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REVIEW

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Taste preferences and diet palatability in cats

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ABSTRACT

The taste of food is an essential characteristic for cats and has been shown to affect food selection. However, understanding of food selection by cats using taste characteristics is far from complete. Therefore, the aim of the present review was to summarize the current knowledge on food preference and the role of taste on this selection in domestic cats. Appetite regulation is one of the determinants of palatability in cats and involves a highly complex interplay between hypothalamus, adipose tissue, and digestive tract. However, knowledge on this interplay is scarce in cats. When evaluating different foods for cats, behavioural responses such as facial expressions involving the movements and positions of ears, tongue, and head can provide increased insight into the effectiveness of formulating a more palatable diet. This paper also reviews food additives currently used in industry for enhancing the palatability of cat foods. In summary, a better understanding of the factors that affect the food preference in cats is essential to produce high-quality foods because cats will not eat a food with a flavour they dislike even though it is complete and nutritionally balanced.

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1. Introduction

There are two hypotheses about the origin of the domestic cats. The first one presumes that domestic cats originates from Felis silvestris lybica (the African wildcat) and the second hypothesis claims that they should be considered to be the subspecies of Felis silvestris catus which is assumed to have originated from wild cats living in the Middle East (Clutton-Brock 1999; Randi and Ragni 1991). Recent evidence shows that feline domestication approximately occurred 9000 years ago (Vigne et al. 2004). Domestic cat is one of the most popular companion animals throughout the world (Mameno et al. 2017). According to a recent report, nearly 35% of the US households own at least a cat (Pallotto et al. 2018). Approximately 50% of all pet market is comprised of pet food. The global pet food market size was nearly 75 billion dollars and the United States was the largest market which was valued at around 25 billion dollars in 2016 (Phillips-Donaldson 2016).

Although there has been an ongoing debate on whether dogs are omnivore or strict carnivore, the cat is considered to be a strict carnivore. Therefore, cats have a relatively higher protein and essential amino acid requirements than those of dogs (Salaun et al. 2017). Amylase is not present in cat's saliva and their gastrointestinal tract is relatively short compared to omnivores so they can digest meat much faster than vegetables (NRC 2006). Cats lack the enzyme called 'β-carotene 15,15 – dioxygenase' and therefore, they cannot convert beta carotene to vitamin A and need to get vitamin A directly from the food of animal sources (Schweigert et al. 2002). Taurine, an amino acid, is essential for cats and they need to get it through dietary animal sources (Knopf et al. 1978). Cats lack the ability to convert tryptophan into niacin, a vitamin, and therefore it is required to be taken in through diet (Henderson et al. 1949). Arachidonic acid, a fatty acid, is also an essential nutrient for cats since they lack the enzyme necessary to convert linoleic acid to arachidonic acid and therefore their diet should contain sufficient amounts of arachidonic acid (Sinclair et al. 1979). The facts mentioned above support the hypothesis that cats are strict carnivores and therefore their diets need to be formulated precisely in order to supply all these essential nutrients (Figure 1).

Different cats have different preferences towards specific dietary flavours and individual variation in the type of diet given to kittens contributes to differences in diet/flavour selection when they reach adulthood. Therefore, a diet must meet both the nutrients necessary for cats, especially the essential ones, and also flavours that can encourage feeding to be counted as complete and palatable. Without palatability, being complete and balanced diet is not enough for optimal consumption. Thus, diet palatability, which can be increased by using dietary additives such as flavours or natural ingredients, should be high enough to prevent any potential food consumption problems in cats.

2. Eating habits of cats

Despite the domestication process, cats still have the ability to hunt when it is necessary. Because of cats' innate ability to hunt, they would live solitarily without any human interference in the

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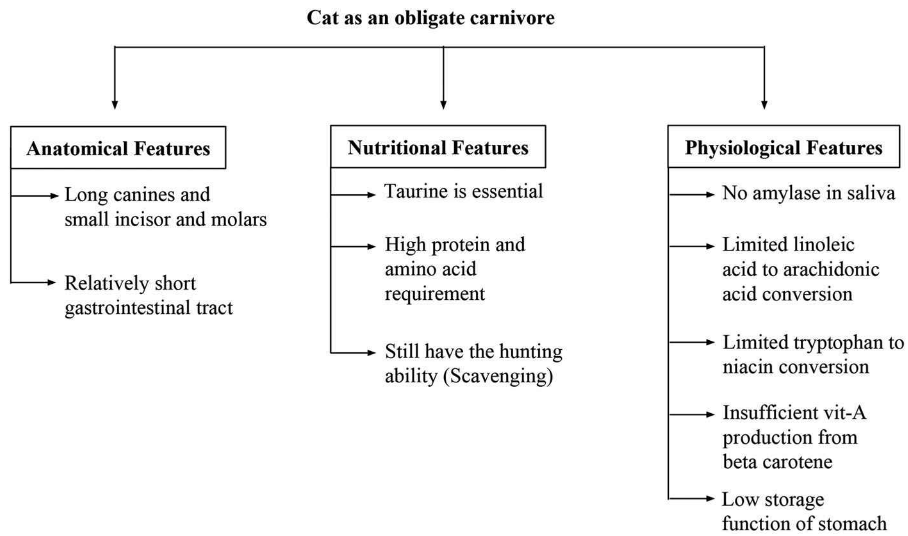

Figure 1. Some of the features of cats supporting the hypothesis that they are obligate carnivores.

