given low or high amounts of energy (starch) by intraruminal infusion, learn to prefer the flavour concentration – low or high – associated with the highest amount of starch infused. When the lambs are then given a gradient of flavour concentrations, they prefer the flavour intensity most similar to the intensity of the flavour associated with the highest amount of starch previously infused (Villalba and Provenza, 2000d).

[Q4] Animals also generalize across broad classes of experience. Lambs that experience toxicosis, even if it occurs only once after eating a novel food, become more reluctant to eat novel foods (F.D. Provenza, unpublished data). Conversely, when lambs experience positive nutritional consequences every time they eat a novel food, they more readily eat novel foods (Launchbaugh *et al.*, 1997).

Discriminating nutritious from toxic foods within and among meals

DISCRIMINATING AMONG NOVEL FOODS BASED ON THE AMOUNT OF EACH NOVEL FOOD EATEN IN A MEAL. The amount of food eaten and the novelty of a food's flavour interact with postingestive consequences to enable animals to discriminate nutritious from toxic foods within a meal. When goats naive to the blackbrush shrub first eat a meal of blackbrush – twigs of both CSG and OG – and then experience toxicosis due to the high tannin concentrations in CSG, they subsequently avoid CSG in part because it is most different from the more

familiar OG (Provenza *et al.*, 1994b). The amount of each twig eaten within a meal also influences their behaviour. As soon as a goat eats a meal that contains more CSG than OG, and it eats enough CSG to experience malaise from the tannins in CSG, it subsequently avoids CSG, the twig type it ate in the greatest amount (Provenza *et al.*, 1994b). This behaviour is learned very quickly but not simultaneously by all goats. Some naive goats eat more CSG than OG initially in a meal, and others do the opposite, but all goats learn about the consequences of eating CSG and OG within 1–2 days of beginning to forage on blackbrush.

Animals also must ingest a threshold amount of a novel food for the body to assess the specific biochemical characteristics of the food, and nutritional state influences the response. Sheep exposed for only 20 min/day to two novel foods, one more nutritious than the other, surprisingly preferred the less nutritious of the two foods because it was more familiar and they ate little of the more nutritious food. This response occurred only when sheep were fed a basal diet adequate in energy and protein. When offered only the two novel foods for 8 h/day, they quickly learned to prefer the more nutritious of the two foods (Villalba and Provenza, 2000b). Importantly, animals will include a familiar but less nutritious food in their diet when the food is only a minor part of their diet.

Thus, sheep discriminate based on familiarity, nutritional state and amount of food eaten, factors that undoubtedly influence preferences as nutritional qualities, toxicities and abundances of foods change daily and seasonally. More generally, when nutritional state is adequate, familiarity breeds content, novelty breeds contempt and animals are neophobic – they are more cautious of novel foods. Conversely, as nutritional state becomes inadequate, familiarity breeds contempt, novelty breeds content, and animals become neophilic – they sample novel foods more readily.

DISCRIMINATING DIFFERENT DOSAGES AND COMBINATIONS OF NUTRIENTS AND TOXINS. How animals discriminate among foods varying in nutrients and toxins also has been investigated with goats conditioned with different combinations of nutrient–toxin (postingestive feedback) as they ate the branches of four species of

conifers (flavours) (Ginane *et al.*, 2005). On conditioning days, animals were fed a conifer species, and as they ate, they were dosed with a mixture of two stimuli: one nutritious (sodium propionate) and the other toxic (lithium chloride). For each goat, four dosage combinations of nutrient–toxin were each paired with a different species of conifer, and a different species was offered each day on 4 successive days per week for 5 weeks.

The goats reacted strongly to the toxin, and the effect was evident early in the study. One encounter with a food plant paired with the toxin was sufficient for the goats to perceive the variation in the four different intensities (doses) of feedback, to associate each conifer species with each intensity and to decrease preference progressively for each species paired with increasingly higher doses of toxins. When all four conifer species were offered simultaneously, animals selected based on the intensity of their previously experienced postingestive effects, indicating that the links between postingestive effects and degree of avoidance of toxic foods are well developed in goats, allowing them to make appropriate choices when faced with a series of foods of varying potential toxicity.

