The Evolutionary Basis for the Feeding Behavior of Domestic Dogs (*Canis familiaris*) and Cats (*Felis catus*)[1–3]

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ABSTRACT   The dentition, sense of taste and meal patterning of domestic dogs and cats can be interpreted in terms of their descent from members of the order Carnivora. The dog is typical of its genus, *Canis*, in its relatively unspecialized dentition, and a taste system that is rather insensitive to salt. The preference of many dogs for large infrequent meals reflects the competitive feeding behavior of its pack-hunting ancestor, the wolf *Canis lupus*. However, its long history of domestication, possibly 100,000 years, has resulted in great intraspecific diversity of conformation and behavior, including feeding. Morphologically and physiologically domestic cats are highly specialized carnivores, as indicated by their dentition, nutritional requirements, and sense of taste, which is insensitive to both salt and sugars. Their preference for several small meals each day reflects a daily pattern of multiple kills of small prey items in their ancestor, the solitary territorial predator *Felis silvestris*. Although in the wild much of their food selection behavior must focus on what to hunt, rather than what to eat, cats do modify their food preferences based on experience. For example, the "monotony effect" reduces the perceived palatability of foods that have recently formed a large proportion of the diet, in favor of foods with contrasting sensory characteristics, thereby tending to compensate for any incipient nutritional deficiencies. Food preferences in kittens during weaning are strongly influenced by those of their mother, but can change considerably during at least the first year of life.   J. Nutr. 136: 1927S–1931S, 2006.

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Both the domestic dog *Canis familiaris* and the domestic cat *Felis catus* are members of the order Carnivora. As its name implies, this group includes many species that specialize in carnivory, but this is not an absolute rule for the majority, most of which are omnivores; there are even some herbivores in this Order, such as the pandas (Ailuridae) and some frugivores, such as the kinkajou *Potos flavus* (Procyonidae) and the African palm civet *Nandinia binotata* (Viverridae) (1). The ancestral Carnivora were probably small nonspecialist omnivores, but some of the modern families consist of species that are obligate carnivores, notably the cats (Felidae) and the seals (Phocidae). Most species within the dog family, Canidae, subsist mainly on prey, although this can be predominantly invertebrate in species such as the fennec *Fennecus zerda* and the crab-eating fox *Cerdocyon thous*. The jackals *Canis aureus*, *C. adustus* and *C. mesomelas*, from the same genus as the domestic dog, are all omnivores, and the coyote *C. latrans* can subsist on fruit and other plant materials when prey is difficult to find (2). The diet of the ancestral species of the dog, the wolf *Canis lupus*, consists predominantly of meat in most habitats in which it is currently found. However, the dentition of the modern wolf is not dissimilar to that of jackals (3), and is consistent with a more omnivorous diet. Before persecution by humans, wolves were able to occupy a wider range of habitats than they do today; thus, it is possible that they formerly consumed a more wide-ranging diet.

Domestic dogs and cats, although both carnivores, therefore originated in different branches of the Carnivora, and have inherited rather different legacies of food preferences and food selection behavior.

Feeding behavior and food selection in domestic dogs   It is generally agreed that dogs were the first species of animal to be domesticated, but precisely when, why, and how domestication took place is still under debate (4). Archaeological evidence suggests that dogs first became distinguishable in appearance from wolves ~14,000 y ago; their mitochondrial DNA points to a much older common ancestor, perhaps >100,000 y ago. This discrepancy can be resolved if the appearance of domestic wolves/dogs did not diverge from that of free-living wolves until the shift from hunter-gatherer lifestyles to the early stages of agriculture; at this point this is speculative. There is also argument about the purpose for which dogs were first kept by people. Whatever the details of their origin, today's dogs are extraordinarily diverse in form, their range of sizes and conformations

exceeding those of all the other species in the Canidae combined. Less visible, and less well documented, is an underlying diversity of physiology and behavior (5). It is therefore always risky to generalize about "the dog" when discussing any aspect of behavior. Although anecdotally some breeds and types of dogs differ from others in their feeding behavior, there is little published evidence that would enable this variation to be explained.

