

The odour profile of feedstuffs as modulators of feed preference in herbivores

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Summary

The food available to grazing herbivores is typically heterogeneous, and therefore animals have the opportunity to select a diet with a higher concentration of nutrients and a lower concentration of toxins than the average of that available. In order to select or reject a feed, an animal will use a potential food's odour, flavour and visual appearance as cues to trigger learned preferences and aversions. No single sense alone is sufficient to predict feed intake or choices, as feed preferences originate from a functional interrelationship between smell, taste, sight and post–ingestive feedback. In the sensory evaluation of feedstuffs by animals, olfaction is likely to be an important factor because it can provide rapid and detailed information about the biochemical properties of the food without the animal actually having to eat it, thereby minimising the risk of toxicity. Odour detection is likely to be more sensitive in livestock than in humans, yet we have not fully explored the potential use of odour as a way of manipulating feed preferences and increasing intake. In this paper, we discuss the advantages to animals of using olfaction in diet selection, the physiology of odour detection, and conclude by considering some practical implications and opportunities for increasing animal production.

Keywords: feed preference, palatability, odour, olfaction, grazing herbivores

Introduction

The sense of smell (olfaction) is one of the most important means by which animals (including humans) receive information about the environment. It is widely recognised that odours (or pheromones) play an important role in insect and animal reproduction behaviour (Rekwot *et al.* 2001), neonate–mother interactions (e.g., Distel and Hudson 1985) and in the detection of predators. In this review, we consider the role of odours in assisting herbivores to find, recognise and discriminate between foods.

Most of the literature on olfaction and food preferences is focussed on insects. For example, moths (Masante–Roca *et al.* 2002), mites (De Boer *et al.* 2005) and lacewing (Reddy 2002) are known to discriminate between volatiles of different plant origin. In moths, plant volatiles are detected by projection neurons on the antennal lobe (Anton and Hansson 1995; Greiner *et al.* 2002; Masante–Roca *et al.* 2002). For insects to use plant odours to locate host plants makes intuitive sense given strong interactions that exist between specific plants and particular insect species. Further, considering the sophistication of the mammalian olfactory system, it seems likely that plant odours could play an important role in the location and selection of feedstuffs in this class of animals.

The size of the nasal epithelium is a good indicator of the degree of an animal's sense of smell because the number of olfactory receptor cells per unit surface area is a constant. Therefore, in long–nosed mammals such as horses, cattle and sheep, olfactory senses are likely to be well developed and are used in conjunction with other signals to respond to their environment. Indeed, olfaction plays a major role in general animal awareness, which is defined as 'a state in which complex brain analysis is used to process stimuli or constructs based on memory' (Sommerville and Broom 1998). The links between olfaction and memory allows animals to develop learnt behaviours based on associations between the sensory characteristics of feedstuffs and metabolic experiences; in other words, a characteristic odour profile can trigger memory processes, and thus help an animal assess whether a familiar feedstuff is associated with favourable or unfavourable metabolic consequences following its ingestion.

Sensory perceptions in the control of feed intake

As control of feed intake and feed selection involves an intricate and complex interplay of messages emanating from the feedstuff and the animal consuming

it, no single criterion alone is sufficient to predict feed intake or feed choice. In order to select or reject a feed, an animal uses a food's odour, flavour and visual appearance as cues to trigger innate and learned preferences or aversions that are based on known post-ingestive consequences of eating that feed (Forbes 1998; Forbes 1999). Thus, eating is initiated by a combination of systemic metabolic stimulation and sensory stimulation.

Feed preferences originate from the functional interrelationship between smell, taste and sight and post-ingestive feedback. This interrelationship is dependent on the animal's physiological status (e.g., pregnant, lactating, working) and a food's chemical characteristics (Provenza 1995; Provenza 1996; Provenza *et al.* 1996). An animal uses the senses of smell, taste and sight to discriminate among foods, and the feedback from ingested nutrients and/or toxins calibrates the smell, flavour, sight and texture sensations with the food's homeostatic utility. This enables an animal to acquire preferences for foods that are nutritious and become averse to foods that are either deficient in nutrients or toxic (Provenza 1995; Provenza 1996; Provenza *et al.* 1996). Animals must learn to associate sensory perceptions of food with their nutritional value because their sensory receptors operate at a molecular level and do not respond to combined fractions such as protein, soluble carbohydrates, fat and fibre (Arnold *et al.* 1980). Thus, an animal must be able to seek out and identify food with the desired protein, energy and fibre content indirectly by using learned associations with various sensory cues.

Why use olfaction in diet selection?