Although the goats responded quickly to the toxin, they reacted less strongly to the energy and they did not respond until the last conditioning period, suggesting that they required more time to perceive the energy signal and respond to it within the context of this study. However, their basal diet provided adequate nutrition to meet their maintenance needs for energy, and the conifer species provided additional energy. This combination likely made them much less responsive to the energy infusions than if they had been more deprived of energy (Villalba and Provenza, 1996). Conversely, other studies show that sheep, even fed *ad libitum*, behave based on input from both positive and negative feedback when both signals are associated with the same food cue (Wang and Provenza, 1996, 1997). Thus, in complex situations with many stimuli, animals may need pre-ingestive as well as postingestive clues to discriminate among foods. As argued previously, learning from the mother plays a critical role with regard to learning preferences and aver-

sions to pre-ingestive cues (Provenza *et al.*, 1992).

Initial conditions, individuality, context and homeodynamic utility

Prevailing theories of food (Optimal Foraging Theory) and habitat (Ideal Free Distribution) selection assume that single ‘optimal’ solutions exist for the challenge of foraging (Fretwell and Lucas, 1970; Stephens and Krebs, 1986). In other words, given an array of food alternatives and locations an herbivore will find an optimal diet or habitat, which will be similar for all individuals of a species. However, the value of a food or any combinations of foods varies among similar individuals of the same species due to context – the kinds and numbers of foods available – and due to each animal’s unique experiences with the foods (Villalba *et al.*, 2004). Thus, while animals undoubtedly optimize, an animal’s optimization will depend on its history, necessity and chance, each of which will differ by individual and situation. The kinds and amounts of foods eaten will depend on the utility of those foods within the context of the local environment and the combinations of foods consumed. Thus, animals in the same environment may follow different ‘foraging paths’ depending on their foraging histories and current conditions, and the greater the alternatives, the greater the potential combinations of foods and habitats that can meet individual needs (Provenza *et al.*, 2003a).

Individuality in form and function influences foraging behaviour

Food intake and preference depend on how individuals are built morphologically and how they function physiologically, and marked variation is common even among closely related animals in need for nutrients and abilities to cope with toxins. Foraging decisions are affected by differences in organ mass and how animals metabolize nutrients and toxins (Konarzewski and Diamond, 1994). From the standpoint of nutrients, for instance, the same

dose of sodium propionate that conditions preferences in some lambs conditions aversions in others (Villalba and Provenza, 1996). Likewise, lambs given a choice of barley (high energy) and lucerne (high protein) vary greatly in their preferences (Scott and Provenza, 1999). The same is true with toxins. Doses of tannins that condition an aversion in some goats do not deter others (Provenza *et al.*, 1990). Likewise, some sheep fed high levels of *Galega officinalis* failed to show any symptoms of toxicosis, whereas others were killed by a low dose (Keeler *et al.*, 1988). Such individual variation in ability to tolerate the same dose of different toxins and in metabolism of nutrients and toxins guarantees that no one diet will be ideal for every individual of a species. On the contrary, the degree of benefit or harm a specific food can induce in an animal will vary as a function of the individuals morphological and physiological tolerances and susceptibilities, which in turn will influence diet selection.

Initial conditions and context influence foraging paths

Life flourishes in a liquid region at the boundary of order and chaos, where systems forever push their way into novelty – molecular, biochemical, morphological, physiological, behavioural and organizational (Kauffman, 1995, 2000). The process of maintaining fluidity in the face of uncertainty is much like a hill-climber on a foggy day: animals may not always be able to perceive the optimum so much as the fact that they are travelling uphill (Provenza and Cincotta, 1993). Learning to mix sub-optimal but complementary foods may enable animals to create diets that are unique due to the particular biochemical contexts offered by the foods and the variety of equally successful ways different individuals may meet their nutritional requirements and tolerate toxins. This leads to multiple 'foraging paths' instead of a single solution to the challenge of foraging.