Several breeds of dog have a reputation for being able to consume large meals very rapidly, and it is possible that this is the legacy of competitive feeding in the wolf. When a wolf pack makes a kill of a large mammal such as a caribou, a feeding hierarchy that allows the pack leaders (alphas) to feed first is observed; once they have withdrawn, the juveniles may have to compete with each other for the best of what remains. Rapid feeding may also be an adaptation to scavenging during the early stages of domestication (6). Dogs that retain this tendency can rapidly become obese if allowed to feed ad libitum. Although some breeds may be more prone to such behavior than others, there is also considerable variation among individuals within breeds (7).

In wild animals, food selection is a complex process that begins with the onset of foraging behavior and ends with the consumption of an item of food. In contrast to cats (see below), hunting behavior in domestic dogs was greatly modified genetically during the course of domestication, both in comparison with the wolf, and between types (6). Feral dogs generally subsist by scavenging rather than by hunting (8), suggesting that most dogs do not retain a fully functional repertoire of hunting behaviors. Occasional kills of livestock by feral or stray dogs may be accounted for by the high thresholds for flight in domestic, compared with wild animals. For most pet dogs, the selection of food provided by humans is based upon its appearance, odor, flavor, and texture. Little is known about how wolves use these senses to select among potential foods; thus, it is impossible to judge to what extent food selection behavior in dogs was modified by domestication. The taste systems of dogs and cats are based on what is probably a general carnivore pattern; certainly they are distinct from those found in rats (9) and several other omnivores and herbivores. One major distinction is the much greater sensitivity of the latter to sodium chloride, often a limiting factor in the diet of herbivores but less critical for carnivores because prey automatically contains an adequate level of sodium. Beagles appear to have little preference for salt or appetite for sodium (10), but monovalent cations, including Na+, greatly potentiate taste responses to sugars in dogs; thus, it is unclear how much of a role sodium chloride may have in food selection (11). Among the taste buds of the facial nerve in dogs, the most common units (Type A) respond primarily to amino acids, many of which, such as L-proline and L-cysteine, are described as "sweetish" in humans (12); these units also respond to mono- and disaccharides. Type B units, which are different from those found in rats, respond to carboxylic acids, phosphoric acids, nucleotide triphosphates, histidine, and other Brønsted acids. Type C units respond primarily to nucleotides that are associated with the "umami" taste in humans (13). Type D, which are not found in cats, respond to a small number of "fruity-sweet" compounds, such as furaneol (9). It was suggested that broad links can be drawn between these specializations and carnivory because many of the compounds mentioned occur in raw flesh and in carrion (14), but it is still unclear how the information from the taste buds is integrated into the brain or translated into feeding behavior. Odor must also play a major role in food selection because anosmic dogs show a reduced discrimination between different types of meat (15).

Although such sensory biases may predispose dogs to prefer some foods over others, these preferences must be modified by experience; however, little published research exists in this area. Dogs fed the same diet for long periods often display enhanced preferences for other diets (16,17), an example of the so-called "novelty effect," which will be discussed further in relation to cats (see below). Neophobia, initial rejection of apparently palatable foods that have never been experienced before, does occur in some breeds of dogs, but not in others (14). The most powerful effects of experience on feeding behavior in any species are one-trial aversions, in which sickness following a meal induces complete and persistent refusal of the same food at subsequent encounters. Experimentally, this is often demonstrated by adding an emetic such as LiCl to a food; it was suggested that dogs are less ready to learn such aversions than are other species (18), but subsequently it was discovered that LiCl has other behavioral effects on dogs (19), including inducing aggression; thus it is possible that these effects may interfere with aversion learning.

