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ORIGINAL ARTICLE

Impact of macronutrient composition and palatability in wet diets on food selection in cats

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Summary

Cats are obligate carnivores adapted to high-protein diets, but are commonly fed diets rich in carbohydrate. The aim of this study was to examine the food intake choices of cats when diets with different protein and carbohydrate contents were offered. Thirty-nine cats participated in voluntary dietary intake studies. Four foods were formulated to provide between 24% and 53% of metabolizable energy as protein, between 43% and 11% as carbohydrate and holding dietary fat constant with a contribution of approximately 36%. Foods were offered either singly to evaluate voluntary food intake or in pairs to compare food intake between pairs of diets. Cats regulated their macronutrient intake to attain an overall diet composition that provided 53% of metabolizable energy as protein, 11% as carbohydrate and 36% as fat. The protein contribution corresponded to approximately 6 g of protein/kg body weight/day. High-protein/low-carbohydrate diets were always eaten preferentially over low-protein/high-carbohydrate foods. When low-protein/high-carbohydrate diets were offered, cats limited their food intake to limit daily carbohydrate intake to less than 3 g of carbohydrate/kg body weight. This carbohydrate ceiling may limit protein and even energy intake when only low-protein/high-carbohydrate diets were offered. The inclusion of palatability enhancer in the diets increased food intake but did not change protein or carbohydrate intake patterns, indicating that macronutrient intake can be regulated regardless of the use of palatability enhancers in cats. We conclude that cats can discriminate between diets based on macronutrient composition and regulate their intake to maintain maximal protein intake but limit carbohydrate intake.

Keywords diet selection, domestic cat, nutrition, carbohydrate, protein, palatant

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Introduction

Pets require adequate nutrition to ensure a good health, vitality and longevity. Nutrient requirements vary considerably depending on the species, size, stage of life and physical activity. Although both dogs and cats belong to the order of Carnivora, dogs belong to the Canoidea superfamily and cats to the Feloidea superfamily (MacDonald et al., 1984). Whereas Canoids' diets vary from herbivorous (Giant panda) to omnivorous (bears and dogs), all Feloids have evolved as strict carnivores. As comprehensively reviewed by MacDonald et al. (1984), Morris (2002), Case et al. (2011) and Verbrugghe and Bakovic (2013), the evolution of cats to a strictly carnivorous diet has resulted in metabolic adaptations and particular nutritional requirements. The nutritional idiosyncrasies of cats include a high-protein requirement and a need for some nutrients of animal origin (such as taurine, arachidonic acid and vitamin A as retinol). The literature also reviews that cats are anatomically adapted to that diet as indicated by their dentition with large canines to sever the neck of their prey and their taste perception and preferences (Boudreau and White, 1978; Bradshaw, 2006). In a natural environment, wild cats consume protein-rich prey with very low carbohydrate content (1-2% of metabolizable energy provided by carbohydrate) (MacDonald et al., 1984; Eisert, 2011) to fulfil their nutritional needs.

However, domestication led to a modification of cats' way of life and feeding. Today, many domestic cats are fed with commercial dry or wet diets including palatants. Whereas no dietary requirement for carbohydrate has been recommended in cats (National Research Council, 2006), commercial cat foods contain various amounts of carbohydrate for technical

and economical reasons. Commercial feline diets contain less protein than carcasses of select birds and small mammals (mean crude protein content of 62.19% in dry basis) (Kremen et al., 2013) and carbohydrate may contribute up to 45% of the metabolizable energy of cat food formula, which is also true for dogs (Axelsson et al., 2013). As carnivores adapted to a diet based on prey, cats are not physiologically adapted to high-carbohydrate diets, as shown by the low expression of enzymes responsible for carbohydrate digestion (Morris et al., 1977; Kienzle, 1993a; Kienzle, 1993b; Zoran, 2002; De Oliveira et al., 2008). However, they are able to digest well-processed starch (Kienzle, 1993a).