Initial conditions affect the evolution of systems (Glass and MacKey, 1988), and in the case of foraging, first impressions matter. Initial experience and the availability of alterna-

tives influence the preferences of lambs with 3 months of experience mixing foods with tannins, terpenes and oxalates compared with those of lambs naive to these foods (Villalba *et al.*, 2004). During the studies, all lambs were offered five foods, two of them familiar to all of the lambs (ground lucerne and a 50:50 mix of ground lucerne:ground barley) and three of them familiar only to experienced lambs (a ground ration with either tannins, terpenes or oxalates). Within each group, half of the experienced and half of the naive lambs were offered the familiar foods *ad libitum*, while the remaining lambs were offered only 200 g of each familiar food daily. Throughout the study, naive lambs ate less of the foods with toxins if they were fed *ad libitum* as opposed to restricted access to the nutritious alternatives (66 vs. 549 g/day), and experienced lambs did likewise (809 vs. 1497 g/day). In both cases, however, lambs with experience ate significantly more of the foods containing the toxins, whether access to the lucerne–barley alternatives was *ad libitum* (811 vs. 71 g/day) or restricted (1509 vs. 607 g/day). These differences in food preferences and intake persisted during trials a year later. In a companion study, when access to familiar foods was restricted to 10%, 30%, 50% or 70% of *ad libitum*, animals ate more of the foods with toxins along a continuum (10% = 30% > 50% = 70%), which illustrates that animals must be encouraged to learn to eat unfamiliar foods that contain toxins (Shaw *et al.*, 2005). Thus, initial conditions – past experiences and contexts – that encourage animals to learn to mix diets that contain toxins and nutrients help explain the partial preferences of herbivores, and they provide implications for managing plant–herbivore interactions (Provenza, 2003a).

In a related study, sheep learned to eat a low-quality food with toxins and a high-quality food in two different temporal arrangements (Villalba *et al.*, 2005b). In one case, sheep were fed the high-quality food for 12 days followed by food with toxins 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

both foods, only the high-quality food or only the food with toxins. Sheep that initially ate both foods in a meal always ate more food with toxins than 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 toxins. 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 toxins and thus consumed more food.

Finally, nutritional context influences what lambs learn about foods with tannins and terpenes. In one study, for instance, a group of lambs was fed a low-quality food containing tannins while on a basal diet low in nutrients; several weeks later they ate the same low-quality food containing terpenes while on a basal diet adequate in nutrients. Conversely, lambs in another group first ate terpenes and then ate 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 – tannin or terpene – they ate while on the basal diet high in nutritional quality. Thus, preference for plants high in toxins is affected by the nutritional state of an animal during exposure to the plant, which is influenced by the choices in the landscape (Provenza *et al.*, 2003a), which in turn influences future choices (Provenza *et al.*, 2003b).

Nutritional Wisdom Revisited: From Instinct to Experience***

[Q5]

Looking back

During the last century, nutritional wisdom came to imply that animals ‘instinctively’ selected specific substances to maintain homeostasis (Fig. 13.4). This notion was referred to as ‘genetic programming’ of ingestive behaviour (Schmidt-Nielsen, 1994), and as the ‘sub-conscious but irresistible desire’ to restore biochemical equilibrium (Katz, 1937). With livestock, the archetypal example of nutritional wis-

dom is the well-characterized appetite for sodium (Richter, 1976), linked to both a specific gustatory transduction mechanism (Schulkin, 1991) and humoral signals acting in the central nervous system (Stricker and Verbalis, 1990). The sodium model of nutritional wisdom was extrapolated to livestock by scientists attempting to explore ‘instinctive appetites’ for other minerals and vitamins.