The evolutionary origins of feeding behavior in domestic cats The domestic cat *F. catus* is derived from the north African wildcat *F. silvestris lybica* (20), which is a more specialized predator than the wolf. It has also been domesticated for a much shorter period than dogs, and is consequently much less modified from its wild ancestor. In fact, the strict definition of domestication, i.e., that breeding, care, and feeding are totally controlled by humans, producing a reproductively isolated population (21), can strictly be applied only to pedigree cats (22). Nonpedigree ("mongrel") cats generally select their own mates, and readily interbreed both with free-living feral domestic cats, and, where they co-occur, with wild *Felis silvestris* (23). Pet cats, unlike pet dogs, have also retained the ability to hunt effectively.

That they are descended from a specialist predator is readily apparent from their dentition (3), which is dominated by large canines, used to sever the neck vertebrae of mammalian prey, and carnassials for shearing flesh from bone; the incisors and molars are relatively small. Unlike wolves, they are exclusively solitary hunters, and therefore usually take prey with much lower body-mass than their own, necessitating several kills per day. This is reflected in the ad libitum meal-patterning of domestic cats, which take several small meals, spread throughout the 24 h of the day (24).

However, domestic cats are more fundamentally constrained in their choice of foods by the absence of certain key metabolic enzymes, which appear to have been lost in the common ancestor of all of the extant species in the cat family. These losses result in very narrowly defined nutritional requirements (25), which in the wild can be satisfied only by a diet that consists largely of vertebrate prey. It is only perhaps in the last half-century, as these requirements have been elucidated by nutritionists and applied by pet food manufacturers, that domestic cats have been able to rely upon obtaining a balanced diet from human provisioning alone. This is likely to be the main selective pressure that has caused them to retain their ability to hunt. Before the widespread availability of refrigeration, surplus meat and fish would have been available only sporadically in all but the richest households; thus, those females that left the most descendants would be those that could obtain key nutrients by hunting (22).

Taste systems in cats The sense of taste in cats is based upon the carnivore pattern, as described above for dogs, but with further specialization, which can be accounted for in terms of its more specialized nutritional requirements (14,26,27). The same amino acid–sensitive units occur as in dogs, but in cats, these are stimulated by some amino acids and inhibited by

others, such as L-tryptophan, which are hedonically bitter to humans (28). These inhibitory amino acids are generally rejected by cats, which tend to prefer those that are excitatory, such as L-lysine, at least when tested in pure solutions (29). Also different from the dog, and highly unusual among mammals, is the insensitivity of these units, or any others that have been characterized in cats to date, to sugars. Cats also do not easily select foods on the basis of their sugar content (14,30).

The acid-sensitive units in cats are broadly similar to those in dogs, as are the nucleotide-sensitive units. Rather than the "fruity-sweet" sensitive units found in dogs, cats have a type of receptor that responds optimally to quinine, tannic acid, and alkaloids, approximately analogous to (but not homologous with) the "bitter" taste in humans.

Overall, these differences between cats and dogs can be interpreted as a refinement of the carnivore pattern in parallel with narrow specialization for obligate meat-eating. For example, the loss of sensitivity to sugars is unlikely to be problematic for an animal that cannot obtain much nutritional benefit from fruits, and might enable more precise estimation of the amino acid balance within a food, unaffected by any potential masking by sugars (14). However, this must remain speculative until more is understood about the integration of taste information of different types, and its translation into food preferences.

Effects of experience on food selection in cats Within the constraints imposed by their nutritional requirements, domestic cats take a wide range of prey, including some invertebrates (31). Some of these will be nutritionally incomplete or even potentially toxic; it has therefore presumably been adaptive for cats to be able to alter their preferences depending upon their recent feeding experiences. Cats living in association with humans have more potential foods to choose from than those that, like their wild ancestors, hunt exclusively; thus it is possible that domestication has resulted in the refinement of the behavior available to ensure a balanced diet. Long-lasting one-trial aversions were recorded toward the emetic LiCl (6), to concentrated sucrose that induced diarrhea (32), and to thiamine- and arginine-deficient diets (33,34). However, not all deficiencies in essential nutrients have this effect, as shown by cats fed taurine-deficient diets for up to 3 y without loss of appetite (35), despite the responsiveness to taurine of the acid units on the cat's tongue (12).