wild (Bourgeois et al. 2006). Long canine teeth and shorter incisors and molars make cats very effective at hunting their prey and stripping the meat from its bones (Van Valkenburgh and Ruff 1987). Cats can hunt preys that are smaller in size several times daily in the nature. Fitzgerald and Turner (2000) showed that cats would kill 12 small animals (rodents mostly) on average in order to meet their daily energy and nutrient requirements. This instinctive behaviour must have been inherited from its ancestors and probably helps explain the habit of eating frequent and small meals observed today in domesticated cats (Bradshaw and Thorne 1992). In contrast, dogs are prone to eat big meals and mostly use this opportunity as a socialization period like humans. Cats are considered to be a strict carnivore and their diets mostly consist of muscle and organ meat of other animals (Lei et al. 2015). Consequently, the percentage of metabolizable energy that is provided from proteins and fats are very high (up to 90–95%) and carbohydrates should not contribute to the metabolizable energy by more than 10%. However, carbohydrate sources are less expensive and most commercial dry foods contain a lot more carbohydrate (around 40%) than cats' normal requirement (Hilton 1987). Cook et al. (1985) reported that a diet with high palatability and low protein content was preferred over a less palatable but complete and balanced diet. Therefore, the palatability of diet plays an important role in optimizing energy and nutrient intake in domestic cats through ensuring enough food consumption. Odour, taste, texture, and particle size are additional factors that play role in food intake preferences by cats (Hullar et al. 2001; Small and Prescott 2005).

3. Appetite

Appetite, by a broad definition, covers a lot of aspects such as palatability, eating frequency, size of eating episodes, energy density of foods eaten, and diversity of food consumed by cats (Arora and Anubhuti 2006; Figure 2). Appetite regulation is mainly controlled by signals produced both in hypothalamus and peripheral organs such as adipose tissue and digestive tract (Erlanson-Albertsson 2005). Hormones or cytokines produced by adipose tissue have become widely known as adipokines and they are involved in the regulation of appetite, energy balance, glucose, and lipid metabolism (Zoran 2010). Leptin is a protein hormone secreted from adipose tissue that has been shown to decrease appetite and often referred to as a 'adipostat' in cats (Appleton et al. 2000; Shibata et al. 2003). Since leptin is secreted from adipose tissue, the higher body fat levels are associated with higher plasma leptin concentrations (Appleton et al. 2000). Leptin works as a negative feedback mechanism in cats to limit food consumption and helps decrease accumulation of more fat in the body. Therefore, circulating leptin levels has been reported to be positively correlated to body fat levels in cats (Hoenig and Ferguson 2002). Although leptin receptors are widely distributed throughout the body, they are mainly located within the satiety centre of

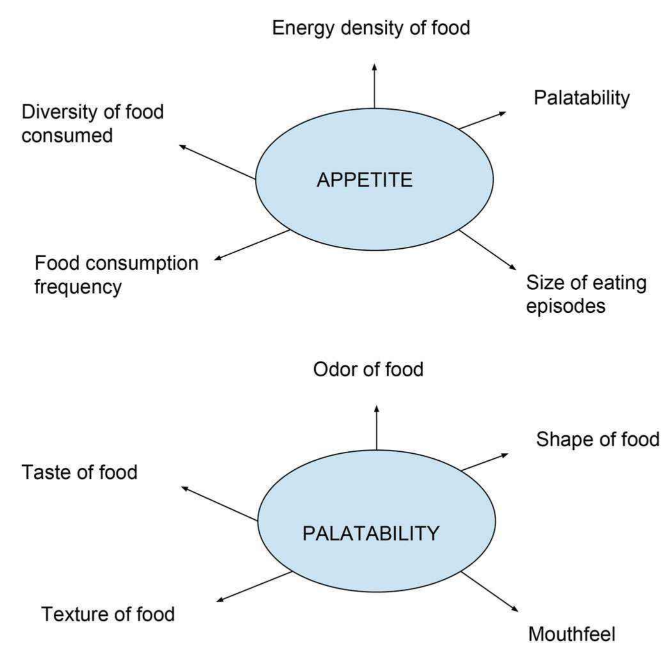

Figure 2. Schematic representation of the main factors involved in appetite and diet palatability in cats.

hypothalamus (Houseknecht and Portocarrero 1998). The binding of leptin with the receptors located within the hypothalamus results in the release of two different types of neurotransmitters; the first type stimulates anorexigenic neurones, and the second type suppresses the orexigenic neurones. Therefore, leptin plays a key role in reducing appetite and thus controlling food intake in cats (Appleton et al. 2000; Coppari et al. 2005). Adiponectin is another cytokine and acts as a food consumption regulator together with leptin in cats and recently has been shown to be a target molecule for the treatment of obesity and diabetes in cats (Ishioka et al. 2009). The same authors found that obese cats had lower plasma adiponectin concentration when compared to non-obese cats. Tvarijonaviciute et al. (2012) reported a significant increase in plasma adiponectin concentration after a weight loss in obese cats. Although there is some evidence to indicate the involvement of adiponectin in fat accumulation in cats, its role on food intake or appetite remains to be further studied, especially in obese cats with increased appetite. A schematic figure summarizing the role of leptin and adiponectin is shown in Figure 3.

Ghrelin (a gut hormone) increases appetite and plays a role in the control of food intake and its plasma concentration has been shown to be inversely correlated with dietary fat concentrations in cats (Backus et al. 2007). Another gut hormone named cholecystokinin activates peripheral and central cholecystokinin receptors and causes satiety and acts as a mechanism to limit food intake in cats (Bado et al. 1991). Neuroendocrine hormones named glucagon-like peptide-1 and peptide tyrosine are also released from intestinal cells in response to food intake and are involved in the satiety response but there is a lack of research on their role in regulation of appetite and therefore on energy expenditure in cats. The analogues of glucagon-like peptide-1 are used to decrease body weight through a speculated loss of appetite in humans, however whether the same effect occurs in cats remains currently unknown (DeFronzo et al. 2008; Hoelmkjaer et al. 2016).