There are a number of reasons why the ability to detect odours can be beneficial for food selection. Odour can be detected rapidly and thereby provide a means of influencing short term feeding behaviour. Rapid decision-making may be a useful trait if a feed source were only temporarily available, such as would occur during a competitive feeding situation. If animals have limited time to assess a feedstuff because of competition with other animals, then the capacity to make a rapid assessment of the food on offer would be important in helping the animals make appropriate choices under pressure. The decision to select or reject a particular feedstuff can be made without actually consuming the feed, enabling them to avoid toxic species. In an experiment on the capacity of roe deer to select between different plant species, animals used odour to recognise and avoid undesirable plants (arum and euphorbia) once they had learnt the consequences of eating these plants (Tixier *et al.* 1998). Similarly, preferred plants, once smelled, were hardly ever refused.

The physiology of odour detection allows animals to integrate a complex suite of odours that may reflect the biochemical composition of the food. Although animals can detect individual odorants, the way in which

the olfactory system processes information also allows animals to 'generalise' the inputs to the central nervous system from a mixture of odours. Thus, the olfactory sense is able to distinguish among a practically infinite number of chemical compounds at very low concentrations (Leffingwell 2002), and neural processes link the detection of odour to memory. The physiology of odour detection is discussed in more detail in the following section.

An additional, but perhaps less quantifiable, benefit of using olfaction is that it enables the animal to select different components of the diet during periods of low light intensity or at night. Grazing animals typically start consuming their largest meal before sunrise when there is insufficient daylight to allow for easy visual discrimination between plants in a mixed sward. A second major grazing period typically occurs late in the afternoon, with smaller less regular grazing periods at other times throughout the day. Although many factors influence this grazing pattern, it is tempting to speculate that the main grazing periods may coincide with the time of day when odour detection is easiest. The production of volatile compounds by plants is likely to peak after respiration during daylight hours, and volatile compounds are more likely to be emitted from plants during the warm period of day because volatilisation increases with temperature. In addition, the cool, dense air of the early morning and evening may limit the dispersal of volatile compounds and thus 'trap' them at a level that can be detected by animals. The higher moisture content of morning air may help to provide conditions at the olfactory epithelium that enhance binding of odorants to receptors.

The physiology of odour detection

The perception of gas-phase molecules involves the olfactory and trigeminal systems. The trigeminal system is responsible for the perception of sensations such as irritation, stinging, burning, tickling, warm, cool and pain (Doty *et al.* 1978; Doty and Commetto-Muiz 2003). Trigeminal perception occurs via free nerve endings found in the nasal and oral cavities, with the nasal cavity being the more sensitive of the two (Silver and Finger 1991). Odorants are volatile chemical compounds that are carried into the nasal cavity with inhaled air and come into contact with the olfactory epithelium. Odorants dissolve in the mucous layer on the epithelium, in some cases aided by odorant binding proteins. The receptors are highly sensitive and act through a standard G-protein cascade, causing cation channels to open and action potentials to be fired. Olfactory neurones in the olfactory epithelium project upwards through the cribriform plate to the ipsilateral olfactory bulb. Interestingly, this region is one of the few places that new neurones are regenerated in the adult.

Individual cells will respond to a range of odours; each odour has a characteristic 'fingerprint' of activity across the entire epithelium. It is commonly held that

each neurone expresses one olfactory G-protein coupled receptor, but this is still unresolved (Mombaerts 2004). Odorant receptor (OR) genes comprise the largest gene family in the mammalian genome. Humans possess about 350 OR genes and 560 OR pseudogenes (Glusman *et al.* 2001), mice possess 1000–1300 OR genes, and other mammals may have over 4000 receptors. Given that nearly three-quarters of human OR genes may be dysfunctional (Rouquier *et al.* 1998), we may be much less sensitive to smell than many animals, including livestock, and there is a possibility that we have underemphasised the importance of odour detection in feed preferences of livestock.

A key feature of the physiology of odour detection is that individual receptors are not required for each odour: the pattern of bound receptors in the olfactory epithelium provides the brain with the information necessary to recognise a specific smell. Slight changes in the chemical structure of odours can activate different combinations of receptors. For example, octanol smells like oranges but the chemically similar compound, octanoic acid, smells like sweat (Leffingwell 2002).