Domestic cats, therefore, have mechanisms that enable them to avoid repeating disadvantageous feeding experiences. It is more doubtful whether they are able to deliberately seek out foods that they know from experience have a particular nutritional composition, perhaps to compensate from an incipient deficiency in one nutrient or another. It has even been argued that from an evolutionary perspective, such mechanisms are unlikely to exist in specialist predators such as the cat family (36). Many cats do, however, show a growing aversion toward foods that have formed a large part of their diet in the past, sometimes referred to as the "novelty effect," but more accurately termed a "monotony effect," because it is the perceived palatability of the repeated food that is mainly affected. This strategy should reduce the probability that an unbalanced diet is taken because no 2 foods with markedly different flavors should contain the same nutritional deficiencies, even if these cannot be directly detected by cats. Powerful monotony effects were detected in both kittens and adult cats, and in both catteries (6,37) and free-ranging populations (38). The strength of this effect on preference appears to be greater in free-ranging cats, such as those on farms or taken in as strays, than in cats raised exclusively on nutritionally complete diets (39). Experience of the effects of accidentally taking a nutritionally incomplete diet, and subsequently correcting the imbalance by seeking out a food of contrasting flavor, may therefore increase the tendency to adopt the same strategy on subsequent occasions.

Effects of genetics and early experience on the food preferences of cats From an evolutionary perspective, the very specific dietary requirements of the cat family predict relatively little genetically based variation in flavor preferences. A case could be made for possible polymorphisms affecting prey preferences; for example, there could be some genetic basis for the specialization of some cats for hunting birds, and others for mammalian prey (40), although this does not appear to have been investigated. However, it is not easy to see how this would be assisted by polymorphisms in flavor preferences. In the wild, cats should focus their efforts on what they can catch, rather than what they find pleasant to eat. Rather, it could be predicted that all cats should have a similar flexible set of learning mechanisms that enable them to avoid repeating disadvantageous feeding events, such as the ingestion of toxins, and to repeat the ingestion of nutritionally balanced foods, such as modern commercial products. In support of this idea, differences in food preferences between populations of cats are more readily explained by feeding experience than by genetics (38).

Apart from their nutritional completeness, prepared pet foods bear little resemblance to the natural prey of domestic cats; obvious differences include a lower energy density and the sensory properties produced by thermal processing. Nevertheless, kittens can be weaned onto prepared foods easily, suggesting that their early food selection behavior is plastic and easily modified. Apart from direct experiences during and after ingestion, it is likely that kittens are most strongly influenced by the food preferences of their mothers (41), in parallel with the more well-established link between prey brought to the kittens by the mother, and their subsequent hunting abilities (42).

It is possible that the mother's influence begins before weaning because both her amniotic fluid and her milk will contain flavors from her diet. Wyrwicka (43) trained mother cats to eat unusual foods, including mashed potato and banana; when offered a choice between meat and the mother's diet, most of the kittens preferred the latter. Puppies weaned onto restricted and unusual diets also preferred these diets to more "natural" foods such as meat (44). Acceptance by kittens of flavors that differ so much from those typical of nutritionally complete foods (i.e., flesh) is evidence against the presence of innate flavor templates. The influence of the mother may extend to simply whether she is nearby; kittens introduced to tuna when their mother was present ate at the first or second exposure, whereas other kittens introduced to tuna when isolated from the mother required several exposures before they started eating (45). These biases in preference in favor of the mother's diet, termed the primacy effect (41), may be due to neophobia (46) to all other foods.