An approximately 15% less food intake has been reported in summer compared to winter in cats during a 4-year cohort study that was conducted in the south of France where there is a Mediterranean climate (Serisier et al. 2014). These authors indicated that the seasonal consumption differences did not affect the body weights and therefore they speculated that the change in energy requirement was responsible for the food intake difference. Therefore, exact detailed mechanism responsible for these changes is still unclear in cats.

4. Sense of taste in cats

While cats' sense of taste helps them evaluate the nutrient content of a food, it also protects them from eating toxic, harmful or indigestible ingredients as much as possible. Chemical sensors that respond to a variety of chemicals are called taste buds which are located in tongue, palate, pharynx, and larynx in cats (Shin et al. 1995). They have relatively small numbers of taste buds (approximately 470) compared to dogs, cows, and humans which have around 1700, 20,000, and 10,000 taste buds, respectively. Therefore, cats have a weaker taste sensitivity compared to most other animals (Davies et al. 1979; Ganchrow and Ganchrow 1987; Robinson and Winkles 1990). Taste buds can detect five basic tastes which are classified as salty, sour, bitter, sweet, and umami (Li 2013). Although cats have a functional sense of taste like most mammals; they lack sweet taste receptors and show no preference for sweet compounds such as sucrose (Li et al. 2005). The reason for the lack of sweet taste perception has

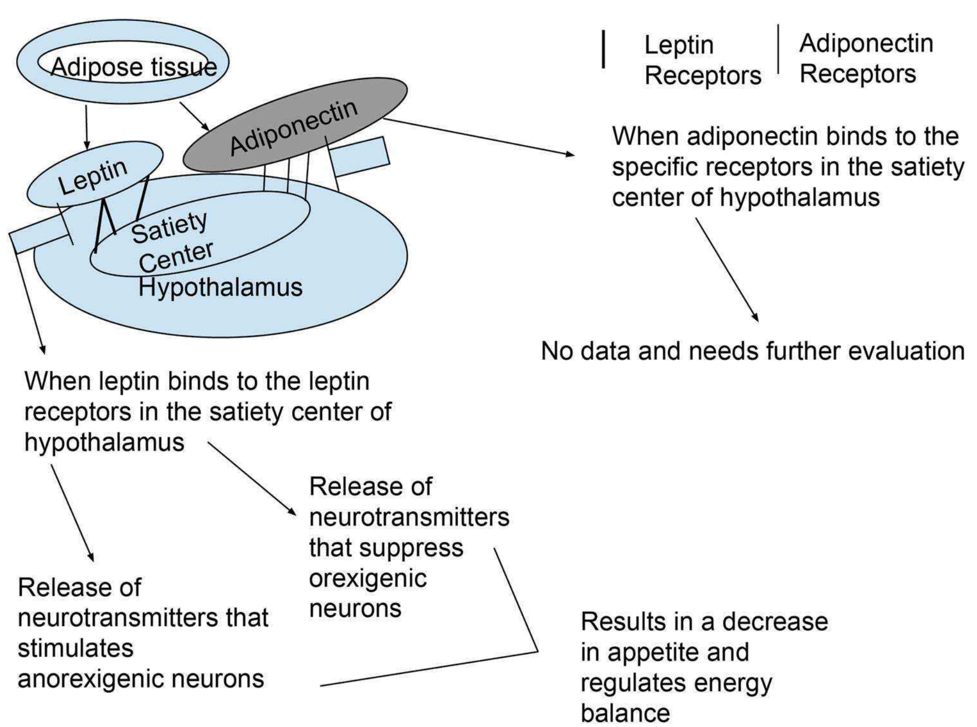

Figure 3. Schematic representation of the role of leptin and adiponectin in appetite control in cats.

been largely attributed to the deletion of Tas1r gene of sweet taste receptors found in taste buds (Li et al. 2005, 2006). Results of a recent study indicate that a mutation is responsible for the deletion of TIR 2 gene very early in the evolution of cats (Adler 2014). Therefore, they do not show any preference for glucose, sucrose, and fructose naturally. Cats have been also reported to reject non-nutritive sweeteners like saccharin and cyclamate (Bartoshuk et al. 1975). Domestic cats have been reported to have at least seven different functional bitter taste receptors but they tend to reject bitter foods where the opposite is true for dogs and most other mammals (Sandau et al. 2015). Electrophysiological records showed that water is not tasteless to cats (Bartoshuk et al. 1971). The very few number of taste buds found in cats led them to perceive the taste of food using other complementary senses. Among these alternative senses, odour appears to be the most important one. It is a well-known fact that cat's sense of smell is 14 times better than humans. The reason for the better sense of smell was largely attributed to having 2 times more receptors in the nasal epithelium of cats (Padodara and Jacob 2014). Additionaly, cats have a vomeronasal organ, which is also called Jacobson's organ located in the roof of their mouth which has a duct that connects it to both nose and mouth. Vomeronasal organ lying along the base of the nasal cavity, with an average length of 15 mm, opens into mouth by vomeronasal duct on the lateral side of incisive teeth through nasal septum laterally (Chung et al. 2018; Salazar et al. 1995). Vomeronasal organ is almost entirely surrounded by a cartilage. This organ compensate for low taste detection ability of cats since they have very few numbers of taste buds on their tongue and cats use his nose, mouth, and vomeronasal organ collectively to arrive at a decision on the taste of food item (Salazar et al. 1996). When a cat smells food, they open their mouth, put their chin in lower position, curve the tip of their nose, then communication starts between the vomeronasal organ and nasal cavity through the vomeronasal duct, while cat

