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Taught by animals: how understanding diet selection leads to better zoo diets

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Wild animals invariably obtain their nutrient requirements, regulate their ingestion of toxins and even self-medicate. This review suggests that, while size and morphology dictate gross diet, the ability to select a diet is learnt. Animals learn to distinguish nutritious foods from less beneficial or toxic items through the positive and negative consequences of ingestion. In this process, early life experiences appear to be critically important. Zoo animals can rarely be provided with their wild diets and caretakers substitute nutrients from other sources. Thus, a suitable range of ingredients should be provided to give the animals a stimulating and nutritious diet that ensures excellent health.

Key-words: conditioned food aversion, diet selection, foraging, herbivore, herbivory, life experience, nutrition, plant secondary compounds, PSM, zoos

tion was fully understood, zoo environments could be engineered to allow the animals to choose their own diets from a selection of suitable components. This would offer the added advantages of allowing the animals to exhibit an important range of natural behaviours and providing diets that are nutritionally similar to those with which the species have evolved. In this article diet selection in animals is reviewed and suggestions are made as to how this knowledge can be applied in order to provide better diets for zoo animals.

Although confronted with a vast array of food items, wild animals usually obtain the nutrients they need. Some animals, particularly herbivores, do this while regulating their ingestion of toxins. In contrast, for both practical and economic reasons, humans decide what animals in captivity should eat and this is done without the benefit of the sensory capabilities of the animals and their individual and evolutionary experience with natural foods. If natural diet selec-

ANIMAL NUTRITION
The subject of this review is not animal nutrition but the processes by which animals fulfil their nutritional requirements. These subjects may be difficult to disentangle so we start with an overview of nutrition that introduces diet selection. For an account of animal nutrition, specific to zoo animals, the reader is referred to the review by Hume (1995) and several chapters in the volume edited by Kleiman *et al.* (1996).

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The nutrient requirements of all animals fall into two categories. The first contains the essential nutrients, like essential amino acids and essential fatty acids, various vitamins and minerals; distinct molecules that animals must obtain from their diets. The second category is the non-essential nutrients; compounds that animals must obtain in order to generate their energy requirements and to synthesize specific molecules, like non-essential amino acids. These nutrients are non-essential because many molecules can serve the same purpose. For example, an animal may obtain its energy by oxidizing fat, carbohydrate or protein, while carbon chains from several molecules can be resynthesized into non-essential amino or fatty acids. Some dietary components are needed for healthy digestive functioning even though they appear to detract from the quality of the diet (e.g. fibre and grit) (Leus & Macdonald, 1995). For example, Giant anteaters *Myrmecophaga tridactyla* in captivity frequently suffer from diarrhoea if their diet is not supplemented with considerable amounts of grit (Moeller, 1990). Likewise, a lack of fibre in the diets of herbivores in captivity can disrupt normal digestive function and allow teeth to overgrow (Hume & Barbosa, 1993). Similarly, many animals, particularly granivorous birds, deliberately eat stones that lodge in the digestive tract and aid physical digestion.

Evolution has led to an astounding diversity of animal life making it remarkable that all animal tissues, from single-cell organisms to vertebrates, have similar nutritional requirements (Moir, 1968). For example, most animals require the same nine or ten essential amino acids. Irrespective of outward appearance, all animals are composed of the same fundamental components (i.e. cells), so the similarity of nutrient requirements is not completely remarkable. Evolution has largely conserved the biochemical processes that allow cells to function. Thus, similar cells in all animals contain mito-chondria for respiration, which requires, among other things, enzymes composed of amino acids. In turn, the catalytic activity of enzymes requires co-factors, such as the metal atoms zinc, copper and iron, or co-enzymes, which are often vitamins.

Thus, the prime variable separating animals nutritionally is not the nutrients they need but the ability to meet their requirements from vastly different sources. Evolution continues to create infinite nutritional niches filled by animals with profound adaptations in their digestive systems and in their methods of gathering food. Just considering vertebrates, this process has given rise to birds that obtain their nutrition from mistletoe, vultures that consume decaying flesh, ant-eating mammals and reptiles, snakes that swallow prey many times their size, whales and sharks that feed on krill, fish-eating bats, bats that feed on blood, and herbivores, like rabbits and ringtail possums, that obtain substantial nutrition from eating their own excrement.

This diversity is an evolutionary response to the variable availability of nutrients in foods. Many dietary items do not contain all the nutrients required by an animal in the correct proportions and many have properties that reduce their nutritional quality. These 'anti-quality factors' (Launchbaugh *et al.,* 2001) include toxic compounds, compounds that reduce the availability of nutrients by binding to them (e.g. tannins) and compounds that are indigestible to most animals and thereby dilute the nutrients in the food. Animals show two different responses on two different scales to these challenges. Individual animals can avoid foods possessing anti-quality factors and choose to eat something else (i.e. diet selection) but the scope of this selectivity is determined by the evolutionary response of that species to anti-quality factors. One example of such a response is provided by ruminants, which have evolved digestive systems that counter many of the physical and chemical

defences evolved by plants on which they feed.

