

AND THEY CALLED IT PUPPY... FOOD PREFERENCES AND BEHAVIOURS

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TIM WATSON examines the role of early feeding practices and how they can positively influence adult dog eating behaviours through early learning

ADVISING clients how to feed their new puppy is simple, isn't it? You hand over a glossy "puppy pack", often accompanied with a free sample, and direct them to the products you stock. Apart from considering whether to feed wet or dry food, or a mix of the two, there's not much more to discuss. Or is there?

There is emerging evidence that what and how a puppy is fed can influence its short and longterm health, as well as determining attitudes to food later in life. Important factors appear to be feeding frequency as well as food type and the variety of foods offered. It is now clear the feeding behaviour of adult dogs is shaped by early experiences, especially during puppyhood ([Figure 1](#)).

Feeding behaviour

The feeding behaviour of our dogs and their food selection is quite different to their ancestors and wild relatives. Although the exact time that dogs were domesticated by humans is unclear, there is archaeological evidence of dog remains in the Middle East about 12,000 years ago (Dayan, 1999) and in western Russia more than 15,000 years ago (Germonpre et al, 2009). Research has indicated that today's dogs have derived much of their genetic background from grey wolves in the Middle East (vonHoldt et al, 2010).

The process of domestication appears to have brought about a significant shift in canine feeding behaviour (Bradshaw, 2006). The ancestors of domestic dogs would have hunted in packs, feeding on small and large prey, and browsing on berries, fruits and other parts of plants when prey was difficult to find. Wild dogs, such as wolves, jackals and coyotes, display similar feeding habits today. In contrast, feral dogs generally survive by scavenging rather than hunting.

It is believed this shift reflects genetic modification, or adaptive divergence, of specific genic regions relating to feeding behaviour during the course of domestication when the ability to scavenge would have allowed the early domestic dogs to survive on the broad array, but sometimes limited quantities, of food available around human encampments (Coppinger and Schneider, 1995).

Domestic dogs also differ markedly from their ancestors and wild relations in how they select foods. For domestic dogs, dietary selection appears to be based upon the appearance, odour, flavour, texture and nutrient composition of the foods available. It is these properties that determine the acceptance or palatability of dog foods.

In contrast, there is little evidence that palatability plays any role in the selection of foods by wolves and other wild dogs, even though the nutritional requirements of domestic dogs and wolves are similar. The ready availability of prey and knowing that a food is safe to consume is much more important for a wild animal's survival than sensory characteristics.

The reason for this divergence probably lies in the fact that domestic dogs were selected for traits other than their predatory skills and that, similar to the impetus for changes in feeding behaviour, these dogs had to become opportunistic feeders, adapting their food preferences for the variety of foods available around human habitats.

Freedom to choose

It is believed odour plays a major role in the choices made by domestic dogs, along with flavour. Dogs typically prefer meat over vegetable proteins, appearing to especially like the flavour components in meat proteins (Haupt et al, 1978).

The taste system of dogs is carnivorous in nature, but appears to have become modified. For example, there is potential to detect sugars, as seen in omnivorous species, and dogs seem to prefer cooked over raw meats (Lohse, 1974). Appearance and texture contribute less than odour and flavour in determining a food's attractiveness to dogs.

The role that nutritional quality plays in food selection by domestic dogs is poorly understood, although there is evidence that dogs do learn to select foods based upon protein content. Many species have been shown to develop learned aversions or learned preferences in response to the nutritional adequacy of foods. This is essentially the ability of the animal to respond to sensory

cues it learns to associate with a positive or negative physiological response to a food.

Several studies have shown that, when given freedom to choose from a variety of foods with differing protein content, dogs consistently select diets that provide between 25 per cent and 30 per cent of metabolisable energy as protein (Romsos and Ferguson, 1983; Torres et al, 2003), which is considerably in excess of their minimum protein requirement. The reasons for this are not yet clear, although the authors postulate a learned preference based on metabolic reinforcement of maintaining plasma amino acid homeostasis.

Recent work has indicated a protein-leverage hypothesis, whereby food selection is based on the macronutrient profile, which is well recognised in humans, mice and other omnivores (Sørensen et al, 2008), may also be present in carnivores, such as the mink, and is thus a more widespread phenomenon than previously recognised (Mayntz et al, 2009).