Odour and feed preferences of livestock

Research into the area of feed preferences and feed intake regulation have primarily focused on the ability of an animal to develop a learned association between components that affect the sensory characteristics of a food and the ultimate nutritional utility of the food. However, little is known about the smell and taste responses of ruminants to various naturally occurring chemical constituents of herbaceous plants (Arnold *et al.* 1980). In early studies with sheep, Arnold *et al.* (1980) showed evidence of differences in feeding behaviour due to odour, as various herbaceous odorants affected the choices made by normal sheep but had no effect on

the food choice of anosmic sheep. They also reported evidence of large short-term effects on the feed preferences of sheep resulting from the addition of odorant pads containing volatile herbaceous compounds such as cedar wood oil, tannic acid, propionic acid and glycine to the feed bins of the animals (Figure 1). These odours reduced feed preference during the first hour of testing and sometimes for the first six hours of testing, but over the ensuing three days the aversion was usually reduced. Of the odorants tested, the aversion remained significant for 72 hours only for glycine. This suggests that some odours act as powerful regulators of short-term preference, but if the odours are not associated with any 'metabolic discomfort' (Forbes and Provenza 2000), the aversion is temporary. Since many other odours used by Arnold *et al.* (1980) did not induce this short-term aversion, the result summarised in Figure 1 cannot be attributed to a general aversion to a new smell (neophobia). The odours that did not affect feed preference presumably did not trigger the combination of odorant receptors necessary for the central nervous system to initiate food avoidance. Arnold *et al.* (1980) also provided evidence that plant odour can, in addition to its effects on feed preference, also have a marked effect on voluntary feed intake of ruminants. The authors demonstrated that feed intake over a series of 18 three-day periods was significantly increased in the presence of odours from butyric acid and amyl acetate, but significantly decreased in the presence of odours from coumarin and glycine. The observed increase in intake suggests that certain odours can override satiety mechanisms, at least temporarily. However, this only occurs when energy intake is below the capacity of the animal to use energy. It is not known whether the increased intake found by Arnold *et al.* (1980) would have persisted if the odours were provided continuously rather than in bouts of three-day periods.

In grazing herbivores, there is evidence that odour is used strategically in feed selection. Field experiments

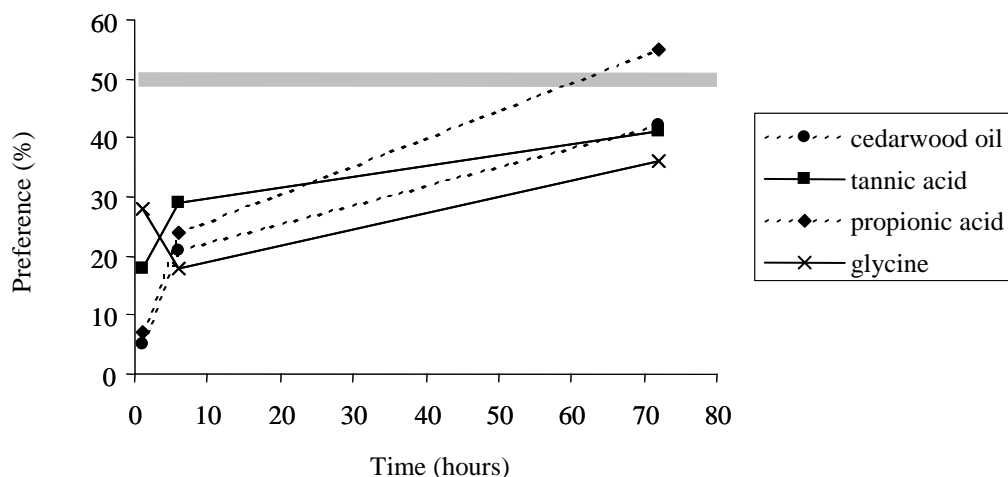


Figure 1 Changes in feed preference of sheep in response to the odours from four compounds (adapted from Arnold *et al.* 1980). The horizontal shaded bar indicates a preference value of 50%, which implies no preference for or against the odour.

often highlight the phenomenon of marked selectivity of animals towards specific plant species or components. Cattle grazing eight endophyte-free tall fescue cultivars were observed to move through the different plots with their muzzles in the forage canopy, occasionally taking a bite, apparently detecting volatile components (Shewmaker *et al.* 1997). Mayland *et al.* (1997) quantified compounds emitted from fresh tall fescue cultivars that differed in grazing preference and found that preference scores were significantly correlated ($r^2 = 0.97$) with emissions of 6-methyl-5-hepten-2-one, (Z)-3-hexenyl propionate and acetic acid.