Plant cells may be divided on a functional basis. One part contains cellulose and other polysaccharides of the cell walls (fibre), and the other part, the cell contents, includes much of the protein, soluble carbohydrates and plant toxins. While some animals select plant parts for the cell contents and avoid or discard the fibre (e.g. Giant panda *Ailuropoda melanoleuca),* others utilize the abundant energy source provided by plant cell walls. This metabolism requires a microbial synergism because vertebrates do not have enzymes for degrading plant fibre. This microbial ecosystem has static requirements, such as slow passage of digesta through an anaerobic chamber kept at near neutral pH. The ecological advantages this system confers upon the animal are enormous. Apart from making available an otherwise unobtainable energy source and perhaps detoxifying some plant secondary metabolites (PSMs), microbial metabolism may exchange poor-quality plant protein or even non-protein nitrogen for high-quality microbial protein. Inappropriate feeding can make this ecosystem highly inefficient. For example, when high-quality protein is fed to foregut-fermenting herbivores, it is degraded and resynthesized into microbial protein of similar quality, causing large losses of energy during the chemical transformations (Van Soest, 1982).

This example demonstrates the precarious nature of providing zoo animals with a single complete diet in lieu of an appropriate choice of items from which they can select their own diet. Likewise, it demonstrates the risks inherent in changing the diets of animals in captivity without the knowledge to support the practice.

Domestic ruminants, such as Sheep *Ovis aries,* cattle *Bos* sp, goats *Capra* sp and Buffalo *Bubalus bubalis,* occur in most human civilizations. In the less developed parts of the world these animals eat plant fibre that is of little use to people. As long as the gut microbes obtain nitrogen and soluble carbohydrates, the animals thrive and can even eat substantial amounts of cardboard, as cows do in many Indian cities. Further supplementation with a molasses and urea block, which the animals voluntarily lick, can further stimulate the microbes and induce feeding so that a working animal also produces considerable amounts of milk (Preston & Leng, 1987). In more developed countries, such animals usually graze but many are held in barns and feedlots, where they eat concentrated commercial diets. These diets supply the nutrient requirements of the animals in a rather inefficient way. For example, ruminants are not physiologically nor morphologically adapted to cope with high-quality feeds, so they metabolize grains inefficiently. The two feeding systems, roughage or concentrates, are simultaneously stable and precarious. Foregut fermenters that eat extremely poor roughage without a source of soluble carbohydrates and nitrogen may reduce or even cease feeding (Van Soest, 1982). Alternatively, if these animals are suddenly offered a highly digestible diet like grain, there will be serious disruption of the microbial population and the animal may die. Furthermore, feeding diets with insufficient fibre may cause metabolic diseases because of the rapid microbial metabolism (Van Soest, 1982). These metabolic problems largely disappear if the animal is allowed to choose its diet from a selection of *appropriate* foods.

Some foods are inappropriate for animals in captivity because digestive adaptations and feeding strategies have evolved in particular environments, and are not always optimal in other contexts. For example, the Giant panda naturally feeds on a highly specialized diet consisting almost exclusively of bamboo but *occasionally* supplemented by small animals and carrion (Schaller *et al.,* 1985), which provide a valuable supplement to their poor-quality diet. However, if Giant

pandas in captivity are *routinely* offered energy-dense foods, such as rice and animal products, obesity and digestive disorders can result (Bush & Montali, 1993; Kirkwood, 1993).

Related to metabolic problems are four adverse nutritional states that are often difficult to distinguish. (1) *Malnutrition* describes a deficiency of a particular nutrient (Hume, 1995), including macronutrients, such as amino acids, or micronutrients, such as vitamins and minerals [e.g. calcium and vitamin D deficiencies that lead to rickets and osteomalacia (Vickers, 1968; Morrisey *et al.,* 1995)]. (2) *Undernutrition* generally refers to inadequate intake of energy or of protein, caused by undereating or a poor-quality diet. (3) *Overnutrition* occurs when energy absorption exceeds energetic demands [which are greatly reduced in captivity compared with activity in free-living individuals (Nagy, 2001)] and it can result in obesity, poor reproductive performance and disrupted metabolic processes (e.g. Hume & Barbosa, 1993; Schwitzer & Kaumanns, 2001). (4) *Toxicity.* Herbivores, in particular, are faced with a staggering array of PSMs and different species and individuals have varied abilities to detect and tolerate them. Nutrients, such as vitamin A (Schweigert, 1995), vitamin D [e.g. in horses (Sályi, 2002)], copper (Bremner, 1998) and selenium [e.g. in aquatic birds (Spallholz & Hoffman, 2002)], may also become toxic if overingested, while rejection of foods containing toxins may cause undernutrition.

Wild animals routinely select nutritious diets while regulating their intake of toxic compounds within manageable limits and, given appropriate circumstances, zoo animals can also avoid these adverse nutritional states.

THEORETICAL FRAMEWORKS FOR ORGANIZING AND SUMMARIZING THE UNDERSTANDING OF DIET SELECTION

Humans have probably tried to understand how other species choose their diets since times preceding the domestication of animals. There are many theories on diet selection (Provenza & Balph, 1990; Moore & Foley, 2000) and five of these are outlined here and compared as to their usefulness in facilitating a better understanding of how zoo animals can be offered more appropriate diets.