Based on this assessment, it has been assumed that cats avoid carbohydrate-rich diets and prefer food with high protein content. The geometric multivariate analysis concept allows the study of the interactions between protein, fat and carbohydrate on animals' food preference (Hewson-Hughes et al., 2011, 2012, 2013). Hewson-Hughes et al. (2011) have demonstrated that cats are able to regulate their food intake to reach a target diet with a macronutrient energy composition of 52% protein, 36% fat and 12% carbohydrate. However, the effect of palatability enhancers on this selection of diets has not yet been investigated. The objective of our study was to examine cats' food selection when offered diets with various protein/carbohydrate ratios and to investigate the effect of a palatability enhancer on food selection. We hypothesize that palatability of wet diet may modify macronutrient selection in cats.

Materials and methods

Animals

All experiments were conducted with 39 adult cats maintained every as a qualified and validated palatability panel for wet and dry diets using a procedure of qualification checking repeatability and discrimination every 3 months. The centre specialized in the evaluation of petfood palatability is modelled on the real-life home environment and is committed to the well-being of pets and to the observation of the feeding behaviour. This study followed Diana Pet Food animal care guidelines. Cats were originally obtained from local welfare organizations and housed at a dedicated palatability facility. The selected kittens were in good health and tolerant towards both conspecifics and human contact. They were trained with our experimental procedures and tasted different types of food. The population of cats kept in the expert panel is representative of cat population in Europe (~80% of European cats and 20% of purebred cats; FACCO/TNS SOFRES survey, 2012) and balanced in terms of age (from 2 to 15 years) and sex. There were 15 males and 24 females, all neutered, with body weight ranging between 2.6 and 6.2 kg (Table 1). Cats were weighed every week, and weight maintenance was measured throughout the protocols. Only cats that were fed regularly on wet food were used in the experiments. Cats were housed and fed individually in purpose-built lodges (97 × 93 × 90 cm) 16 h per day (from 16:00 to 08:00) and were kept together in social groups of nine or 10 cats without food for the remaining 8 h with a free access to an enriched outdoor courtyard. They had access to drinking water at all times. The metabolizable energy requirements (kcal/d) of cats were calculated according to the National Research Council (2006) recommendations for adult cats using the formula: Energy requirement = 100 × body weight$^{0.67}$.

Diets

Eight wet diets were manufactured according to a standard process for canned cat foods at Diana, Elven, France. Diets D1, D2, D3 and D4 were formulated to have variable protein and carbohydrate contributions to the total metabolizable energy of diets while keeping fat contribution at approximately 36% (Table 2). Diets D1PE, D2PE, D3PE and D4PE had the same protein, carbohydrate and lipid contributions to total metabolizable energy as diets D1 to D4, respectively, but 1.5% by weight of a liquid palatability enhancer was added to these diets. Diets were formulated with animal products including pork liver, pork lung, chicken liver, chicken heart and chicken carcass. Wheat flour was used as the carbohydrate source. Vitamins and mineral mixes were added. The same raw materials were used for all experiments, which ensure a similar ingredient's acceptability in all formula. Diets were analysed in duplicate for their contents in protein (EU 152/2009), fat (EU 152/2009), starch (NF V18-121, 1997), ash (NF V04-404, 2001),

Table 1 Demographic table of cat panel (n = 39 cats, 15 males and 24 females)

	Mean	SD	Minimum	Maximum	Lower quartile (25th percentile)	Upper quartile (75th percentile)
Age (year)	7.8	4.1	2.0	15.0	4.0	12.0
Weight (kg)	4.5	0.9	2.6	6.2	4.1	5.4

Table 2 Analytical nutrient composition of canned diets and individual nutrient contributions to metabolizable energy (ME) of experimental diets. Values are means ± SD