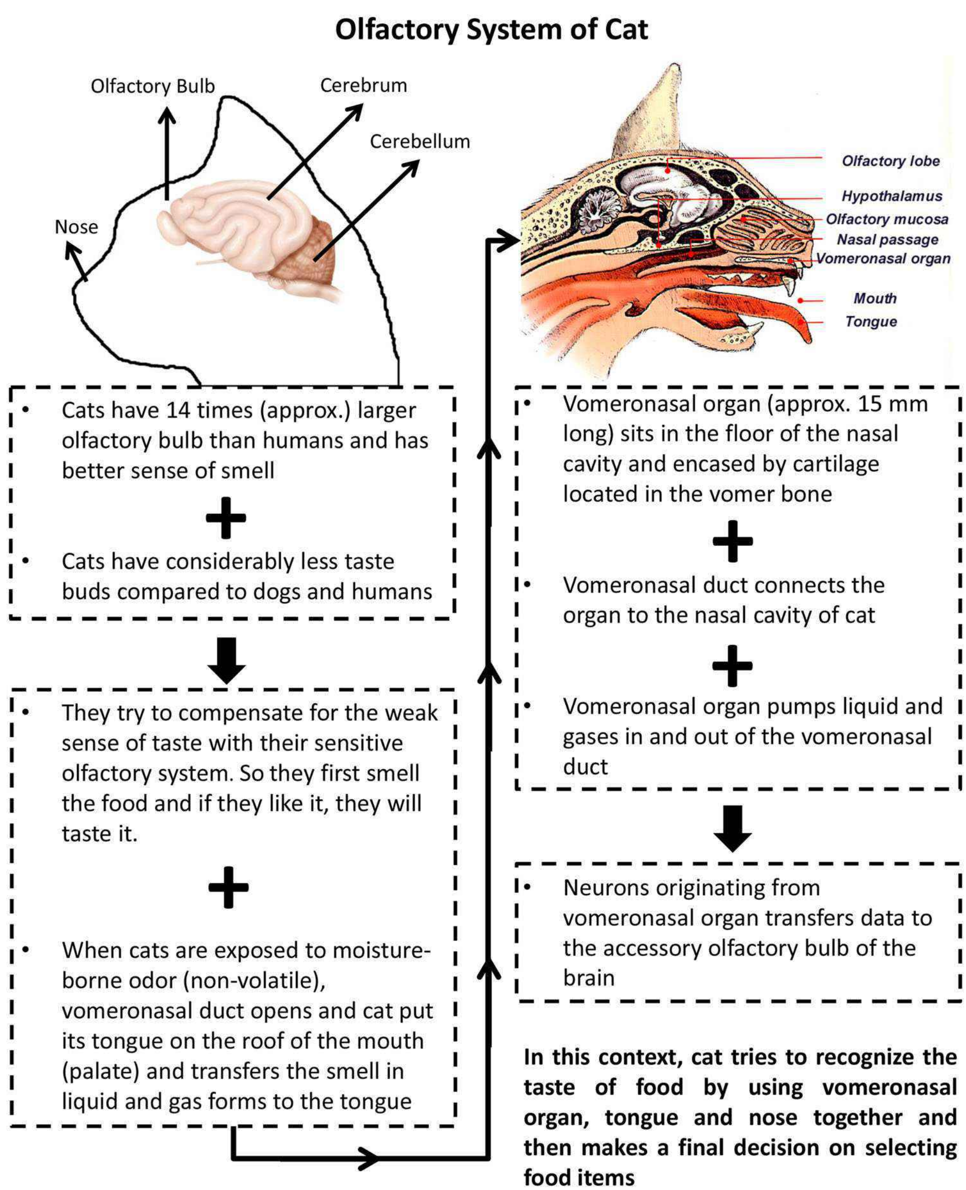

Figure 4. Parts of cat's olfactory system and its role in determining the taste of Foods.

rubs its tongue against palate and transfers the smell to the tongue where taste buds are located. Thus, cats use vomeronasal organ, nose, and tongue together to describe the taste of a compound since its limited capacity for the utilization of taste by low numbers of taste buds (Papes et al. 2010). The vomeronasal organ also functions in determining pheromones and play a major role in determining sexual behaviour in cats (Doving and Trotier 1998; Hart and Leedy 1987). Parts of cat's olfactory system and its role in determining the taste of foods are summarized in Figure 4.

4.1. Taste preference in cats

Cats were reported to prefer fish and commercial food over rat in a laboratory setting (Houpt and Smith 1981). Beauchamp et al. (1977) reported that the increased preference for foods with large amounts of protein and fat might be considered proof that cats are obligate carnivores. Cats uses odour information generated from food as an effective tool to identify the source of food to be eaten. If a cat finds an odour of a food more attractive than another, he will keep eating it without tasting the other food (Hullar et al. 2001).