These efforts made researchers doubt that livestock possessed nutritional wisdom. Lactating dairy cows did not instinctively ingest recommended levels of calcium and phosphorus when offered dicalcium phosphate; indeed, many of the calcium-deficient animals never approached the novel source of calcium, and for those that did, intakes of calcium varied greatly (Coppock *et al.*, 1976). Moreover, some animals consumed large amounts of dicalcium phosphate even when neither calcium nor phosphorus was needed (Coppock, 1970). These results were consistent with earlier findings that sheep did not rectify a phosphorus deficit by consuming supplemental dicalcium phosphate (Gordon *et al.*, 1954). Nor did dairy cows offered choices consistently select appropriate minerals and vitamins, though the cows fed different diets did not perform differently during the 16-week trials; the researchers concluded that longer studies were needed due to the ability of cows to store many minerals and vitamins in the body (Muller *et al.*, 1977). Finally, lambs did not eat sufficient amounts of needed minerals, and because they tended to overconsume some minerals, researchers recommended feeding a complete ration, or if that is impossible, to offer *ad libitum* a complete mineral mix (Pamp *et al.*, 1977). Collectively, these studies fostered the notion that domestication had produced animals more responsive to food flavour than to nutritive value, and that acceptability rather than appetite or craving for minerals and vitamins influences free-choice consumption (Pamp *et al.*, 1976). In other words, domestication erased ‘nutritional wisdom’ and the ‘innate ability’ to select needed nutrients, a trait that through evolution still confers survival value to wild herbivores.

To add to the confusion, other research suggested that livestock have specific appetites for minerals, and observations by livestock

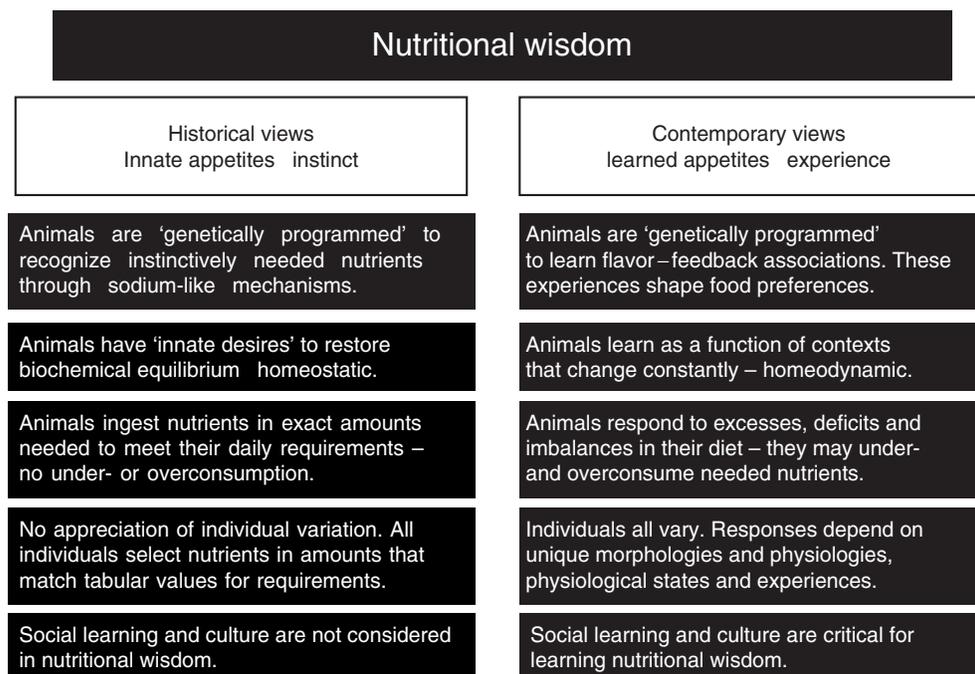


Fig. 13.4. Historical views of nutritional wisdom were based on innate appetites and instinctive drives to restore homeostasis through selection of the 'right' substance – homeostatic behaviour imbedded in the genes through evolution. When researchers attempted to extrapolate these views and the 'sodium model of nutritional wisdom' to study specific appetites for other minerals and vitamins in livestock, their efforts largely failed to show nutritional wisdom because they did not consider the many factors that enable the wisdom of the body. More recently, the concept of nutritional wisdom has been expanded to the idea that food intake, food preferences and palatability involve interrelationships among a food's flavour and postgestive feedback emanating from cells and organs in response to nutrients and toxins in a food, the biochemical characteristics of other foods in the diet, an animal's current physiological condition and its past experiences with the food.