	Diets without palatant				Diets with palatant			
	D1	D2	D3	D4	D1PE	D2PE	D3PE	D4PE
Dry matter g/100 g	19.0 ± 0.6	18.9 ± 0.5	19.2 ± 0.6	19.1 ± 0.6	18.9 ± 0.6	18.9 ± 0.6	18.9 ± 0.5	18.9 ± 0.6
Crude protein g/100 g	10.8 ± 0.5	8.3 ± 0.5	6.7 ± 0.3	4.4 ± 0.2	10.6 ± 0.5	8.5 ± 0.4	6.7 ± 0.4	4.5 ± 0.2
Crude fat g/100 g	3.1 ± 1	3.4 ± 1	3.1 ± 1	2.5 ± 0.9	2.9 ± 1	3.2 ± 1	2.6 ± 1	2.5 ± 1
Carbohydrate* g/100 g	2.3 ± 0.2	4.2 ± 0.2	6.0 ± 0.3	8.1 ± 0.4	2.3 ± 0.1	4.2 ± 0.2	6.2 ± 0.3	8.0 ± 0.3
Crude fibre g/100 g	Traces[†]	Traces	Traces	Traces	Traces	Traces	Traces	Traces
ME kcal/100 g	72.2 ± 3.6	72.6 ± 3.6	70.8 ± 3.5	65.0 ± 3.2	69.8 ± 3.4	71.6 ± 3.6	67.2 ± 3.3	65.0 ± 3.2
Contribution of macronutrient to ME								
Protein	53%	40%	33%	24%	53%	42%	35%	24%
Fat	36%	40%	37%	33%	35%	38%	33%	33%
Carbohydrate	11%	20%	30%	43%	12%	20%	32%	43%

*Carbohydrate is determined by difference as nitrogen-free extract.
[†]<2 g/100 g.

crude fibre (EU 152/2009) and water (NF V04-401, 2001) (Table 2). Modified Atwater coefficients of 3.5 kcal/g, 3.5 kcal/g and 8.5 kcal/g were used to calculate the respective contribution of protein, carbohydrate and fat to the metabolizable energy of diets (National Research Council, 2006).

All diets were formulated to cover the recommended allowance for adult cats at maintenance (National Research Council, 2006). Diets were formulated with raw materials and ingredients commonly used in pet food industry to be representative of the existing range of commercially available diets (Fig. 1); diets D1 and D1PE correspond to canned foods rich in animal-based raw materials whereas diets D4/D4PE correspond to the formulation of canned diets or kibbles with higher content in wheat flour. Each diet was offered to cats in excess amount so that animals had enough available food to meet their nutritional requirement in one bowl: for single-diet trials, 500 g of food/cat/d was offered (350 kcal/bowl), and for diet comparison trials, 400 g of each food/cat/d was offered in each bowl (280 kcal/bowl).

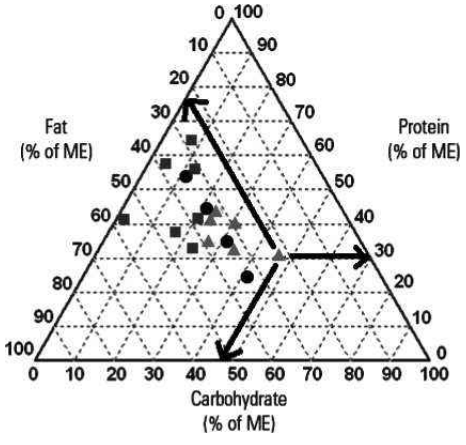

Fig. 1 Contribution of protein, carbohydrate and fat to the metabolizable energy content of diets used in this study (black circles) compared to representative dry commercial food (triangles) and wet commercial diets (squares). As an example by following arrows, macronutrients contribution to metabolizable energy of one dry commercial food is 30% from protein, 48% from carbohydrate and 22% from fat.