1. *Euphagia* refers to animals possessing 'innate hungers' for nutrients and an instinctive avoidance of anti-quality factors. Together these abilities would allow animals to detect nutrients and toxins, and assemble a balanced diet. A prerequisite of this model is the ability of animals to sense individual compounds in their food. Herbivores can discriminate foods that differ in digestible energy or nutrients (Launchbaugh *et al.,* 2001) but this is a learnt ability. While evidence suggests that animals do have innate hungers for sodium and calcium (Krieckhaus & Wolf, 1968; Coldwell & Tordoff, 1993, 1996), euphagia is not useful as a general model of diet selection and it is not feasible to assume that zoo animals are born with complete nutritional wisdom.

2. *Hedyphagia* also relies upon instinctive knowledge of what is 'good' and 'bad' to eat but postulates that animals choose their diet according to its hedonic value, or the pleasure it gives. The central tenet is that natural selection has caused nutritious foods to taste agreeable and less nutritious or toxic foods unpleasant. Hedyphagia proposes, for example, that sweet foods are pleasing to the senses because they contain high concentrations of simple carbohydrates, whereas bitter foods are displeasing because they tend to be toxic (e.g. many alkaloids). While the hedonic value of foods undoubtedly plays an important role in diet selection, hedyphagia fails to explain diet selection in general. Regardless of their initial reaction to a flavour, animals can develop aversions to sweet foods and preferences for bitter foods (Arnold & Hill, 1972; Glendinning, 1994; Pfister *et al.,* 1996). There is little evidence that animals can innately

recognize the nutritional or toxic properties of foods using their sensory abilities alone (Launchbaugh *et al.,* 2001).

3. *Morphophysiology and size* combine to impose limits on an animal's diet that ultimately define its dietary niche. Because each species has its own array of anatomical and physiological adaptations that are related to diet selection, this provides a sound theoretical basis for the nutrition of animals in captivity (e.g. Hume & Barbosa, 1993; Hume, 1995; Leus & Macdonald, 1995).

A simple example, involving only conspicuous morphological and physiological differences, can separate animals into two major trophic groups. Carnivores are specialized at locating, capturing, subduing and eating other animals. Their dentition allows them to tear and cut their highly nutritious diet, while a simple digestive tract processes it. Herbivores eat less nutritious diets that frequently contain high proportions of indigestible plant cell-wall material and they possess extensive gastrointestinal adaptations to process these diets.

Within the herbivores, body size alone explains much of the variation in diet selection, with smaller herbivores usually selecting a more nutritious diet than larger herbivores. This trend occurs in several mammalian groups, such as primates (Harvey & Clutton-Brock, 1981), ruminants (Hofmann, 1973) and macropodoid species (Sanson, 1978). The relationship between diet and body size has a physiological basis. With increasing size, metabolic requirements become relatively smaller, whereas gut capacity retains its relative size. Therefore, larger herbivores have a larger gut and frequently have a higher herbivory rating; that is, they eat less nutritious food than smaller herbivores.

There are many exceptions to the body-size rule. Eland *Taurotragus oryx* (700 kg), Giraffe *Giraffa camelopardalis* (800 kg), Moose *Alces alces* (600 kg) and European bison *Bison bonasus* (850 kg) are all large browsers or intermediate species. In contrast, Oribi *Ourebia ourebi* (15 kg), Springbok *Antidorcas marsupialis* (30 kg), Speke's gazelle *Gazella spekei* (15 kg), Common ringtail possum *Pseudocheirus peregrinus* (1 kg), Greater glider *Petauroides volans* (1·3 kg) and Koala *Phascolarctos cinereus* (9 kg) all have high herbivory ratings. (Plates 1 and 2.) How do we explain these deviations from the classical body size–herbivory rating model? There is remarkable diversity in both form and function within the gut of herbivores (Hofmann, 1989; Clauss *et al.,* 2002), as well as gut plasticity (Karasov & Hume, 1997), and similar variation in other anatomic, metabolic and behavioural features of herbivores. This is well illustrated by: (1) the long neck of the giraffe and the bipedal stance Gerenuk *Litocranius walleri* take when feeding, which allow both to select browse; (2) the ability of species to store nutrients or to migrate when conditions become unfavourable (Hofmann, 1989); (3) variation in energy expenditure (Blaxter, 1989); (4) feeding synergisms between populations of different species (De Boer & Prins, 1990). All of these factors provide scope for animals to deviate from the body-size rule.

A more subtle example exposing the fallibility of relying solely on body size and morphology to predict diet comes from two similar-looking 4–6 kg wallabies, the Tammar wallaby *Macropus eugenii* and the Parma wallaby *Macropus parma,* which are both primarily grazers (Hume, 1999). The Tammar wallaby occurs in maritime semi-arid habitats with a Mediterranean climate, whereas the Parma wallaby occurs in wet sclerophyll forests with moist or rainforest understories (Strahan, 1995). Physiological adaptations separate the species. The Tammar wallaby's nitrogen requirement is half that of the Parma wallaby (Hume, 1986) and the species also has a capacity to concentrate urine, enabling it to drink sea water (Purohit, 1971). These adaptations allow

Plates 1 and 2. Body size explains much of the variation in herbivore diet selection, as smaller herbivores usually select more nutritious diets than larger ones, although there are many exceptions to this. For example, the Springbok *Antidorcas marsupialis (top)* **is a small gazelle with a higher herbivory rating than the Giraffe** *Giraffa camelopardalis (bottom),* **which is a much larger browser.** *Ben Moore.*

it to survive in a far harsher environment where high-quality foods and fresh water are rare in summer.