Frequency of food consumption is different in domestic dogs to their wild ancestors and relations, with research showing a relationship between meal patterns and the availability of food (Bradshaw and Thorne, 1992). Beagles, poodles and basenjis have all been shown to adopt a nibbling pattern of food consumption when freed from any constraints over access to food (Mugford and Thorne, 1980), which contrasts markedly with the gorging behaviour of predatory dogs. The extent to which this behaviour is replicated across the domestic dog population is unknown. The adoption of frequent small meals by some domestic dogs when food is freely available might suggest some advantage for this pattern of food intake, such as optimising digestive capacity and maximising nutrient availability. Regardless of its origins, this observation indicates the feeding of several small meals is more likely to satisfy the natural feeding behaviour of some dogs than a single large meal.

The selection of foods is also strongly influenced by previous experiences. Dogs fed the same diet for long periods often display preferences for other diets – the so-called novelty effect – whereas other dogs will apparently reject novel foods in the process referred to as neophobia. Some of these differences appear to be breedspecific (Bradshaw, 1991).

Puppy development

Behavioural development of puppies can be categorised into four phases: neonatal, transitional, socialisation and juvenile (Nott, 1992; [Figure 2](#)).

The neonatal phase, which encompasses the first two weeks of life, is dominated by feeding and sleeping, with approximately 30 per cent of the puppy's time spent feeding. The sole source of food is maternal milk and individual puppies have around 12 meals per day.

During the third week of life, the transitional phase, there is rapid neurological and physical development. Puppies are able to crawl, may attempt to walk, and can lap milk from a saucer. Teeth erupt at this time and puppies begin to take their first solid food.

As they move into the subsequent period of socialisation, which extends to 10 weeks of age, puppies remain dependent on maternal milk, but feed less frequently – six to eight meals per day. Importantly, feeding and sleeping no longer dominate the puppy's life and exploration becomes an important activity.

The socialisation stage represents the start of a significant developmental window in terms of how feeding behaviour and preferences are shaped. The variety of foods offered and the frequency of feeding during this period can have a significant influence on future feeding preferences.

Early studies of preference in puppies

Initial behavioural studies confirmed the belief that food preferences displayed by puppies tend to be influenced by early experiences. Limiting exposure to foods of varying odour and taste during the first six months of life (the socialisation and juvenile periods) was found to lead to very narrow and fixed food preferences, whereas feeding puppies a mix of foods with different flavours and textures resulted in them being much more accepting of novel foods (Kuo, 1967).

Subsequent work showed that such a view might be an oversimplification, since there are significant differences between individuals in their readiness to try new foods. Furthermore, the relative palatability of any novel food can have a substantial impact on response. For instance, puppies raised on a highly palatable diet are less likely to select a novel food when it is of inferior palatability, whereas a new diet will have a much bigger impact on food selection when the habitual diet is not very palatable (Mugford, 1977; Ferrell, 1984).

The conclusion from these early studies was that providing puppies with a varied diet – in terms of both flavour and texture – always reduces, and usually eliminates, any tendency for food preferences to become fixed (Thorne, 1995). The result is puppies grow into adults that are generally receptive to new foods and that are not fussy or discriminating in nature.

Recent studies

Further evidence that domestic dogs have diverged in behaviour from their wild relatives has emerged from a study of handraised dogs and wolves (Gácsi et al, 2005; [Figure 3](#)). Groups of dog puppies and wolf pups were reared and socialised in identical ways and their attitudes to humans and dogs – both familiar and unfamiliar – as well as inanimate objects was observed.

Compared to wolves, dogs displayed more communicative signals, such as vocalisation, tail wagging and gazing at the human's face, which might potentially facilitate social interaction. In contrast, the wolves tended to show more aggressive behaviour, particularly towards humans and regardless of whether they were familiar, and were prone to avoiding potential social interaction.

These observations indicate that, even at an early age, there are distinct differences in the way

puppies interact with humans compared with their wild ancestral relatives. Importantly, the occasion of feeding appears to offer great opportunity for early social interaction between young puppies and humans.

Another piece of behavioural research relates to how food preferences might be communicated between dogs. Using pairs of dogs, the investigators fed one dog a dry food flavoured with either basil or thyme and then allowed the two dogs to interact before offering the other dog the two flavoured foods (Lupfer-Johnson and Ross, 2007). The second dog in each pair was then found to show a significant preference for whichever diet was consumed by the first dog, indicating that dogs prefer food smelled on a companion's breath. This ability to learn about, and trust, chemosensory stimuli is likely to be advantageous in acquiring information about what foods are safe to consume.