Voluntary food intake experiments

Single-diet trials

Two series of single-diet trials were performed to evaluate the consumption of diets D1 to D4 without palatability enhancer (first series) and of diets D1PE to D4PE containing palatability enhancers (second series). For the first series, cats were allocated to four groups of nine or 10 cats per group. For each group, the order of diet presentation was randomized using a Latin square design so that cats were cycled through four 4-days periods in which they were assigned to a single food. After this 16-days protocol, cats were proposed more classical diets for a period of 9 days in order not to get used to our diets. Then, the second series of 16 days was performed with the same cats with the same procedure as the first one for diets containing palatability enhancer. Food was available during 16 h from 16:00 to 08:00 during individual housing. Uneaten food was collected every day and weighed.

All the results in this study are expressed in g of macronutrient or kcal of metabolizable energy per kg of cat body weight per day (g/kg BW/d or kcal ME/kg BW/d) in order to be able to compare individual data

for food or nutrient intake of the 39 cats with various body weights.

Pairwise diet comparison trials

For pairwise diet comparison trials, all 39 cats were offered the same two diets provided in two stainless steel bowls at the same time. Each pair of diets was presented on two consecutive days. Any uneaten food was weighed every day at 08:00 at the end of the 16 h-feeding period to calculate the amount of each diet eaten.

Diet formulations were the same as those used for single-diet trials. Diets containing palatability enhancers (D1PE, D2PE, D3PE and D4PE) were offered to the cats in six pairs of diets so that each diet was compared with each of the other three diets.

Texture and olfactory analyses

Texture analyses were performed using a Texture Analyser TA Plus (Ametek). Samples of canned food were cut using a Warner–Bratzler shear blade set. Maximal strength, work, rigidity and deformation were recorded. A qualified human sensorial panel that knows sensorial methods and products was asked to classify each of the foods and describe their smell in Napping® methodology.

Statistical analyses

For all criteria except texture, a mixed model was used to assess the effects of treatment on nutrient intake. Diet composition, day, palatability enhancer inclusion, diet composition*day interaction, diet composition*palatability enhancer inclusion interaction and day*palatability enhancer inclusion interaction were included as fixed effects. Cat was included as a random effect. Analyses were performed with SAS version 9.2 (SAS/IBM). This model was run using SAS mixed procedure with an unstructured correlation matrix to model the within-cat errors. Parameters were estimated using restricted maximum-likelihood method with the Newton–Raphson algorithm. Denominator degrees of freedom were estimated using Satterthwaite's approximation. Differences were considered significant at $p < 0.05$.

For texture, an analysis of variance was used to assess the effects of treatment. Diet (8 modalities) was studied as fixed factor. Analyses were performed with STATGRAPHICS Centurion XVI.I using the one factor ANOVA procedure. Differences were considered significant at $p < 0.05$.

Values in figures are means ± standard errors of the mean (SEM). If the factor is significant, post hoc tests have been performed next, using least significant difference (LSD) tests.

Results

Food intake

Protein content had a significant influence on the amount of food consumed by cats ($p < 0.0001$). For single-diet trials, both with and without palatability enhancer, low-protein/high-carbohydrate diet was associated with lower food intake. As the energy density of the eight diets was similar at around 70 kcal/100 g (Table 2), a decrease of the food intake therefore corresponds to a decrease of the energy intake from an average of 40 kcal/kg BW/d (170 kJ/kg BW/d) for diet D1 to an average of 21 kcal/kg BW/d (88 kJ/kg BW/d) for diet D4 (Fig. 2). Similarly, when palatability enhancer is added to compositions, energy intake is higher for diet D1PE with 41 kcal/kg BW/d (173 kJ/kg BW/d) compared to diet D4PE with 23 kcal/kg BW/d (98 kJ/kg BW/d) (Fig. 2). Food intake was stable during the 4 days, and cats were fed each diet, so day effect was not significant, $p = 0.2$.

For each pairwise diet comparison trial with diets containing palatability enhancer, cats always preferred the diet with the higher protein/lower carbohydrate content ($p < 0.01$). The cats preferred diets in the following order ($p < 0.01$): D1PE (most preferred), D2PE, D3PE and D4PE (least preferred). In the three tests where D1PE was offered, cats regulated their food intake to attain a food intake that provided 50% of ME as protein, 14% as carbohydrate and 36% as fat (Table 3). Furthermore, the larger the difference in protein contents between two diets, the greater the contribution of the higher protein diet to food intake.