An understanding of the morphological factors influencing diet selection offers zoo animal caretakers a way to identify the nutritional needs of an animal and the foods that the animal might be able to use to assemble a healthy and balanced diet. What it cannot explain, however, is how animals *know* what to eat and what to avoid. What mechanisms allow an animal to decide whether or not to eat a particular food item, to know when to stop eating that food and to assemble a balanced diet from an array of possible food items?

4. *Optimal foraging theory* models (reviewed by Stephens & Krebs, 1986) are mathematical models that are used in an attempt to identify the rules used by animals to make foraging decisions. These rules take various forms, depending on the currency being optimized (e.g. energy or nutrient gain, time minimization), the decisions made by foragers (e.g. which items to eat, how long to remain at a foraging location) and the constraints of foraging (e.g. thresholds for nutrients or toxins). More advanced models incorporate digestive physiology and interactions between the foraging animal and

the resource it eats (e.g. Whelan *et al.,* 2000).

While it is useful to predict how an animal will forage, two key aspects of optimal foraging theory models limit their usefulness. First, decisions about the suitability of food items must be made by the researcher before predictions can be made and, second, these models classify foods as either acceptable or unacceptable without grounds for accommodating the partial preferences exhibited by most animals (Provenza *et al.,* 2003). Finally, the theory ignores how an animal knows what it is foraging for and how it knows when it has found its optimal diet.

5. *The learning model of diet selection* is the most flexible explanation presented here because it can predict which food items animals show a preference for, the origins of those preferences and how and why they change. This model can explain why animals do not always choose the 'best' diet immediately and why preferences fluctuate.

As the name suggests, the central premise of this explanation is learning. Animals learn from conspecifics and from experience. For example, by using the positive and negative consequences of ingesting individual foods they learn to distinguish nutritious foods from less beneficial or toxic items. In keeping with the concept of hedyphagia, each food can be ascribed a value but in the learning model this value is not intrinsic but reflects the experience of the animal. Moreover, this value is dynamic and is constantly being 'tuned'. Animals develop aversions to eating foods that elicit negative effects, such as nausea or gastrointestinal malaise resulting from the action of toxins or nutrient imbalance. In contrast, animals develop preferences for foods that result in a sense of well-being because they are nutritious or ameliorate sickness by rectifying nutrient deficiencies or countering the effects of toxins.

Aversions and preferences can vary in strength and lie at two ends of a continuum. Animals develop conditioned food aversions and preferences as they incorporate novel foods into their diet throughout their lifetimes, and continually adjust them so as to ensure a balanced diet when faced with fluctuating availability and quality of foods. To this end, animals display a range of sampling and foraging strategies (Provenza *et al.,* 1998).

As the detailed examples presented will illustrate, a strong body of evidence supports the learning model of diet selection. An understanding of the model is vital to those designing zoo diets because, in many instances, its predictions may run counter to those of the previous models discussed. Animals choose what to eat, not on the basis of an innate nutritional wisdom but on the basis of their own individual experiences with that food item. As a result, a certain degree of patience must be exercised while animals undergo this learning process and an appropriate learning environment must be provided. The flexibility of learning means that animals are certainly capable of incorporating novel foods into their diet, even where those foods are 'unnatural' or lie outside the evolutionary experience of the species. However, morphological and physiological adaptations mean that some preferred foods would be more suitable than others.

While most or maybe all animals can learn from post-ingestive experiences and modify diet selection accordingly (Day *et al.,* 1998), herbivores routinely encounter foods with low concentrations of nutrients and which also contain toxins.

PLANT SECONDARY METABOLITES AND DIET SELECTION IN HERBIVORES

Plants have evolved an array of defences to avoid being eaten and these can be referred to collectively as anti-quality factors (Launchbaugh *et al.,* 2001), including physical defences, such as thorns, and chemical defences or PSMs, which work in various ways. For example, anti-quality

factors may intoxicate the animal [e.g. cyanide (Cheeke, 1998)] or they may make it difficult for herbivores to extract nutrients, such as when tannins bind to plant protein.

Foley *et al.* (1999) pointed out that refractive and potentially toxic factors are ubiquitous, so it is usually unrealistic for herbivores to avoid them. Animals select nutritious items from plants that contain those negative factors that they cope with best. In this way, herbivores regulate the amount they eat so that their intake of PSMs does not exceed a threshold (Provenza, 1995a; Lawler *et al.,* 1998a). For example, Common ringtail possums and Common brushtail possums *Trichosurus vulpecula* stop eating when they have ingested a threshold amount of jensenone, a secondary metabolite of *Eucalyptus* (Lawler *et al.,* 1998a). Likewise, Ruffed grouse *Bonasa umbellus* regulate their intake of coniferyl benzoate, a PSM of Quaking aspen *Populus tremuloides* (Jakubas *et al.,* 1993), cattle *Bos taurus* restrict their consumption of the alkaloids in Tall larkspur *Delphinium barbeyi* (Pfister *et al.,* 1997) and sheep fed diets containing lithium chloride (LiCl) regulate their feeding to avoid toxicity (Wang & Provenza, 1996a). The ability of herbivores to regulate their intake of potential toxins is contingent upon them forming an association between the negative consequences of the toxin and a sensory stimulant, such as the odour, taste or texture of the food (Provenza, 1995a). The system fails when: feedback is inappropriate for the animal to associate the toxin with the flavour, feedback occurs too long after ingestion of the food or no reliable sensory cues exist. Although regulating the intake of toxins is vital for all herbivores, the consequences of failure are variable, because the ability of an animal to cope with toxins depends primarily on its capacity for detoxifying them and that, in turn, depends on time. These are known as kinetic constraints.