producers and veterinarians were not always consistent with the research findings, which suggested that livestock lacked nutritional wisdom. Deficits of phosphorus and calcium were linked directly with bone ingestion to restore phosphorus and calcium levels in the body (Denton *et al.*, 1986; Blair-West *et al.*, 1992; Schulkin, 2001). Likewise, practitioners and veterinarians such as Holliday (2003) recounted experiences such as the following from an occasion when Holliday was working with a client, a dairy producer named Carl:

One year inclement weather made planting and harvesting hay and grain crops a great gamble with the result that feedstuffs that fall and winter looked good but had low nutritional

value. By late winter Carl consulted me with two seemingly unrelated problems: (i) his cattle were eating almost 2 lb of a mixed mineral per head per day! (ii) about 10 days before they were due to calve, his heifers would abort a live calf. The calf, with some care, would live, but in spite of all we could do the heifer would die within 2 or 3 days. After the third one in a row had died, I did what every smart vet would do. . . . I passed the buck and sent a dying heifer to the University Vet School for autopsy. Their diagnosis came back *starvation!* Carl took good care of his animals and was feeding them all they could eat. This diagnosis was like an insult to Carl and difficult for either of us to accept. We could have accepted a diagnosis of malnutrition because of the poor crops that year but starvation seemed a little too harsh.

We then turned our attention to the mineral consumption problem. Available in that area at that time was a 'cafeteria' mineral programme in which each mineral was fed separately on the theory that each animal could then eat only what it needed to balance its own needs. Carl decided to try this programme. His mineral feeder was in the middle of his cow lot and he had to carry each bag of minerals through the lot to empty into the feeder. Things went well for the first few trips and then several of the normally docile cows suddenly surrounded him, tore a bag of mineral from his arms, chewed open the bag and greedily consumed every bit of the mineral, the bag and even some mud and muck where the mineral had spilled out. . . . astounding behaviour for a bunch of tame dairy cows!

What was in the bag, you ask? . . . a source of the trace mineral, zinc. During the next several days they ate several bags of this zinc source while completely ignoring all other minerals. Gradually they began eating normal amounts of the regular mineral. From that day on his heifers calved normally and things gradually returned to normal. . . . Apparently, the difficult growing season had resulted in crops that were deficient in zinc or perhaps high in zinc antagonists. The basic mineral mix had a small amount of zinc in it but to get the zinc they needed, they had to consume large amounts. This gave them too much calcium. Calcium interferes with zinc absorption, which in turn increased their need for zinc. Even though their quest for zinc impelled them to eat the mixed mineral, every mouthful they took increased the imbalance. Inevitably, symptoms began to show up in the most vulnerable group . . . young heifers, still growing and in the last stages of pregnancy. . . . Finally they just gave up and checked out all for want of a few grams of zinc. The decrease in feed conversion associated with zinc deficiencies coupled with the poor quality feed would result in malnutrition even when feed intake appeared to be adequate. I realize that other secondary factors may have been involved here, but the main factor was a zinc deficiency as evidenced by the remission of symptoms when zinc was supplied.

Holliday concludes with the following:

For me this incident epitomizes the concept that, given the chance, animals can balance rations better than computers or nutritionists can. Many nutritionists tend to discount the

ability of animals to balance their ration, asserting that by the time they feel the need to eat a certain item they are already in a deficient state. From their point of view, I suppose they have a point. The fallacy in their reasoning may be that they expect the animal to choose for the level of production that man desires while the animal chooses only what it needs to be healthy.