Carbohydrate intake

When the protein level of a diet decreased while its carbohydrate level increased, the carbohydrate intake approximately doubled from 1.3 ± 0.04 g carbohydrate/kg BW/d when eating diet D1 to 2.6 ± 0.1 g carbohydrate/kg BW/d for diet D3 and D4 (Fig. 3), even though the amount of food eaten decreased. Interestingly, carbohydrate intake for diets D4 and D4PE was not higher than the one for diets D3 and D3PE, respectively, despite different protein and carbohydrate contents.

Protein intake

Protein intake decreased by a factor of four as protein content of the diets offered decreased by a factor of

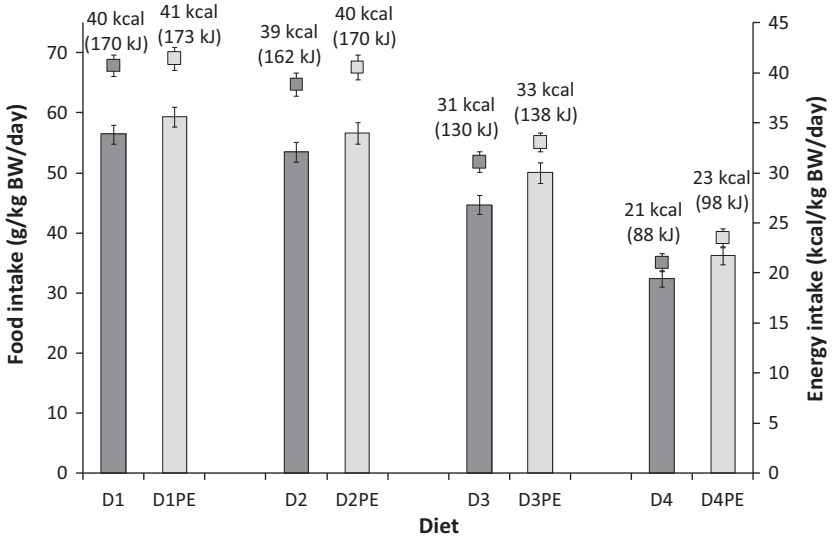

Fig. 2 Food intake (bars) and corresponding energy intake (■ squares) of diets without palatability enhancer (D1, D2, D3 and D4, dark grey) and with palatability enhancer (D1PE, D2PE, D3PE and D4PE, light grey) during single-diet trials. Values are means ± SEM, $n = 156$. Kcal = kcal of ME. Atwater coefficients of 3.5 kcal ME/g protein and carbohydrate and 8.5 kcal ME/g fat were used to calculate the contribution to metabolizable energy.

Table 3 Contribution of protein, carbohydrate and fat to energy intake during pairwise diet comparison trials. Values are means ± SEM, $n = 78$

Pairwise diet comparison trials	Total energy intake (kcal ME/kg BW)	Contribution of macronutrients to energy intake (%)			Contribution of the higher protein diet to daily protein intake (%)
		Protein	Carbohydrate	Fat	
D1PE *versus* D2PE	40.1	50 ± 2.1	14 ± 0.5	36 ± 1.4	78
D1PE *versus* D3PE	46.9	51 ± 2.1	14 ± 0.5	35 ± 1.4	92
D1PE *versus* D4PE	48.8	52 ± 1.9	13 ± 0.4	35 ± 1.2	98
D2PE *versus* D3PE	49.0	41 ± 1.4	22 ± 0.7	37 ± 1.3	88
D2PE *versus* D4PE	43.0	40 ± 1.5	23 ± 0.7	37 ± 1.4	94
D3PE *versus* D4PE	37.7	33 ± 1.2	34 ± 1.2	33 ± 1.1	90

ME, metabolizable energy; BW, body weight.

two in the single-diet trials. Protein intake decreased from 6.1 ± 0.2 g/kg BW/d to 1.4 ± 0.1 g/kg BW/d for diets D1 and D4, respectively, and from 6.3 ± 0.2 g/kg BW/d to 1.6 ± 0.1 g/kg BW/d for diets D1PE to D4PE, respectively (Fig. 4). The effect of protein content on protein intake was significant for single-diet trials both with and without palatability enhancer ($p < 0.0001$).