4.2. Behavioural responses to different tastes in cats

Measuring just preference and consumption patterns when concerning the palatability of a diet may not be complete without assessing behavioural responses of cats. When evaluating a cat's behavioural responses to a food item, the facial expressions should be the very first one to be evaluated. Facial expressions include the motion of face, tongue, eyes, and nose. Relationship between these expressions and taste of a food can be used in the analysis of palatability and proved to be helpful when combined with preference and consumption data in cats. Behavioural responses related to food consumption may be classified into three: (a) those related to the taste of food; (b) those related to consumption; and (c) those related to satiety (Figure 5). Touching the food with paws and biting are good behavioural examples related to the taste of any substance for cats. Behavioural responses during feeding including eye and face movements can be indicative of the palatability of the food they consume. Most house cats are likely to play with their prey when they are not hungry and they play to practice their hunting skills. Therefore, playing with food or prey can be given as an example for behavioural responses related to satiety in cats (Levine et al. 2016; Leyhausen 1979). Hanson et al. (2016) reported an increase in the duration of 'half-closed eyes' when they consume a food they prefer. The same authors also noted that when cats eat something they like, they tend to do the behavioural responses such as nose licking, tongue protrusion, smacking lips longer compared to food they do not prefer. Becques et al. (2014) investigated the behavioural responses when given highly palatable or less palatable dry food to cats during 20 h period a day. They concluded that feeding the highly palatable diet resulted in a significant decrease in the length of sniffing the food which corresponds to less hesitation to consume it when compared to less palatable diet on the two first visits to feeding station of first day. After cats eat something they like, they do the licking of the lip region more frequently. On the other hand, after they consume a food they dislike; licking their nose, moving their tail to the right and left, and increased grooming are the behavioural indicators which may be seen at higher frequencies (Savolainen et al. 2016). Similarly Van den Bos et al. (2000) reported a significant increase in total duration and frequency of lip-licking after consuming a more palatable diet compared to a less palatable diet. The novelty effect or 'neophilia' is mostly occurred with cats that have been fed a single food or diet for a long time. These cats were reported to show a higher preference for a new diet when they were given a chance to select between the diet they used to eat and a new one. This response has been attributed to cats' evolutionary habit towards consuming more than one food source to prevent any nutritional deficiencies (Bradshaw 2006; Stasiak 2002). The duration of preferring the novel food depends on its palatability. In contrast, some cats show resistant to a new diet, especially when they were fed one type diet or flavour for years, this form of behaviour is called 'neophobia'. This type of behaviour has been reported to be a strategy of cats to avoid any toxic or poisonous food item. This type of diet

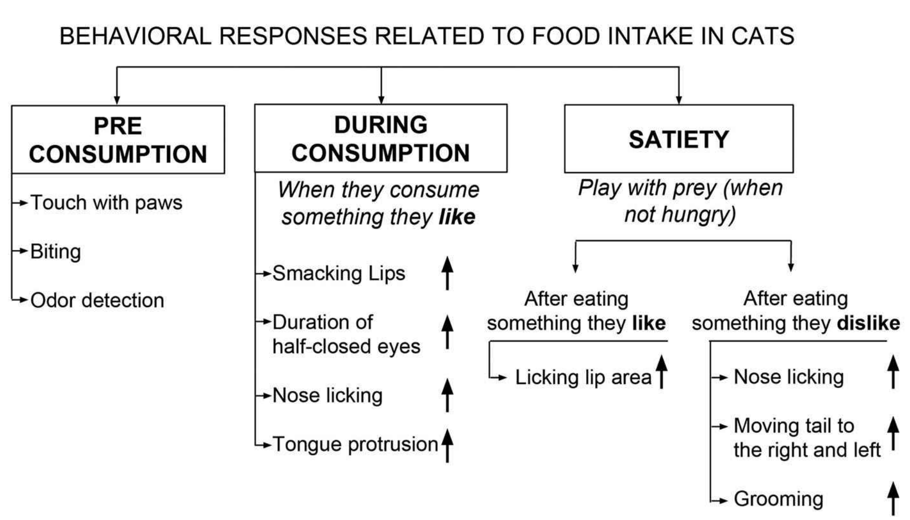

Figure 5. A schematic of the relationships between food intake and behavioural responses in cats during pre-consumption, consuming, and satiety stages.

rejection is most commonly reported under physiological, emotional, or environmental stress in cats. Giving a new type of food during a visit to veterinarian, or when a cat has a disease or pain can be good examples of this effect (Bourgeois et al. 2006; Bradshaw 1991; Bradshaw et al. 1996). Thus, it is always a good idea to introduce a new food under positive and usual circumstances to avoid neophobia situation.

5. Palatability

Palatability can be defined as the overall pleasant sensations related to the hedonic or sensory attributes obtained from ingested food that contributes with its acceptability in animals (Hall et al. 2018; Stubbs and Whybrow 2004; Yeomans et al. 1997). Lists of variables affecting palatability have been identified in cats in the literature and are discussed below in this review. However, complex interactions between many factors related to animal and food have been a major issue for the pet food industry.

6. Factors affecting food palatability in cats

6.1. Animal-Related factors affecting food palatability in cats

6.1.1. Preweaning feeding and its influence on feed preference in adult cats

According to Bradshaw (2006), cats observe their mothers' feeding practices which can affect their food preferences later in the adulthood period. Hamper et al. (2012) fed cats with either raw or canned diet from post weaning 9 weeks to 20 weeks. Then, the same cats were fed with only dry food between 7 and 23 months of age. Cats demonstrated a reduced acceptance of canned (moist diet) food after 23 months of age. It was concluded that feeding neither raw nor canned food earlier affected the transition from dry food to moist food during adulthood. Stasiak (2001) fed one group of cats with tuna only while the other group was fed with beef only during a 3-week-old to 6-month-old period. After feeding only one type of food, cats were retrained using the alternated food. Stasiak (2001) demonstrated that both the beef and tuna cats preferred tuna in stages with alternated food. However, when cats were nondeprived of a food taste during 6-month period, no difference in attractiveness of food tastes observed. Therefore, they concluded that the deprivation of different food tastes could reveal an inborn food choice. Feeding cats through a stomach tube during the first 75 days of their lives had a detrimental role on sensory system that activates the reward mechanism, although they could able to learn to perceive the food reward as attractive (Stasiak and Zernicki 2000). Bradshaw et al. (2000). showed that the house cats had an aversion towards raw beef while the farm cats consumed a little of the hard-dry food which might have been difficult to ingest. Therefore, they speculated that the way of life and prior dietary experiences play a role in food preferences in adult cats.