Selectivity under grazing conditions may be most noticeable with forages that have a high degree of morphological variability, such as browse bushes (e.g., sheep grazing saltbush or cattle grazing tagasaste). In a recent study in South Australia where sheep grazed saltbush (*Atriplex nummularia*), video footage revealed individual sheep inserting their muzzle into bushes and sometimes recoiling without eating (J. Franklin-McEvoy, W. Bellotti, N. Edwards and D.K. Revell, unpublished data). On other occasions, the plant was eaten after this initial inspection. Work is currently in progress to identify the basis for this selectivity of saltbushes; the odour profile of the bush appears to be an important determinant. Preliminary results indicate that a negative association exists between naphthalene emitted from saltbush leaves and the degree of preference shown towards the bushes. In addition, the emission of this compound from saltbush leaves sampled 19 days after grazing was approximately double that of leaves sampled from ungrazed bushes. Naphthalene has seldom been described as a natural product, but is found in some plant species in chemical forms such as methylnaphthalene, which is aromatic; for example, Daisy *et al.* (2002) reported the presence of naphthalene in *Magnolia* flowers. Furthermore, naphthalene is known to have antimicrobial-, insecticidal-, insect repellent- (Hoffman *et al.* 2002), anthelmintic- and vermifugal properties. Other volatile plant compounds, including dimethylsulphoniopropionate or oxalic acid, may also be involved in the selectivity of sheep offered saltbush. The likelihood that secondary compounds or volatile plant compounds are involved in feed selection is strengthened by the work of Tiong *et al.* (2004), who found that although *Atriplex amnicola* was generally more preferred by sheep than *A. nummularia*, it had significantly lower *in vitro* digestibility of organic matter, higher fibre content, and lower nitrogen content. This suggests that selection between saltbush species is not explained by conventional nutritive value traits. Alternatively, the sheep may have developed their preferences when the plants possessed different nutritional characteristics (e.g., at an earlier stage of plant growth), and this learnt behaviour may have persisted for some time because olfactory cues did not change in parallel with nutritive value. If so, one would expect that preferences would continue to adjust over time to reflect the nutritional value of the plants.

We are currently conducting a large number of preference tests with dairy cows and horses fed oaten hays differing in nutritive value. Observations have confirmed that the animals smell the different feeds on offer before making a selection. Part of this study involves feeding horses oaten hays that differ in preference, *in vitro* digestibility and water-soluble carbohydrate content. Preference tests (Cox 2004) involved offering two hays simultaneously for short-term periods (8 minutes) or for longer-term periods (3-hour periods on five consecutive days). Hay preference (short- or longer-term) was not related to any single nutritive value trait except crude protein content ($r^2 = 0.72$). However, preference was strongly related to the abundance of two volatile compounds emitted from the hay that had gas chromatography retention times of 5.59 minutes and 19.13 minutes. The volatile compound with a retention time of 5.59 minutes was negatively correlated ($r^2 = 0.77$) to both the preference and crude protein content of the hays, suggesting that the horses may have used the odorant to identify and avoid low protein hays. Such a phenomenon would be consistent with the finding that rats can self-select for dietary protein based on olfactory stimuli (Heinrichs *et al.* 1990). This compound has not been identified, but appears to have a mass spectrum similar to that of naphthalene. The other volatile compound (retention time of 19.13 minutes) was positively related to hay preference ($r^2 = 0.83$). The identity of this compound is also yet to be confirmed, but appears to be a decane. Decanes have been linked to the odours from peaches that attract insects (Natale *et al.* 2003), and it is conceivable that horses also found the odour attractive, or that it was positively related to a previously identified favourable nutritional trait of the hay.

It has been proposed that when presented with a wide range of feedstuffs that exerts multiple stimuli (positive and/or negative), animals will require substantial pre-ingestive cues to perceive the values of individual foods (Ginane *et al.* 2005). Given that herbivores select diets that are higher in nutrient concentration and lower in toxin concentration than the average for the plant material available, the pre-ingestive cues must relate to post-ingestive consequences (Provenza 1995). There are survival and production advantages for animals that are able to detect antinutritional factors from the odour profile, and many antifeedants are indeed volatile, even at low temperatures (Bryant *et al.* 1992). For example, volatile sulphur compounds can deter feeding because of an association with predator odours (Bullard *et al.* 1978; Nolte *et al.* 1994; Provenza *et al.* 2000). Volatile compounds can be inhaled directly into the lungs and transported into the bloodstream, posing a direct risk of toxicosis at high concentrations.

Less attention has been directed to considering whether the odour fingerprint of plant material is used by animals to help select plants (or plant components) of high nutritional value. Possession of this ability would

have production advantages to animals in the same way that being able to detect and avoid antinutritional factors would be beneficial. Volatile organic acids detected by an animal's olfactory system may provide a valuable cue to the energy content of the feed (e.g., the odour from butyrate was found to be favourable by sheep; Arnold *et al.* 1980) and aromatic amino acids may be useful indicators of protein content. Linking the odour fingerprint to the nutritional value of forages or fodder is an area that warrants further investigation. Whilst olfaction is only one of many senses used to evaluate feeds, it may be a powerful driver of diet selection and learning behaviour in grazing/foraging herbivores.