Palatability enhancer effect

The comparison of diets with the same nutritional value and being different only with the absence or presence of a palatant showed that the addition of this palatant significantly increased food intake ($p < 0.0001$) and energy intake ($p = 0.0006$) for all diet compositions (Fig. 2). For all diets, the addition of palatability enhancer increased caloric intake by approximately 2 cal per cat per day.

Texture analysis

Maximal strengths needed to slice wet diets were higher for high protein/low carbohydrate formula (Fig. 5). Diets D1, D2, D1PE and D2PE are hard whereas diets D3, D4, D3PE and D4PE are softer. The addition of palatability enhancer does not significantly affect the texture of wet diets.

Human olfactory sensorial analysis

Consumers' sensory perception of diets was evaluated through qualitative analysis of diets' smell. The human sensorial panel used descriptors such as liver, grilled and meat for formulas with the highest protein/lowest carbohydrate contents whereas formulas with the lowest protein/highest carbohydrate contents were described as vegetable, bread and cereals (results not shown).

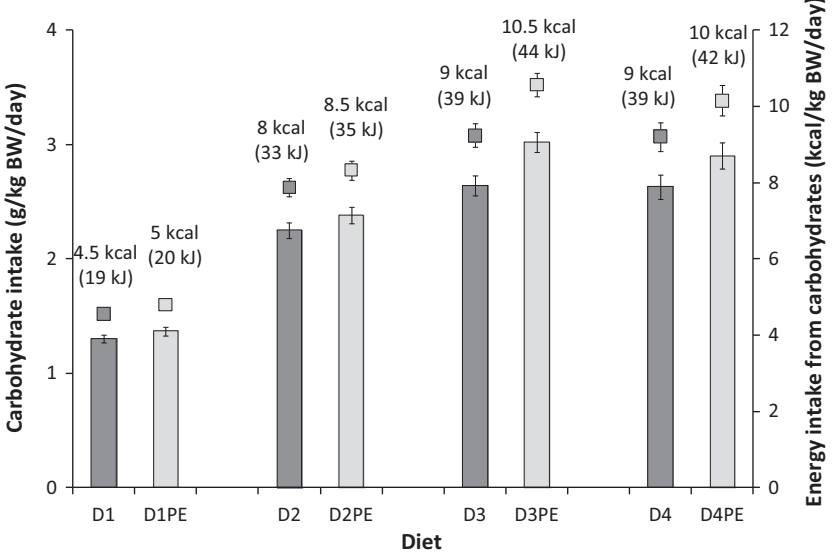

Fig. 3 Carbohydrate (bars) and corresponding energy from carbohydrate intake (■ square) of diets without palatability enhancer (D1, D2, D3 and D4, dark grey) and diets with palatability enhancer (D1PE, D2PE, D3PE and D4PE, light grey) during single-diet trials. Values are means ± SEM, $n = 156$. Kcal = kcal of ME. Atwater coefficients of 3.5 kcal ME/g protein and carbohydrate and 8.5 kcal ME/g fat were used to calculate the contribution to metabolizable energy.