The extent to which kittens are neophobic toward a new food appears to depend upon the degree of contrast between its sensory attributes and those of the foods they or their mother are accustomed to eating. Weaning onto varied diets results in puppies and kittens with broad food preferences (44). The simplest explanation for this is that the possibility of strong contrasts, which might trigger neophobia, is reduced because any new food is likely to show some similarity to one or other of the foods already experienced. It is unclear whether wide experience actually makes young animals less neophobic per se.

Kittens and puppies raised on a single type of commercial pet food often show strong preferences for other commercial foods on the first few occasions they are offered (6); presumably, in this situation, the broad similarity between the products means that there is little or no neophobia, and the "monotony effect" (antiapostatic selection) dominates.

These powerful consequences of early experience do not, however, rule out genetic effects. Because of the effects of maternal behavior on kittens at weaning, paternal effects would be required to produce unambiguous evidence for genetic effects on flavor preferences. In a preliminary study conducted by the author, 12 cats from 5 litters sired by 2 different fathers (7 males, 5 females, all neutered, 4–5 y old, maintained as a single colony since weaning) were offered 10-min preference tests between a commercial cat food (Whiskas) and the same food with 10% by weight raw lamb's kidney added immediately before presentation. In a nested ANOVA, preferences (arcsine-square-root transformed) were characteristic of litters ($P = 0.006$) but not of sires ($P = 0.52$). Although it is possible that the 2 sires were genetically similar in this attribute, the much larger maternal effect suggests that early experience dominates. However, when the same preference test was offered to 10 sibling pairs of pet cats (14 males, 6 females, all neutered, 2–8 y old), all living in different houses, no littermate similarity was detected ($P = 0.36$). Together, these trials suggest that litter-specific (presumably maternally influenced) food preferences may persist into adulthood only when the feeding experiences of the littermates remain virtually identical.

In a study of 8 litters of pet cats, significant ($P < 0.05$) littermate similarities in preferences for the same pair of foods were detected at 7 wk of age postweaning, but before the kittens were living in individual homes. In a ninth litter, the queen, which was fed fish almost exclusively by its owner, repeatedly refused to eat in this preference test; 3 of 4 of the kittens in that litter also refused to eat in their test, compared with 4 kittens in the other 8 litters (Fisher Exact Test, $P = 0.03$). This supports the idea that kittens identify what is edible from what their mothers eat. When tested at 4 mo of age, after dispersal to individual homes, the preferences of the kittens correlated moderately with those they had shown at weaning (Pearson $r = 0.557$, $P < 0.01$), but the littermate similarity was no longer significant. There was little correlation ($r = 0.216$, $P = 0.29$) between 4 mo and 1 y, but preferences at 1 and 2 y were very similar ($r = 0.769$, $P < 0.0001$). These changes are consistent with the hypothesis that the preferences of pet cats are initially influenced by the feeding habits of the mother, but are subsequently modified by the range of feeding experiences made available by the owner. Eventually they become less variable, as the purchasing habits of the owner come into dynamic equilibrium with what cats will and will not eat. The owners of cats that, for whatever reason, exhibit a strong "monotony effect" may tend to buy a wide variety of foods, because any one food is refused after a few consecutive servings. Owners of cats that are more fixed in their likes and dislikes, for example, because they are prone to neophobia, may come to identify those foods by trial-and-error, and purchase them repeatedly.

Conclusions When feeding, domestic cats and domestic dogs both display the legacy of their origins in the Carnivora. This is especially true for cats, where narrow nutritional requirements have resulted in the retention of much of the behavioral repertoire of their wild ancestor, including hunting, but also sexual behavior. Cats are also equipped with flexible behavioral strategies, based on accumulated experience, aimed at achieving a balanced diet whatever the types of food available. Although kittens do display strong food preferences, based largely on the foods they encountered during weaning, these are readily modified by experience in adulthood. It is less easy to generalize about dogs, however, simply because of the great diversity of form and behavior within this species, resulting from its long history of domestication and the many different functions for which dogs have been bred.

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