Practical implications

Training animals by exposure to odour cues

In young animals, the learning of associations between odour and other characteristics of food can be enhanced by experiences with their mothers (Provenza *et al.* 2003). Preferences in the adult appear to be enhanced by olfactory enrichment in the post weaning period (at least in rats; Hennessy *et al.* 1977). Exposure of young animals to identifiable odours associated with a positive outcome (gustatory or post ingestive), and the subsequent addition of this odour to an otherwise unfamiliar feed may help overcome avoidance of new feeds. Grass juice odour, or flavour obtained from either water (Tien *et al.* 1999) or methanol (Dohi *et al.* 1997) extracts of pasture, can stimulate feed intake by sheep because familiarity of odour or flavour reduces the time taken to commence ingestion of an unfamiliar feed.

Using familiar and positive odours to stimulate increases in short-term intake has application to situations when feed is changed abruptly. Animals can adapt to such changes but do not do so immediately; it may take years for them to adapt to new forage mixtures or grazing regimes (Provenza *et al.* 2003). Short periods of reduced intake and performance can have profound

effects on animal production. We found that weaner fallow deer exhibited a reduction in the rate of bodyweight gain for 1–2 weeks after weaning (Fisher, Tow and Revell, unpublished data). This depression was not compensated for under the grazing situation that prevailed in our study, demonstrating that a temporary decline in performance prolonged the time taken to reach market weight. A temporary decline in feed intake is often observed when grazing animals are moved onto new pasture; naïve animals spend more time grazing but actually eat less and walk greater distances (Lyons and Machen 2005), with consequential effects on animal production.

Further studies are required to evaluate the potential of using odour or flavour preferences to increase feed intake in the short-term when animals move onto a new pasture base. We know that the addition of undesirable odours can reduce intake of grazing animals—for example, cattle avoid pasture treated with effluent slurry (Laws *et al.* 1996) and avoid pasture contaminated with the faecal or urine odours associated with predators (Pfister *et al.* 1990)—but we have not invested much research activity in trying to enrich the odour profiles of pastures. Using familiar odours or flavours could perhaps reduce the decline in feed intake typically observed when animals are introduced into a feedlot. In this regard, it is important to consider the training or exposure of animals to an odour that has been previously associated with a positive post-ingestive outcome rather than trying to identify an odour or flavour that is somehow inherently appealing to the animal. Studies with pigs at weaning generally suggest that flavour additives are not reliable stimulants of post-weaning intake. This may be because a flavour (or odour) will not be 'positive' unless the animals associate it with some positive effect, either nutritional or social. Hinch *et al.* (2004) recently showed the potential of using odour from a water extract of lucerne to increase the intake of wheat when the grain is first offered to adult ewes. In dairy cows, avoiding a temporary reduction in feed intake could have

Table 1 Correlations between volatile compounds with gas chromatography retention times of 5.59, 19.13 minutes (RT 5.59 and RT 19.13), crude protein content and preferences of hays by thoroughbred horses (Cox 2004).

		RT 5.59	RT 19.13	Crude protein content	Preference
RT 5.59	Pearson correlation	1	−0.842**	−0.773*	−0.774*
	<i>P</i> value		0.009	0.024	0.024
RT 19.13	Pearson correlation	−0.842**	1	0.537	0.828*
	<i>P</i> value	0.009		0.170	0.011
Crude protein content	Pearson correlation	−0.773*	0.537	1	0.718*
	<i>P</i> value	0.024	0.170		0.045
Preference	Pearson correlation	−0.774*	0.828*	0.718*	1
	<i>P</i> value	0.024	0.011	0.045	

*Correlation significant $P < 0.05$ level (2-tailed)

**Correlation significant $P < 0.01$ (2-tailed).

significant production and economic benefits, as a short-term drop in intake can have both an immediate and persistent effect on milk production. Hence, any dietary change, such as the source of hay used, should be monitored carefully and, where possible, new feedstuffs should be phased into the existing ration rather than changed abruptly. Moreover, exposing animals to a variety of nutritional experiences when they are young may help them make transitions between different feedstuffs later in life.

Plant–animal interactions following herbivory

Odours are likely to play an important role in plant–animal interactions because of changes to plant chemistry induced by herbivory. Managing the dynamic relationships between plants and grazing animals therefore requires an understanding of how animals respond to changes in plant–derived cues. Plant defence mechanisms may not deter herbivores that have adapted to them, but they may limit the intake by animals that are not pre-adapted (Wratten *et al.* 1981). Plant response to herbivory is inducible (Larcher 1995), with the severity of attack determining the plant response. Immediately upon mechanical damage, plants emit significant amounts of green-leaf volatiles (Turlings *et al.* 1998), which may be quantitatively and qualitatively different from the blend emitted when intact (Dicke and van Loon 2000). The induced release of volatiles is not limited to the site of damage but can occur systemically, and these volatiles from herbivore-infested plants may even induce defences in neighbouring plants.