6.1.2. Hunger level

Physiological state of hunger has been shown to affect feeding behaviour in cats (Peachey and Harper 2002). Van den Bos et al. (2000) reported that cats prefer to eat more palatable food regardless of their hunger level. However, they also showed that cats consume the less palatable diet depending on their hunger level.

6.1.3. Age of cat

Aging results in a significant decrease in olfactory receptors and fibres, thereby reducing the sense of smell. In addition, aging also has been associated with a concomitant loss of taste in cats (Boyce and Shone 2006). Despite this, voluntary eating behaviour of cats has been found to be stable in response to aging (Taylor et al. 1995). Feeding a more palatable diet, moistening dry food by adding warm water, and feeding fresh food more frequently have proven to be effective ways of encouraging old cats with appetite problem to consume a satisfactory

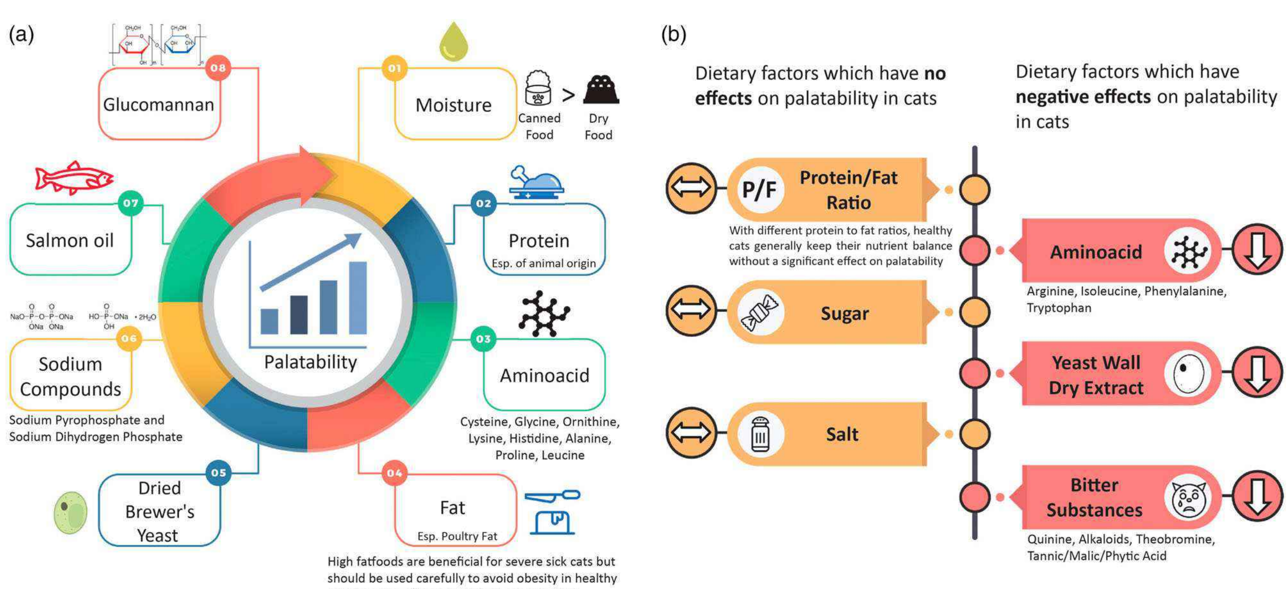

Figure 6. (a). Dietary factors which have positive effects on palatability in cats. (b). Dietary factors which have no or negative effects on palatability in cats.

amount of food to maintain a constant nutrient balance (Laflamme 2005).

6.2. Dietary variables that affect the palatability of diets for cats

Dietary factors contributing to diet palatability are summarized in Figure 6(a,b).

6.2.1. Moisture

Although cats can consume dry or semi-moist foods without a problem, they mostly prefer wet or canned food over dry foods since the moisture level of canned food is very close to that of meat (70–85%) (Zaghini and Biagi 2005).

6.2.2. Protein source and content

Kittens were reported to show an impressive regulation of protein intake and also have an upper limit for carbohydrate intake which constrains them to deficits in protein and fat intake on carbohydrate-rich foods (Hewson-Hughes et al. 2011). There is a strong positive correlation between the protein level of the food and its palatability, especially when protein sources of animals are used (Zaghini and Biagi 2005). Diets formulated for cats are known to vary greatly in protein sources and they can be classified into either vegetable or animal origin. Soybean and soybean-derived products are the main vegetable-based protein sources in cat diets, especially in vegetarian diets; however, they also have low palatability that limits inclusion in diets for cats (Redmon et al. 2016). One common industry practice is to use other foods or additives such as porcine liver or polyphosphates to increase the overall palatability of the cat diets (Zentek and Schulz 2004). On the other hand, collagen tissue has been used in relatively low-priced cat foods as a source of animal protein. However, it also has a very low palatability compared to muscle meat sources and again the addition of another high palatability ingredient is necessary (Paßlack et al. 2017).

6.2.3. Protein/fat ratio

It has been shown that cats are able to regulate and balance their protein and fat intake regardless of its flavour (fish, rabbit or orange) even with different protein to fat ratios (from 10:90 to 70:30) that contribute to the energy density of the diet (Hewson-Hughes et al. 2016). Therefore, the authors concluded that macronutrient composition and organoleptic features of diet mostly play independent roles in diet selection by cats but these factors might interact in some cases.