How are diets of animals limited by the rate of detoxification of secondary compounds? Freeland & Janzen (1974) argued that the rate of detoxification is crucial in diet selection. This theory has two ramifications as it suggests that, first, detoxification capacity determines dietary niche and, second, better detoxification allows an animal to ingest more PSMs and hence more food. A simple demonstration of this second point involves the PSM benzoic acid, the detoxification of which requires conjugation predominantly with glycine (Hutt & Caldwell, 1990). When Common brushtail possums were offered diets containing supplementary glycine they ate more benzoic acid (G. J. Pass, W. J. Foley & S. McLean, unpublished data). Further ramifications of this theory are that herbivores with few resources for detoxification should eat mixed diets and spread a presumed array of PSMs, or complementary toxins, over several detoxification systems. In other words, if PSMs impose separate kinetic constraints that an animal can cope with individually, it should be able to eat more of the combined foods than it could of any single item. There is circumstantial evidence for this concept. Common brushtail possums allowed to feed simultaneously from diets containing ground *Eucalyptus melliodora* leaves and ground *Eucalyptus radiata* leaves ate more than when they were presented with either diet singly (Dearing & Cork, 1999). Similar results were observed in Mule deer *Odocoileus hemionus* when offered Sagebrush *Artemisia* spp and Juniper *Juniperus occidentalis* (Smith, 1959). Of course, factors other than PSMs may explain these results so, while the theory is generally accepted, in the absence of detailed toxicological studies there is little evidence for or against it (Foley *et al.,* 1999).

Further evidence for kinetic differences between species comes from those animals that eat *Eucalyptus* foliage, a food that often contains high concentrations of PSMs. The four major *Eucalyptus* foli-

vores, Koalas, Greater gliders, Common ringtail possums and Common brushtail possums, eat *Eucalyptus* foliage to different extents. Greater gliders and Koalas tend to eat only *Eucalyptus,* while the diet of the Common brushtail possum, a generalist herbivore, includes variable amounts of *Eucalyptus* and other tree foliage (Kerle, 1984). According to Freeland & Janzen's (1974) theory, these species may be expected to have different detoxification capabilities and Boyle *et al.* (2001) found that the extent to which each of these species is able to oxidize the *Eucalyptus* terpenes, cineole and *p*-cymene, increases with the degree of specialization on *Eucalyptus* foliage. However, it is not clear whether these differences reflect varying capacities for detoxification nor whether they impose limitations on feeding.

There is ample evidence, from many taxa, that the ability of an animal to cope with anti-quality factors depends on its nutritional state and its diet (Illius & Jessop, 1995). For example, lambs ate more food containing LiCl when the dietary energy concentration increased (Wang & Provenza, 1996a, 1997). Supplementing the diet of sheep with extra energy and protein enabled them to eat more terpene-rich Sagebrush (Banner *et al.,* 2000) but there was no effect on feeding attributable to energy or protein supplementation alone (Burritt *et al.,* 2000). Perhaps the most widespread PSMs are tannins, which by definition bind protein. Blue jays *Cyanocitta cristata* fed low-protein diets with tannins lost body mass but feeding tannins to Blue jays in conjunction with high-protein diets eliminated this loss (Johnson *et al.,* 1993). Finally, Witmer (2001) suggests that supplementary protein (Eastern cottonwood *Populus deltoides* catkins) allows Cedar waxwings *Bombycilla cedrorum* to ameliorate the effects of PSMs and meet the cost of maintaining normal acid-base balance better when consuming the highly acidic fruits of the Guelder rose *Viburnum opulus.*

Detoxification capacity is not necessarily static and, given time, animals may increase their ability to detoxify PSMs. One way this happens is through the induction of specific detoxification enzymes, such as the cytochrome P450 group (Pass *et al.,* 1999). Common brushtail possums fed diets supplemented with *Eucalyptus* terpenes contained higher concentrations of cytochrome P450 in their livers than possums fed the diet without supplementation (Pass *et al.,* 1999).

Many ecologists believe that the sheer diversity of PSMs and detoxification systems prevents us from understanding how these components interact to determine food intake (Levey & del Rio, 2001). However, regardless of the PSM, there are common features of detoxification: it takes time and there are negative consequences that may be shared by all animals (Foley *et al.,* 1995). These attributes may be the common currency explaining how animals integrate a diversity of PSMs into their diets. The implications of kinetic constraints for the diets of animals are clear. First, when toxins are encountered in mixed diets, animals can often eat more and cope better with toxins. Second, animals have evolved strategies to detoxify toxins and need not avoid them entirely; in fact, exposure to these compounds is often necessary to optimize detoxification systems.

THE IMPORTANCE OF AVERSIONS AND LEARNING IN DIET SELECTION

There are many examples of foods that humans consume that exert unpleasant effects even before they are eaten (e.g. blue cheese and certain fruits, such as the durian) but which actually provide useful nutrition; other foods seem innocuous to the senses but may be extremely toxic (e.g. various fungi or tropical fish infected with ciguatera). Foods consumed by animals are no different and consequently animals

must integrate aversions and learning when choosing their diets.