The detoxification of antinutritional factors imposes a cost to herbivores, potentially disrupting acid–base homeostasis and, in relatively severe cases, causing loss of body protein and depletion of glucose (Villalba *et al.* 2002). The growth of moth larvae (*Oporinia autumnata*) was retarded when they were fed previously grazed leaves or intact leaves from the same birch plant (Edwards and Wratten 1982). The decline in growth of the larvae was attributed to an increase in leaf phenolics, which has potential to alter taste (condensed tannins are bitter) and odour (tannic acid is volatile).

Animal selection

Animals that are morphologically similar can exhibit wide differences in preference for, and tolerance to, particular plants in a grazing environment (Provenza *et al.* 2003), but the basis for this difference has not been identified. In some cases, there may be a genetic basis to between–animal differences, which could include different genotype–specific nutrient requirements. These would affect the energetic demand of the animal and hence its voluntary feed intake, but it could equally involve genotype differences in the capacity to select dietary components efficiently. The concept of genetically

based odour preferences is illustrated by the olfactory discrimination of familiar twins by lambs (Ligout *et al.* 2004). Marinier and Alexander (1991) suggested that familial associations exist between horses in their efficiency of choosing or sorting between plant species when grazing.

Age decline in feed intake/selectivity

The capacity to detect differences in odour declines with age and, in humans, the loss of odour and flavour has been associated with a decline in food intake. The underlying mechanisms involve degeneration of the olfactory epithelium and abnormalities of the olfactory bulb and central olfactory cortices (Loo *et al.* 1996; Kovács 2004). It is not clear whether livestock or companion animals such as horses experience an age-related decline in olfactory sensitivity as found in humans, primates and rodents, and if so, at what age this commences. If they do, enriching the odour profile of feedstuffs offered to aging animals, especially companion animals that are often maintained for a longer portion of their lifespan than production animals, may compensate for a loss of sensitivity in detecting odours.

Conclusion

If the mechanisms associated with sensory cues and their effects on appetite and ingestive behaviour are better understood, an opportunity exists to manipulate feedstuffs to alter feed preferences. For example, the characteristic reduction in feed intake when animals are first presented with a new feed may be reduced by additives that possess a familiar and positive odour profile. Similarly, a better understanding of the sensory cues used by grazing animals offered a heterogenous diet might help us manage both the animals and the forage resource.

References

- Anton, S. and Hansson, B.S. (1995). Sex pheromone and plant-associated odour processing in antennal lobe neurons of male *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Journal of Comparative Physiology A* 176, 773–789.
- Arnold, G.W., de Boer, E.S. and Boundy, C.A.P. (1980). The influence of odour and taste on the food preferences and food intake of sheep. *Australian Journal of Agricultural Research* 31, 571–587.
- Bryant, J.P., Reichardt, P.B., Clausen, T.P., Provenza, F.D. and Kuropat, P.J. (1992). Woody Plant–Mammal Interactions. In: *Herbivores, Their Interactions with Secondary Plant Metabolites*, pp. 343–370 (eds. G.A. Rosenthal and M.R. Berenbaum). Academic Press Inc., San Diego, USA.
- Bullard, R.W., Leiker, T.J., Peterson, J.E. and Kilburn, S.R. (1978). Volatile components of fermented egg, an animal