6.2.4. Amino acids

The taste buds in cats are innervated by four different cranial nerves in the mouth (Oliveira et al. 2016). The receptors in facial nerve mainly react to tastants such as amino acids, nucleotides, sugar, etc. These reactions may result in either positive or negative response in the central nervous system of cats. Cats have been shown to respond positively to amino acids such as proline, cysteine, ornithine, lysine, histidine, and alanine which results in sweet taste perception in humans (Bradshaw et al. 1996). On the other hand, it was confirmed that 'bitter' amino acids such as arginine, isoleucine, phenylalanine, and tryptophan were widely rejected by cats due to negatively affected receptors in the facial nerve (Oliveira et al. 2016; Zaghini and Biagi 2005). Another report also showed that cats rejected L-tryptophan, although they showed a high preference for L-lysine when given as a pure solution (White and Boudreau 1975). In contrast, Leucine which has a bitter taste in humans is a positive flavour in cats (Beauchamp et al. 1977).

6.2.5. Fat

It is a well-known fact that palatability of food increases proportionally as the fat content is increased. Therefore, increasing the fat content of a diet is a common practice in cats with anorexia. High-fat diet can help meet cats' energy requirement with higher palatability even their food consumption is lower than expected during an anorexic period, except for cats with pancreatitis (Delaney 2006). On the other hand, Kane et al. (1987) did not observe any clear palatability pattern for the low- or high-fat diet in two diet-choice trials. Dietary salmon oil also leads to higher palatability and promote food intake in cats (Filburn and Griffin 2005).

6.2.6. Sugar

In a study using electrophysiological recordings, Bartoshuk et al. (1971) showed that water was not tasteless to cats. Some authors also reported that although cats were indifferent to sucrose, with the addition of small amounts of sodium chloride to suppress the taste of water, cats were able to consume sucrose. Also, cats were reported to consume sucrose or lactose when they were offered in diluted milk (Beauchamp et al. 1977).

6.2.7. Salt and minerals

Cats were reported to be insensitive to salt similar to sugar morphologically and physiologically as opposed to ruminants and most other herbivores (Bradshaw 2006; Li et al. 2006). Therefore, they do not have the appetite for salty food that most mammals have.

Alegría-Morán et al. (2019) reported that mineral components including ash and calcium had negative effects on food preferences in cats by analysing data from a 10-year database of two-feeder food preference tests between 2007 and 2017.

6.2.8. Cellulose

Cats tend to show less preference to foods with kaolin or cellulose (Hirsch et al. 1978). Moreover, Prola et al. (2006) reported that cats fed on a diet with 6% added cellulose could eat the same amount of food compared to control diet without added cellulose; and therefore a significant decrease in energy intake reported for cellulose fed cats. In this regard, this phenomenon can be used to limit energy intake in especially obese cats. Alegría-Morán et al. (2019) indicated that dietary crude fibre could negatively affect their food preferences as a result of a significant linear regression analysis between dietary fibre and diet preference in a 10-year database food preference study.

6.2.9. Dilution of food with liquid

Cats usually do not have a high preference for dilution of their food with a non-caloric liquid (Hirsch et al. 1978; Kanarek 1975).

6.2.10. Warmth and shape of food

Cats prefer to eat dry food at room temperature and they also likely to have more tendency to prefer 'easy to grasp' foods in shape (NRC 2006).

6.2.11. Ph of food

Cats usually show higher preference for acidic (pH = 4.5–5.5) substances (Thombre 2004).

7. Flavour and palatability enhancers

Substances that increase the overall palatability of a food for cats are called 'flavour enhancers' or 'palatability enhancers' and this area of research is of considerable interest by pet food manufacturers.

The palatability of any food item for cats is strongly related to its high quality attributes such as taste, odour, shape, texture, and sensation of mouthfeel (Small and Prescott 2005). The odour perception is very important for cats and plays a key role in choosing whether to eat a food item or not. Cats will use odour to define what foods are appropriate for their need and also will help them perceive toxic substances to their body. In this regard, cats compensate for their relatively low ability to taste foods because of having low numbers of taste buds by using their much more developed olfactory system. It has previously shown that cats prefer salmon alone over cat foods mixed with fish, liver, chicken, or beef flavour (Adamec 1976). Cats can be easily attracted to a food by its odour initially, especially under the conditions when they can smell properly.

Flavour enhancers for cats usually affect food palatability in cats in two different ways. The first one, called flavours that affect 'first choice' which is the first food item tasted by cats in preference tests and these flavours mostly affect olfactory perception of cats and improve attractiveness of the food. The second one, and the most important flavour enhancers are classified as having a 'continuous choice effect' in cats when they are given the same food with the same flavour again and it reflects actual acceptance of a food item by cats in the long run (Tobie et al. 2015). In the continuous choice affect, taste, mouthfeel, texture, etc. have bigger contribution to the palatability of the specific food item with flavour than just the odour of the specific food.

Flavour enhancers in pet food are classified as natural or synthetic. Examples of natural flavours given in the US Code of Federal Regulations are the essential oil, oleoresin, essence or extractive, protein hydrolysate, distillate or any product of roasting, heating or enzymolysis. The same regulation also describes the origin of the natural flavours and they could be obtained from plant materials such as spices, fruits, leafs but also may be obtained from animal products such as meat, poultry, and seafoods. However, to be classified as flavour, their major role must be just for flavouring rather than nutritional (Thombre 2004; Yerger 2003). Flavours do not meet these criteria above are classified as synthetic flavours under the same regulation. The efficacy of these flavours depends on multiple factors including dietary and individual differences. For example, a flavour that enhancing the palatability in dry foods might not be as effective in semi-moist or canned foods. Animal proteins, amino acids, and fat are the most efficacious flavours for cats compared to the flavours of plant origin.

8. Food additives

A vast number of compounds may be incorporated into cat foods for nutritional, functional, and also for palatability purposes. Apart from palatability enhancing, food additives can also be used for purposes such as dental cleaning (eg. phosphates), giving colour to food or freshening breath of cats or even masking unpleasing odour to humans in cat diets (eg. vanilla scent). Most commonly used food additives for palatability purposes are discussed below.