Non-conditioned aversions: short-term avoidance as a result of strong tastes and flavours Pre-ingestive cues, such as taste, odour or irritant properties, neither generate nausea nor result in long-term avoidance but may cause avoidance of food through non-conditioned aversions. A good example in mammals is the burning sensation caused by capsaicin in 'hot' chilli peppers stimulating trigeminal nerve fibres in the mouth. This stimulation often causes the animal to reduce the size or frequency of its meals (Pass & Foley, 2000) but animals will return to that food later. Furthermore, the observation that many bitter compounds stimulate rat *Rattus norvegicus* trigeminal nerves (Liu & Simon, 1998) suggests a broad role for trigeminal stimulation in non-conditioned aversions. It has been suggested this might include the detection of plant terpenoids and the astringency of tannins (Foley *et al.,* 1999). The importance of trigeminal nerve stimulation is not confined to mammals because birds also exhibit non-conditioned aversions mediated this way (Jakubas & Mason, 1991).

Salicin is a bitter phenolic glycoside that induces a non-conditioned aversion in Common brushtail possums (Pass & Foley, 2000). Animals fed diets containing salicin eat less but do not reduce their intake further when additional salicin is placed directly into their stomachs so they do not detect its bitter taste. Salicin had no effect on nitrogen balance or urea metabolism (Pass & Foley, 2000) and there seems to be no other significant costs of detoxification (McLean *et al.,* 2001), suggesting that the bitter taste and possibly stimulation of the trigeminal nerve deters Common brushtail possums rather than any post-ingestive effect. Common brushtail possums seemed unable to overcome this aversion entirely suggesting that learning cannot eliminate it.

Glendinning (1994) put forward a useful hypothesis to explain the differing significance of non-conditioned aversions to animals in different trophic levels. He identified a fivefold difference in bitterness tolerance across 32 mammal species and showed that carnivores, which rarely encounter toxins and have low tolerance to them, have low bitterness thresholds. However, herbivores face a continual barrage of toxins and have high bitterness thresholds. While carnivores can 'afford' to reject bitter foods, the herbivores cannot reject all bitter foods, not least because bitterness and toxicity are poorly correlated. Responses to pre-ingestive cues also differ within these larger trophic groups. For example, despite its potency as a mammalian trigeminal stimulant, birds are insensitive to capsaicin (Mason *et al.,* 1991; Jordt & Julius, 2002). Salicin acts as a feeding deterrent to Common brushtail possums (Edwards, 1978; Pass & Foley, 2000) but not to hares *Lepus timidus,* which frequently browse on salicin-rich foods. Launchbaugh *et al.* (2001) question the existence of any innate system for recognizing the nutritional or toxic properties of food based on flavour or other plant qualities. They point out that unpleasant flavours are not universally repellant (Glendinning, 1994) and that ruminants can develop conditioned food preferences and aversions for both bitter and sweet flavours (Launchbaugh *et al.,* 1993). However, the evidence presented suggests that, in some cases, pre-ingestive cues can influence diet selection. Such a role is not incompatible with the learning model of diet selection. In fact, it adds an extra layer of complexity and should not be ignored by those feeding zoo animals, as pre-ingestive cues may impose constraints on conditioning animals to particular foods. It is also possible that pre-ingestive cues may play a greater role in diet selection by inexpe-

rienced captive animals than in free-living individuals.

Conditioned food aversions: long-term avoidance mediated by nausea Animals form conditioned food aversions when they associate the taste or flavour of food with nausea or other gastrointestinal malaise (Garcia & Koelling, 1966; Garcia, 1989; Du Toit *et al.,* 1991; Garcia & Riley, 1998). For example, *Buteo* hawks avoided black mice when they had a different flavour from white mice and were paired with a dose of the nauseous compound LiCl (Brett *et al.,* 1976). Similarly, animals ranging from slugs (Sahley *et al.,* 1981) and rats (Garcia & Koelling, 1966) to Coyotes *Canis latrans* (Gustavson *et al.,* 1974) and sheep (Provenza *et al.,* 1990) learn to associate flavours with emetic stimulation and then avoid these flavours in subsequent encounters. Why do animals form these associations? Provenza (1995a, 1996) proposed that by forming conditioned aversions animals can regulate their ingestion of toxins and avoid foods that are nutritionally deficient or unbalanced.

Although the experimental use of distinctive flavours, such as aniseed (e.g. Kyriazakis *et al.,* 1997), confirms that herbivores form conditioned flavour aversions, the implications are difficult to gauge. The following example is perhaps more compelling because the compounds involved are secondary metabolites of *Eucalyptus,* which the animals may naturally encounter together. Wild-captured Common brushtail possums and Common ringtail possums can form conditioned aversions to the taste of cineole, a strongly flavoured terpene, based upon the consequences of simultaneously ingesting the toxin jensenone (Lawler *et al.,* 1999). (Plate 3.) Moreover, providing possums with the antiemetic drug, ondansetron, allowed them to eat more jensenone (Lawler *et al.,* 1998b); evidence that possums use cues from the nausea

Plate 3. Folivores of *Eucalyptus* spp, like the Koala *Phascolarctos cinereus,* develop conditioned flavour aversions to strongly flavoured essential oils based upon the consequences of simultaneously ingesting other natural eucalypt toxins that occur in similar concentrations. *Ben Moore.*

and emetic system to regulate their intake of potentially harmful PSMs.