- attractant and repellent. *Journal of Agricultural and Food Chemistry* 26, 155–159.
- Cox, A. (2004). The effects of dry matter digestibility (DMD) and water soluble carbohydrates (WSC) on the short and long term preference and intake of export quality oaten hay by horses. Honours thesis, The University of Adelaide, Australia.
- Daisy, B.H., Strobel, G.A., Castillo, U., Ezra, D., Sears, J., Weaver, D.K. and Runyon, J.B. (2002). Naphthalene, an insect repellent, is produced by *Muscodor vitigenus*, a novel endophytic fungus. *Microbiology* 148, 3737–3741.
- De Boer, J.G., Snoeren, T.A.L. and Dicke, M. (2005). Predatory mites learn to discriminate between plant volatiles induced by prey and nonprey herbivores. *Animal Behaviour* 69, 869–879.
- Dicke, M. and van Loon, J.J.A. (2000). Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomologia Experimentalis et Applicata* 97, 237–249.
- Distel, H. and Hudson, R. (1985). The contribution of the olfactory and tactile modalities to the performance of nipple-search behaviour in newborn rabbits. *Journal of Comparative Physiology A* 157, 599–605.
- Dohi, H., Yamada, A. and Fukukawa, T. (1997). Intake stimulants in perennial ryegrass (*Lolium Perenne* L.) fed to sheep. *Journal of Dairy Science* 80, 2083–2086.
- Doty, R.L. and Commetto-Muiz, J.E. (2003). Trigeminal Chemoreception. In: *Handbook of Olfaction and Gustation 2nd edition*, pp. 981–999 (ed. R.L. Doty). Dekker, New York.
- Doty, R.L., Brugger, W.E., Jurs, P.C., Orndorff, M.A., Snyder, P.J. and Lowry, L.D. (1978). Intranasal trigeminal stimulation from odorous volatiles: psychometric responses from anosmic and normal humans. *Physiology and Behaviour* 20, 175–185.
- Edwards, P.J. and Wratten, S.B. (1982). Wound-induced changes in palatability in birch (*Betula pubescens* enr. Ssp. *Pubescens*). *The American Naturalist* 120, 816–818.
- Forbes, J.M. (1998). Dietary awareness. *Applied Animal Behavioural Science* 57, 287–297.
- Forbes, J.M. (1999). Natural Feeding Behaviour and Feed Selection. In: *Regulation of Feed Intake*, pp. 3–12 (eds. D. van der Heide, E.A. Huisman, E. Kanis, J.W.M. Osse and M.W.A. Verstegen). CABI Publishing, Oxon, UK.
- Forbes, J.M. and Provenza, F.D. (2000). In: *Ruminant Physiology: Digestion, Metabolism, Growth and Reproduction*, pp. 3–20 (ed. P.B. Cronjé), CABI Publishing, Wallingford, UK.
- Ginane, C., Duncan, A.J., Young, S.A., Elston, D.A. and Gordon, I.J. (2005). Herbivore diet selection in response to simulated variation in nutrient rewards and plant secondary compounds. *Animal Behaviour* 69, 542–550.
- Glusman, G., Yanai, I., Rubin, I. and Lancet, D. (2001). The complete human olfactory subgenome. *Genome Research* 11, 685–702.
- Greiner, B., Gadenne, C. and Anton, S. (2002). Central processing of plant volatiles in *Agrotis ipsilon* males is age-independent in contrast to sex pheromone processing. *Chemical Senses* 27, 45–48.
- Heinrichs, S.C., Deutsch, J.A. and Moore, B.O. (1990). Olfactory self-selection of protein-containing foods. *Physiology and Behavior* 47, 409–413.
- Hennessy, M.B., Smotherman, W.P. and Levine, S. (1977). *Physiology and Behavior* 19, 481–483.
- Hinch, G.N., Nolan, J.V., Lynch, J.J. and Hills, J. (2004). Familiar odour and flavour cues reduce feed neophobia in sheep. *Animal Production in Australia* 25, 97–99.
- Hoffman, M.P., Gardner, J. and Curtis, P.D. (2002). *Fibrous Pest Control*, United States Patent Application 20030198659. [Online, accessed 6 November 2004] <http://www.uspto.gov>
- Kovács, T. (2004). Mechanisms of olfactory dysfunction in aging and neurodegenerative disorders. *Aging Research Reviews* 3, 215–232.
- Larcher, W. (1995). *Physiological Plant Ecology*. Springer, Berlin.
- Laws, J.A., Rook, A.J. and Pain, B.F. (1996). Diet selection by cattle offered a choice between swards treated or untreated with slurry: effects of application method and time since application. *Applied Animal Behaviour* 48, 131–142.
- Leffingwell, J.C. (2002). Olfaction — Update No. 5. *Leffingwell Reports Vol 2* (No. 1). [Online, accessed 11 February 2005] <http://www.leffingwell.com/download/Olfaction5.pdf>
- Ligout, S., Keller, M. and Porter, R.H. (2004). The role of olfactory cues in the discrimination of agemates by lambs. *Animal Behaviour* 68, 785–792.
- Loo, A.T., Youngentob, S.L., Kent, P.F. and Schwob, J.E. (1996). The aging olfactory epithelium: neurogenesis, response to damage, and odorant-induced activity. *International Journal of Developmental Neuroscience* 14, 881–900.
- Lyons, R.K. and Machen, R.V. (2005). Interpreting grazing behavior. [Online, accessed 15 February 2005] http://rangeweb.tamu.edu/extension/rangedetect/15385_grzbhv.pdf
- Marinier, S.L. and Alexander, A.J. (1991). Selective grazing behaviour in horses: development of methodology and preliminary use of tests to measure individual grazing ability. *Applied Animal Behaviour Science* 30, 203–221.
- Masante-Roca, I., Gadenne, C. and Anton, S. (2002). Plant odour processing in the antennal lobe of male and female grapevine moths, *Lobesia botrana* (Lepidoptera: Tortricidae). *Journal of Insect Physiology* 48, 1111–1121.
- Mayland, H.F., Flath, R.A. and Shewmaker, G.E. (1997). Volatiles from fresh and air-dried vegetative tissues of tall fescue (*Festuca arundinacea* Schreb.): Relationship to cattle preference. *Journal of Agricultural and Food Chemistry* 45, 2204–2210.
- Mombaerts, P. (2004). Odorant receptor gene choice in olfactory sensory neurons: the one receptor—one