Looking forward

Undoubtedly, in each case above the researchers and the practitioners made accurate observations of the behaviours they observed. Thus, the issue is not who is right and who is wrong, but how contexts and contingencies influenced the behaviours different people observed. All of these interpretations should be reconsidered in light of new understanding of how nutritional wisdom is likely to be manifest, given the many factors that interact to influence food selection. To do so, we must consider how animals learn flavour–feedback associations, including the roles of past experience and the familiar–novel dichotomy, discrimination and generalization, initial conditions and all the dynamic contingencies that apply when animals learn flavour–feedback associations.

It is highly unlikely that several million years of evolution have been erased by a few thousand years of domestication, especially regarding nutritional wisdom. Acquiring nutrients and avoiding toxins is every bit as important as breathing, which has not changed due to domestication, and is similarly influenced by non-cognitive feedback mechanisms. Indeed, feedback mechanisms for detecting and correcting amino acid imbalances appear to be conserved in animals ranging from single-cell organisms such as yeast, to invertebrates, to humans (Hao *et al.*, 2005). Domesticated herbivores forage on rangelands worldwide, and they must choose from the same plant species available to wild herbivores. Given the way livestock are routinely moved from familiar to unfamiliar environments, it is a testament to their ability to quickly adapt that they survive at all (Provenza, 2003a).

As emphasized throughout this review, the concept of nutritional wisdom has been expanded during the last two decades due to research which shows that food preferences are learned through processes involving complex interrelationships between a food's flavour and its postingestive effects, which emanate from cells and organs in response to nutrients and toxins (Provenza, 1995; Fig. 13.4). The sense of taste 'manages' diet selection by qualitatively and quantitatively analysing foods in conjunction with the visceral and central nervous systems, all of which evokes current and past experiences with food. The receptors for taste are situated at the junction between the internal and external milieu, like a Janus head placed at the gateway to the body, one face looking at what is outside and the other looking at what is inside (Scott, 1990). Such dynamic integration of taste with the internal and external milieu offers a new dimension to nutritional wisdom: the ability to modify diet selection as a function of the consequences of food experienced throughout the lifetime of the individual. This is critical from an evolutionary standpoint, given that the average lifetime of a species is several million years and the kinds of foods the species is likely to encounter will vary tremendously over that time frame. What animals need – nutrients, medicines – is relatively constant, but how the various foods are packaged is not. The solution to this challenge was to create animals that learn based on flavour–feedback interactions, and that requires researchers to rethink notions of how nutritional wisdom is likely to work.

Past research with livestock established that the 'sodium model of nutritional wisdom' is not a particularly good example for energy, protein, minerals and vitamins because animals do not instinctively recognize through odour or taste all of these nutrients; nor do they necessarily recognize all of the various configurations of any particular nutrient (Provenza and Balph, 1990). Rather, they must learn based on flavour–feedback associations to ingest foods that contain these substances. Hence, it is not surprising that calcium- or sulphur-deficient animals offered choices of 10 novel minerals – CaCO_3 , K_2CO_3 , Na_2CO_3 , ZnCO_3 , $4\text{MgCO}_3 \cdot \text{Mg}(\text{OH})_2 \cdot 4\text{H}_2\text{O}$, CuCO_3 , MnCO_3 , NaH_2PO_4 , Na_2SO_4 , NaCl –

did not consume appropriate amounts of CaCO_3 or Na_2SO_4 , respectively (Pamp *et al.*, 1977). Sulphur-deficient lambs had to discriminate among four anions – CO_3^- , PO_4^- , SO_4^- , Cl^- – that all contained sodium. As discussed previously, animals generalize among substances that share common flavours and feedbacks (sodium), thus making the task difficult both from the standpoint of a similar flavour and excessive feedback from it (sodium). Equally problematic, sodium is often used as a carrier to mix with other minerals in cafeteria offerings to encourage and/or limit intakes of other minerals as well. The same is true for the calcium-deficient lambs challenged to discriminate CaCO_3 from the six other carbonates. Appropriate learning is more likely when animals are offered substances that differ in both flavour and feedback, and when recovery is paired with eating the substance that rectifies the deficiency. The latter can be learned in part from social models that have learned appropriate behaviours, though that was never considered, despite the fact that that is how humans have learned to prevent deficiencies: long before scientists knew of amino acids, individuals learned to mix rice with beans to get a full complement of indispensable amino acids, and cultures maintained the practice.