Animals not only form aversions to flavours paired with toxins but also will avoid flavours associated with nutrient-deficient foods. For example, rats learn to avoid diets that are deficient in essential amino acids and this again appears to be related, at least in part, to the emetic system (Hammer *et al.,* 1990). After exposure to flavoured foods with differing energy and protein contents, lambs deprived of either energy or protein select an artificial diet to rectify the deficiency (Provenza *et al.,* 1996; Wang & Provenza, 1996a,b). Thus, apart from regulating the consumption of toxins, feedback from the

emetic system may also help animals select a nutritious diet (Provenza, 1995a).

Once formed, conditioned aversions can persist for a long time. Tall larkspur aversions in cattle persisted for more than 2 years (Lane *et al.,* 1990). The initial formation of aversions, however, appears to depend on an animal's familiarity with the food. If a food is novel then aversions form readily, as shown by Burritt & Provenza (1991) who dosed lambs with LiCl and fed them novel and familiar foods together. The animals developed aversions to the novel foods but their preference for the familiar foods remained unchanged. New foods should be introduced gradually to animals in captivity because a bad experience may cause animals to refuse those foods in the future.

Dire consequences may result when animals fail to associate toxic compounds with gastrointestinal malaise because of the delay between ingestion of a food and its post-ingestive feedback (Burritt & Provenza, 1991; Provenza *et al.,* 1992) or when a toxin does not stimulate the emetic system. For example, pyrrolizidine alkaloids take months or even years to stimulate the emetic system (Cheeke, 1998), while cyanide apparently fails to stimulate it (Ionescu & Buresova, 1977). Nonetheless, Common brushtail possums in New Zealand appear to form conditioned aversions to cyanide in poison baits (O'Connor & Matthews, 1995, 1997) and the Water vole *Arvicola terrestris* shows a clear preference for acyanogenic varieties of White clover *Trifolium repens* over cyanogenic ones (Viette *et al.,* 2000), suggesting that other mechanisms may be at play. Although these sorts of compounds are exceptions to the rule, they can pose a threat to captive and free-living animals alike.

Importance of early life experience and learning from other animals Early life experiences, possibly the result of simultaneous changes in neurological, physiological and morphological processes,

appear to have lasting effects on food preferences (Squibb *et al.,* 1990). For example, 4–6 week-old lambs exposed to Mountain mahogany *Cercocarpus montanus* ate more of the shrub later in life than lambs exposed at any other time (Squibb *et al.,* 1990) and goats reared on land dominated by Blackbrush *Coleogyne ramosissima* ate more Blackbrush in a pen trial than goats reared on alfalfa pellets (Distel & Provenza, 1991). Similarly, Kuo (1967) concluded that cats, dogs and Mynah birds raised on restricted diets avoided new foods, while those raised on varied diets ate novel foods more readily. A similar study conducted with rats showed that immature rats given early experience with several flavours in water would accept a novel flavour more readily than those reared with water with only one flavour, while mature rats given several flavours were no more willing to accept the novel flavour than mature rats given only one flavour (Capretta *et al.,* 1975). Thus, the age of an animal when it is first exposed to a food can affect how preferences form and how the animal forages in the future. The implication for feeding animals in captivity is clear: if possible, introduce selections of food items when animals are young. Animals that have been exposed to dietary choices from an early age will be more willing to sample new food items when they are introduced to them and will be better equipped to assemble a healthy, balanced diet from a selection of ingredients. Animals that have spent their lifetimes in captivity on a simple, unvaried diet, however, may not demonstrate the same ability to learn and adapt to novel food items.

There are many examples, relevant to feeding animals in captivity, of how social situations may impinge on feeding. Young animals that receive maternal care or live in social groups, gain skills in diet selection from other animals (Altbacker *et al.,* 1995). This is one way of increasing an animal's acceptance of novel foods (Prov-

enza & Balph, 1988) or of reversing an individual's previous aversions. For example, sheep averted to a proprietary pellet ate more when feeding with non-averted animals than they did when feeding alone (Thorhallsdottir *et al.,* 1990). There are similar observations for social interactions in rats (Galef, 1985b). In contrast, the same social conditioning can prevent animals from accepting food—so-called socially-induced avoidance (Galef, 1985a). The mother, in particular, can shape the food selection of her offspring (Provenza, 1995b) in both positive and negative ways. An extreme example of the latter is protein-deficient kittens *Felis catus* that showed a preference for a protein-deficient diet if they had originally eaten it with their mother (Wyrwicka, 1981). Similarly, lambs offered a choice of two palatable shrubs showed a preference for the one they had eaten with their mother (Nolte *et al.,* 1990). As with conditioned food aversions, these socially-induced preferences can last for many years. Lynch *et al.* (1983) discovered that lambs given wheat when their mothers were present ate much more than lambs removed from their mothers. Even 3 years later, a tenfold difference in wheat consumption remained between the groups (Green *et al.,* 1984).