- neuron hypothesis revisited. *Current Opinion in Neurobiology* 14, 31–36.
- Natale, D., Mattiacci, L., Hern, A., Pasqualini, E. and Dorn, S. (2003). Response of female *Cydia molesta* (Lepidoptera: Tortricidae) to plant derived volatiles. *Bulletin of Entomological Research* 93, 335–342.
- Nolte, D.L., Mason, J.R., Epple, G., Aronov, E. and Campbell, D.L. (1994). Why are predator urines aversive to prey? *Journal of Chemical Ecology* 20, 1505–1516.
- Pfister, J.A., Müller-Schwarze, D. and Balph, D.F. (1990). Effects of predator fecal odors on feed selection by sheep and cattle. *Journal of Chemical Ecology* 16, 573–584.
- Provenza, F.D. (1995). Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *Journal of Range Management* 48, 2–17.
- Provenza, F.D., Scott, C.B., Phy, T.S. and Lynch, J.J. (1996). Preference of sheep for foods varying in flavours and nutrients. *Journal of Animal Science* 74, 2355–2361.
- Provenza, F.D., Kimball, B.A. and Villalba, J.J. (2000). Roles of odor, taste, and toxicity in the food preferences of lambs: implications for mimicry in plants. *Oikos* 88, 424–432.
- Provenza, F.D., Villalba, J.J., Dziba, L.E., Atwood, S.B. and Banner, R.E. (2003). Linking herbivore experience, varied diets, and plant biochemical diversity. *Small Ruminant Research* 49, 257–274.
- Reddy, G.V.P. (2002). Plant volatiles mediate orientation and plant preference by the predator *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae). *Biological Control* 25, 49–55.
- Rekwot, P.I., Ogwu, D., Oyedipe, E.O. and Sekoni, V.O. (2001). The role of pheromones and biostimulation in animal reproduction. *Animal Reproduction Science* 65, 157–170.
- Rouquier, S., Gaviaux, S., Trask, B.J., Grand-Arpon, V., van den Engh, G., Dernaïlle, J. and Giorgi, D. (1998). Distribution of olfactory receptor genes in the human genome. *Nature Genetics* 18, 243–250.
- Shewmaker, G.E., Maryland, H.F. and Hansen, S.B. (1997). Cattle grazing preference among eight endophyte-free tall fescue cultivars. *Agronomy Journal* 89, 695–701.
- Silver, W.L. and Finger, T.E. (1991). Smell and Taste in Health and Disease. In: *The Trigeminal System*, pp. 97–108 (eds. T.V. Getchell, R.L. Doty, M. Bartoshuk and J.B. Snow Jr.). Raven Press, New York.
- Sommerville, B.A. and Broom, D.M. (1998). Olfactory awareness. *Applied Animal Behaviour Science* 57, 269–286.
- Tien, D.V., Lynch, J.J., Hinch, G.N. and Nolan, J.V. (1999). Grass odor and flavor overcome feed neophobia in sheep. *Small Ruminant Research* 32, 223–229.
- Tiong, M.K., Masters, D.G., Norman, H.C., Milton, J.T.B. and Rintoul, A.R. (2004). Variation in nutritive value between four halophytic shrub species collected from five saline environments. *Animal Production in Australia* 25, 327.
- Tixier, H., Maizeret, C., Duncan, P., Bertrand, R., Poirel, C. and Roger, M. (1998). Development of feeding selectivity in roe deer. *Behavioural Processes* 43, 33–42.
- Turlings, T.C.J., Bernasconi, M., Bertossa, R., Bigler, F., Caloz, G. and Dorn, S. (1998). The induction of volatile emissions in maize by three herbivore species with different feeding habits: possible consequences for their natural enemies. *Biological Control* 11, 122–129.
- Villalba, J.J., Provenza, F.D. and Bryant, J.P. (2002). Consequences of the interaction between nutrients and plant secondary metabolites on herbivore selectivity: benefits or detriments for plants. *Oikos* 97, 282–292.
- Wratten, S.D., Goddard, P. and Edwards, P.J. (1981). British trees and insects: the role of palatability. *The American Naturalist* 118, 916–919.