In addition, past studies of nutritional wisdom were based on the erroneous assumption that animals eat to meet what people considered to be their needs for minerals. Thus, to demonstrate an appetite for calcium or phosphorus, researchers expected ruminants to consume minerals from concentrate salts according to National Research Council (NRC) requirements. Recommendations for minerals typically are set higher than animals' needs, and individuals, even within uniform groups, vary greatly in their needs for nutrients such that some animals will consume much more or less than others. Thus, it is not surprising that animals varied greatly in their consumption of minerals in previous studies, that many did not consume minerals at all and that some 'underconsumed' while others 'overconsumed'. Indeed, requirements may be exceeded even with a bite/day of a concentrate salt. The daily phosphorus requirement of a 40 kg lamb of moderate growth potential is 3.9 g (NRC, 1985), which

amounts to only 15 g of NaH_2PO_4 . Preferences for a mineral supplement also depend on the type of mineral offered. For instance, calcium-deficient animals actually avoid phosphorous (Tordoff, 2001). Thus, calcium phosphate salts are not a good choice when studying specific appetites for calcium. For these reasons alone, individuals are unlikely to ingest a recommended daily allowance of minerals.

Finally, researchers did not appreciate that animals respond more strongly to excesses, deficits and imbalances than to daily nutrient requirements. The degree of the mineral deficiency induced in livestock during most early studies to explore nutritional wisdom was likely not enough to induce a response. Learned preferences for nutrients are manifest when animals are in a physiological state of need, and that depends on the specific nutrient in question (Mehiel, 1991; [Q6] Provenza, 1995). The ongoing need for energy is much greater than the need for protein due to the high amounts of energy required daily, and preferences for flavours paired with energy are higher than preferences for flavours paired with protein (Villalba and Provenza, 1999). In contrast, calcium and phosphorus deficiencies develop slowly because daily requirements are low relative to body reserves (NRC, 1985). Animals respond more strongly to daily requirements for energy followed by protein, and then, if at all, to daily requirements for calcium and phosphorus. Responses to calcium and phosphorus are likely to be seen only after long periods of ingesting deficient diets, when a strong need for these minerals develops due to depletion of the ample buffer supplied by body reserves (Ternouth, 1991). When need for a nutrient is not high, animals likely respond more to the novelty or familiarity of the odour or taste than to postingestive effects of the mineral and vitamin supplements, as cattle and sheep evidently did in early studies (Coppock *et al.*, 1976; Pamp *et al.*, 1977). Sheep preferred a less nutritious food in a two-food choice test when their energy requirements were satisfied by a basal diet, and the choice lasted only 20 min/day. However, when their need for energy increased and the choice lasted 8 h/day,

lambs quickly learned to prefer the more nutritious of the two foods (Villalba and Provenza, 2000b). Sheep respond likewise to the specific postingestive effects of phosphorus. They avoid flavours previously paired with NaH_2PO_4 when their requirements for phosphorus are met or exceeded, and they prefer flavours paired with phosphorus during periods of need (Villalba *et al.*, 2005c).

Conclusion

Historically, researchers have been skeptical of the notion of nutritional wisdom. Few believed that cells and organs of the body could influence the palate to select foods that meet needs for nutrients and prevent toxicosis. For nutrients, that skepticism has been perpetuated for several reasons. Cafeteria feeding studies provided no evidence for nutritional wisdom because they were based on the erroneous assumption that animals eat to meet needs for minerals; we did not appreciate that animals respond most strongly to excesses, deficits and imbalances. Recommendations for minerals typically are set higher than animal needs, and individuals, even within uniform groups, vary greatly in their needs for minerals such that some animals will consume much less or more than others. In addition, there has been little appreciation for how animals learn flavour–feedback associations. Studies did not take into account past experiences, familiar–novel dichotomies, amounts ingested within a meal, generalization or initial conditions, and they did not consider the contexts necessary for animals to learn specific flavour–feedback associations. Finally, for toxins people focused on a subset of plants that cause problems – the poisonous plants. We did not understand why animals overingest poisonous plants (Provenza *et al.*, 1992); nor did we realize that all plants contain toxins and that animals learn to limit intakes of most of the plants they encounter (Provenza *et al.*, 2003a).