Early programming

The extent to which exposure to chemosensory cues might exert longer-term influences on food selection, rather than simply communicating safety in the immediate feeding period, has been investigated.

Interest in this field has largely focused on prenatal and postnatal learning of olfactory stimuli, based on the assumption that flavours present in the mother's diet pass into the amniotic fluid and thus are experienced by the foetus. This would then provide the foetus with information on what is natural and safe to consume, based on the mother's normal eating pattern and knowledge of toxic and nontoxic foodstuffs.

Similarly, the flavouring of a mother's milk by her diet provides a further opportunity to communicate food preferences in the early part of life.

Dogs have been shown to learn about odours prenatally, via the maternal diet and amniotic fluid, and for this learning to be exhibited in terms of preferences after birth (Wells and Hepper, 2006). The duration of this learning was investigated in a subsequent study where aniseed-flavoured food was fed to pregnant bitches in the last 20 days of gestation, for the first 20 days of lactation, or both (Hepper and Wells, 2006).

The results showed that postnatal, but not prenatal, exposure to aniseed significantly affected food preference of the puppies after weaning at 10 weeks of age. Although this tended to suggest that any effect of in-utero learning was lost by the time of weaning, there was, in fact, an interaction between pre and postnatal exposure, such that puppies born to mothers fed aniseed during late gestation and early lactation showed the greatest preference.

The authors have suggested prenatal exposure to flavours works to prime the chemosensory system to certain stimuli, thereby increasing their receptivity or sensitivity to the same stimuli after

birth. Furthermore, they speculate this initial in-utero exposure may be quantitatively more important than first exposure via milk in the postnatal period. This subsequent exposure is likely to be critical in developing longer-term learning, since it would ensure a puppy's preferences were not locked on to a dietary component that was only consumed during pregnancy.

These findings have important practical implications for the feeding of pregnant and nursing bitches, since offering a variety of dietary types and flavours will help inform their offspring that these foods are safe to consume. This should, in turn, help the puppies to develop broad food preferences and thus avoid fussy or discriminatory feeding habits.

Conclusions

A 2008 study highlighted the importance owners place on their vets as a respected source of information on their dog's nutrition, health and care (Laflamme et al, 2008). Appreciating the role that early diet nutrition can play in the development of puppy behaviour is an additional means of reinforcing this respect, offering owners an insight beyond the notion that food simply provides nutrients for growth.

While it may be convenient for puppy owners to feed a single diet in one or two daily meals, this will not best serve the puppy's behaviour needs and development. Puppies require multiple daily meals, especially during the weeks after weaning, when six to eight meals per day may be required to meet nutritional requirements. The need for several small meals persists in adulthood, where feeding dogs twice is more likely to satisfy behavioural needs than a single large meal. Offering pregnant bitches and their young offspring foods with a variety of sensory characteristics – including odour, flavour and texture – will help puppies develop preferences for a variety of foods without excessive fussiness or discrimination.

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KEY POINTS

- Early food experiences influence the feeding behaviour of adult dogs, with meal frequency, food type, and variety all having significant effects.
- Domestication has resulted in changes in the eating pattern and food preferences of dogs. This reflects the adaptation of the early domesticated dogs to scavenge on foods available around human encampments rather than hunting for prey.
- Dogs have evolved to select food on the basis of the characteristics that determine its palatability – namely odour, taste, texture and appearance. There is also evidence that nutritional composition plays a role too.
- Feeding behaviour has also altered such that, when freed of constraints to food availability, some domestic dogs naturally choose to consume several small meals through the day as opposed to a single large meal.
- Food selection is strongly influenced by previous experiences, especially during early puppy development (three to 12 weeks of age). Limited exposure to foods during this period may lead to very narrow and fixed food preferences that persist into adult life. Conversely, feeding puppies a range of foods with different sensory characteristics may result in them being much more receptive to new foods.
- Behavioural studies have shown that dogs learn about a food's palatability by interacting with other dogs that have consumed the same food. Furthermore, puppies acquire information on the sensory characteristics of foods at a very early age through the transfer of flavours into amniotic

fluid and milk.

- Recent research has highlighted the importance of feeding practices in meeting both the behavioural and developmental needs of puppies. It is especially important to feed young puppies (from six weeks of age) six to eight meals per day and to offer them a variety of foods with differing sensory characteristics. This will ensure they develop preferences for a range of foods, without excessive discrimination.