8.1. Hydrolysed proteins

Hydrolysis of proteins (mostly meat) by different methods and using them dietary to improve animal performance via different mechanisms (chemical, enzymatic, or microbial) is being studied by different research groups. Disruption of protein molecules results in the production of a vast amount of freely available bioactive peptides which exert a wide range of activities affecting digestion, immune, and central nervous systems (Korhonen and Pihlanto 2006). Soy sauce is one of the earliest and good examples of protein hydrolysates to improve the palatability of foods for humans (Pasupuleti and Demain 2010). Protein hydrolysates are also called 'digest' in animal nutrition and can be in dry or liquid forms with a common dietary application rate of 1–3% as a coating (Nagodawithana et al. 2010). Protein hydrolysates are among the most popular palatability enhancers in commercial cat diets because of its high short peptide concentration and free amino acid content (Folador et al. 2006; Martı´nez-Alvarez et al. 2015). The proteins are broken apart so that the disrupted whole protein structure cannot be recognized by cats immune system and this help reduce the allergies related to these proteins in cats and therefore it is a vital part of any hypoallergenic cat food in the market currently (Cave 2006; Neklyudov et al. 2000).

8.2. Spray-dried plasma

Spray-dried animal plasma is routinely added especially in canned pet food products due to its high water holding capacity, and therefore promoting better foaming, gelling, and emulsifying properties (Rodríguez et al. 2016). Moreover, Polo et al. (2005) reported higher palatability of diets containing spray-dried plasma than diet containing wheat gluten in cat foods.

8.3. Sodium pyrophosphate

Pyrophosphates are chemical compounds that are used as a raising agent or to improve texture, and flavour of foods

(Terenteva et al. 2017). Oliveira et al. (2016) reported that the coating cat food with 0.5% sodium pyrophosphate resulted in a significant increase in food consumption.

8.4. Yeast extract products

Both dried yeast, mostly comes as a byproduct from ethanol industry, and the brewer's yeast, are used as a palatability enhancer in pet food industry worldwide. The palatability increase with the addition of yeast has been attributed to its high glutamic acid concentration which gives the umami or meaty aroma (Nagodawithana 1992). Although Swanson and Fahey (2004) reported an increase in the palatability of diet for cats with the addition of 1% yeast, the same authors also reported a decrease in palatability with the 2% yeast inclusion. In another study, cats given 0.4% yeast wall dry extract had significantly lower diet palatability compared to cats given a diet without yeast extract (Aquino et al. 2010). Thus, the optimal inclusion rate of yeast should be achieved by testing it under different conditions for cat diets.

8.5. Choline

Salt-like taste attributes have been reported for choline chloride in rats and humans. Therefore, it was recommended as a strategy to replace salt with choline to limit the level of salt consumption in humans (Locke and Fielding 1994). Although, cats are known to do not possess appetite for salt, according to Lin et al. (1997) addition of 0.3% choline chloride, which reported to have a salt-like taste in other animals, was helpful in increasing the palatability and overall food consumption of a dry cat food. However, physiological mechanism behind this relationship is not clear.

8.6. Salt

Studies also demonstrated that kittens lack the 'salt appetite' that most omnivorous animals have (Yu et al. 1997). Even sodium-depleted cats reported to show no preference for sodium solution or salted water over plain water. Therefore, cats normally do not show attraction to salty foods and this attribute makes it unsuitable as a palatability enhancer in cat diets. Thus, substantial attention needs to be given to protect cats from any sodium deficiency since they cannot select foods based on their sodium or salt content (Yu and Morris 1999).

8.7. Prebiotics

A significantly higher palatability was found in cats when given 0.6% dietary mannanoligosaccharide as a prebiotic in dry food by Aquino et al. (2010). Inulin is another type of prebiotic and can be used in cat diets (Roberfroid and Delzeene 1998). Decreased plasma ghrelin levels were achieved through dietary use of inulin type fructans in human subjects (Harrold et al. 2013). The same study also revealed that this decrease in plasma ghrelin levels resulted in a significant increase in secretion of glucagon-like peptide-1 which lead to a decrease in hunger and reduced eating highly palatable foods. However, it remains unknown whether and how dietary inulin would affect hunger and therefore food intake and palatability of foods in cats.

9. Conclusion

This review summarized the current knowledge and developments on the understanding of taste preferences, palatability, and factors affecting cats' reactions when selecting and consuming diets. Overall, studies on leptin, adiponectin, ghrelin, and cholecystokinin and how they regulate appetite are necessary for understanding the feline food intake and this might be important in everyday regulation of food palatability in cats. The use of behavioural responses of cats showing during tasting, consuming, and after consuming in combination with preference and food consumption data may be of benefit as to provide a more comprehensive and robust data on determining the palatability of foods for cats. Increasing moisture, protein, certain amino acids, and fat content of cat foods are effective and proven methods to improve palatability. However, cats are insensitive to dietary salt and sugar addition and therefore these ingredients should not be used as a way to increase the palatability of a food or diet for cats. Currently spray-dried plasma, yeast products, choline chloride, and hydrolysed proteins are the commonly used palatability enhancing food additives in cat diets by the pet food industry. Although protein hydrolysates are among the most popular palatability enhancers in the cat food industry, there is no specific bioactive peptide defined as a pure palatability enhancer in cat diets. Therefore, suggested future research directions on food palatability in cats can include developing easy and economical ways to produce specific functional molecules (esp. specific bioactive peptides for different ingredients) which will improve the acceptability of certain ingredients that are not desirable by cats. Taken together, the direction of future research should be towards the promising palatability enhancers with a clear pattern in cats.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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