Any substance can be harmful or beneficial depending on the dose, which is influenced by the chemical characteristics of all

foods in the diet relative to the physiological condition of an animal. In some cases, the combination of substance and amount will be beneficial, whereas in others, the same combination may be harmful. At too high doses, nutrients are toxic, whereas at the appropriate dose, toxins can have medicinal benefits. This is so because at the biochemical level, nutrients and toxins interact with one another – nutrients with nutrients, nutrients with toxins and toxins with toxins. These interactions affect basic metabolic processes, and they cause organisms to experience the consequences of their foraging behaviours as a continuum from pain (aversive) to pleasure (positive). Incentives emanating from the consequences of past behaviours influence the likelihood of future behaviours, and they generate the experiences of emotions and ultimately feelings that arise from different degrees of well-being that emanate from ongoing interactions among cells, organs, individuals, and social and biophysical environments (Damasio, 2003).

The distinction between nutrients, toxins and medicines is artificial because ingesting or avoiding substances are means to the same end – stay well – and that depends on compounds, dosages and their interactions. Nutrients, toxins and medicines are merely labels we use to categorize various phenomena – nutrition, toxicosis and medication. In reality, bodies do not respond to labels, but to various ‘substances’ that benefit or harm the internal milieu, and these homeodynamic endeavors promote states of well-being (Damasio, 2003) and sustain functional integrity (Maturana and Varela, 1980). The active selection or avoidance of substances, regardless of their labels as a function of internal state, supports the notion that bodies have nutritional wisdom.

Nutritional wisdom notwithstanding, predicting the behaviour of individuals is elusive, not because it cannot be well understood, but because it is so multifaceted and dynamic. An animal’s foraging behaviour is a function of its evolutionary history, genetically expressed, in concert with its uniquely individualistic history of the social and biophysical environments where it was conceived and reared. Genes are expressed as a function of interactions with biophysical and social environments, and

because both change constantly and often unpredictably, so too do expressed morphology, physiology and behaviour. Thus, social and biophysical influences that shape the development of individuals from conception to death depend critically on time and timing – the unforeseen and indiscernible role of chance in life (Taleb, 2001). The net result is that food intake and preference depend on differences in how animals are built morphologically and how they function physiologically, and marked variation is common even among closely related animals in need for nutrients and abilities to cope with toxins. Past experience also influences an animal’s propensity to eat different foods. Changes in biochemical contexts spatially and temporally affect what herbivores learn, thereby creating additional variability in behaviour. Experienced animals that have learned to eat a variety of foods differing in nutrients and toxins do so even when nutritious alternatives are available, whereas naive animals familiar only with the nutritious alternatives eat just that subset of foods (Villalba *et al.*, 2004). Nutrients and toxins both cause animals to satiate, and excesses of nutrients, nutrient imbalances and toxins all limit intakes of foods. The amount of a toxin an animal can ingest depends on the kinds and amounts of nutrients and toxins in the forages on offer. Individuals can better meet their needs for nutrients and regulate their intake of toxins when offered a variety of foods that differ in nutrients and toxins than when constrained to a single food, even if the food is ‘nutritionally balanced’. Transient food aversions compound the inefficiency of single-food diets – whether in confinement, on pastures or on rangelands – by depressing intake among individual animals, even if they are suited ‘on average’ to that nutrient or toxin profile (Provenza *et al.*, 2003a). The biochemical diversity of landscapes influences foraging in ways that cannot necessarily be predicted solely by the isolated effect of any single biochemical in the body. Thus, the conventional univariate focus mainly on energy must be replaced with multivariate approaches that recognize multiple biochemical interactions (Simpson and Raubenheimer, 2002; Simpson *et al.*, 2004).

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