Perhaps one of the most interesting aspects of social conditioning is that some of the effects can be traced to pregnancy and lactation. For example, weanling Rabbits *Oryctolagus cuniculus* initially selected foods that their mothers ate during pregnancy and lactation, even when this food was more toxic than other foods offered (Altbacker *et al.,* 1995). Experiments have suggested that experience of tastes *in utero* can affect preferences in rats (Stickrod *et al.,* 1982; Hepper, 1988) and potentially in goats, sheep and cattle (Bradley & Mistretta, 1973; Hill & Mistretta, 1990; Nolte *et al.,* 1992) and that flavours in mother's milk can affect post-weaning preferences of rats, mice *Mus musculus,* pigs *Sus scrofa,* cattle, sheep, rabbits and humans (see references in Mennella & Beauchamp, 1997).

DIET SELECTION IN THE ZOO SETTING
The fact that wild animals choose a nutritious diet while encountering toxins suggests that animals in captivity can do the same if given the necessary raw ingredients. As well as offering nutritional benefits, allowing animals to choose their own diets also serves as an enrichment technique (e.g. Zimmermann & Feistner, 1996; Masefield, 1999).

Some benefits of letting animals choose their diets Fedele *et al.* (2002) showed that goats, when allowed to select their own diets, weighed more and were able to regulate their intake of macronutrients during gestation and lactation better than goats that had been fed a traditional no-choice diet. Likewise, lambs can select diets with consistent protein:energy ratios when presented with individual foods containing markedly different ratios (Wang & Provenza, 1997). The same is true of Sea bass *Dicentrarchus labrax,* which can select an appropriate diet, drawing all three macronutrients from a range of incomplete diets, each containing either one or two macronutrients (Aranda *et al.,* 2000). Perhaps poultry provide the most evidence on choice feeding. Broiler chickens *Gallus gallus* (meat birds) can mix foods containing different concentrations of protein to achieve an optimal average protein concentration (Shariatmadari & Forbes, 1993; Gous & Swatson, 2000), while laying chickens allowed to choose their own diet ate less, yet gained mass faster, had better food-conversion ratios and laid heavier eggs than hens reared on a commercial pullet grower mash (Olver & Malan, 2000). These examples are primarily concerned with macronutrients and domesticated animals but, given the choice, it seems that all animals can select diets that rectify deficiencies and counter toxins. In fact, if free-

living animals did not do this, they would not survive.

We have shown that animals can select diets to regulate their intake of toxins but animals can also select substances of no nutritional value that can ameliorate the toxic and other negative effects of foods. Recently, there has been much interest in the ability of livestock to 'self-medicate' with polyethylene glycol (PEG) to allay the protein-binding effects of tannins. By binding tannins, PEG prevents tannins binding protein, which then becomes available to the animal (Ben Salem *et al.,* 1999a,b). A secondary effect is that the animals eat more (Ben Salem *et al.,* 2000; Landau *et al.,* 2000). Not only will animals self-medicate but also they will adjust the dose; for example, lambs that eat more PEG as the tannin content of their diet increases (Provenza *et al.,* 2000; Villalba & Provenza, 2001). There are other examples of animals self-medicating. For example, lambs fed grain choose to ingest solutions containing sodium bicarbonate and lasalocid to help attenuate the rumen acidosis caused by this diet (Phy & Provenza, 1998). Similarly, free-living Japanese macaques *Macaca fuscata* will ingest soils rich in clay minerals to buffer gastric upset caused by eating supplemented diets rich in soluble carbohydrates and protein (Wakibara *et al.,* 2001). Indeed, many primates practice geophagy as a means of mineral supplementation, adsorption of toxins and treatment of diarrhoea (see review by Krishnamani & Mahaney, 2000). As with other phenomena discussed in this review, self-medication occurs across taxa. Diamond *et al.* (1999) concluded that 11 species of frugivorous New Guinea birds ingested soil because it bound poisonous and/or bittertasting PSMs in their diets. This is an example of one way in which free-living animals can use diet selection to overcome limitations imposed by the inability of their morphology and physiology to cope with certain foods, and thus expand their dietary niche. Providing similar opportunities can allow some zoo animals to do the same.

CONCLUSION

If animals are given the appropriate food items to choose from, they can select diets that satisfy their nutrient requirements without poisoning them, rectify any nutritional deficiencies and increase their capacity to detoxify plant toxins or ameliorate their effects. This is not an ability that animals are born with but is one that must be learnt. A basic set of conditions is required for a healthy psychological development in humans: exposure to a broad range of experiences facilitates learning from mistakes and the development of innovative coping strategies. The impact of these experiences is greatest during the early years when neural pathways are still forming and behaviour patterns are established that will last a lifetime. The developmental journey is not undertaken alone, as parents, siblings and society all have valuable parts to play as role models and as protectors from potentially dangerous experiences. While none of these conditions is essential to an individual's biological survival, they can all contribute to psychological well-being, the richness of life experience and the ability to cope with changing environments. An analogous set of conditions allows zoo animals to develop rich, varied and flexible diets.

For animals to develop appropriate food preferences and aversions and learn how to obtain a nutritious diet from a range of food items, they must become familiar with this range, ideally at an early age. In many cases, interactions with conspecifics will be invaluable but in the case of zoo animals, it will often fall partially or entirely to the caretakers to promote the consumption of some foods and to withhold others. If we understand how the morphology and physiology of a species combine to limit its dietary niche it should be possible to identify its nutritional needs and provide an adequate diet in captivity.

To go one step further and ensure this diet is diverse, palatable and capable of changing with an animal's needs, however, we would do well to learn from those with a vested interest and a lifetime of experience: in other words, we should be taught by the animals.

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