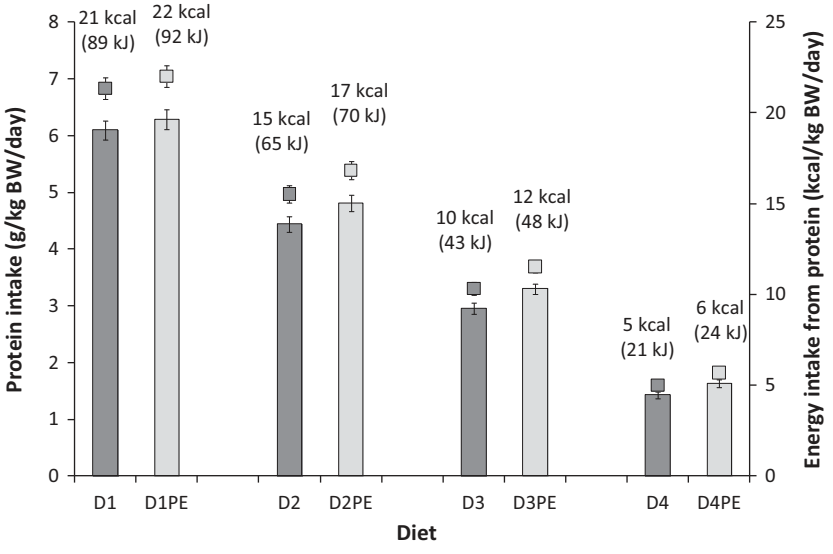

Fig. 4 Protein (bars) and corresponding energy intake (■ square) of diets without palatability enhancer (D1, D2, D3 and D4, dark grey) and diets with palatability enhancer (D1PE, D2PE, D3PE and D4PE, light grey) during single-diet trials. Values are means ± SEM, $n = 156$. Kcal = kcal of ME. Atwater coefficients of 3.5 kcal ME/g protein and carbohydrate and 8.5 kcal ME/g fat were used to calculate the contribution to metabolizable energy.

Discussion

This study builds on recent work (Hewson-Hughes et al., 2011, Hewson-Hughes et al., 2013, Laflamme and Hannah, 2013) examining the underlying factors that govern food preference in cats. Our results support the existence of daily intake targets in cats for protein of at least 50% of ME as protein or 6 g/kg BW/d. Our results are also consistent with a rule of compromise (Simpson and Raubenheimer, 1995) to limit daily carbohydrate intake to less than 3 g/kg BW. Importantly, palatability supplements, which increase food intake, do not appear to impair food selection to optimize macronutrient intake.

This study shows that cats prefer diets with high protein/low carbohydrate content, regardless of whether a palatant is added. In pairwise diet composition trials, cats selected their food to achieve a mixed diet with 51% of metabolizable energy derived from protein, 35% from fat and 14% from carbohydrate. Similarly, the preferred single diet was a diet in which protein, fat and carbohydrate contributed 53%, 36% and 11% to metabolizable energy intake. These percentages closely match previously reported intake targets of 52% of ME as protein, 36% as fat and 12% as carbohydrate (Hewson-Hughes et al., 2011 and Hewson-Hughes et al., 2013) and vary from targets reported in another study based on literature data (Plantinga et al., 2011)

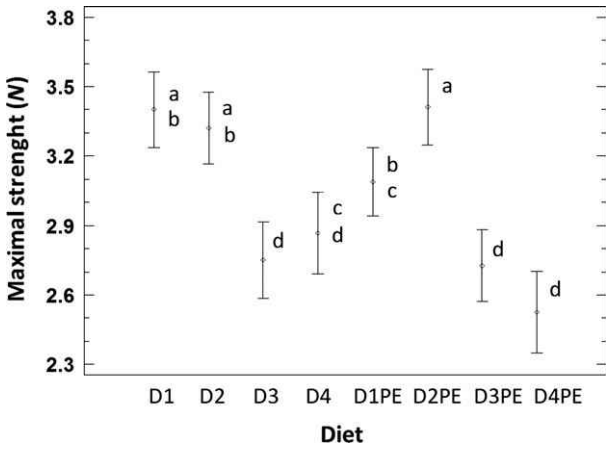

Fig. 5 Maximal strength applied to slice diets without palatability enhancer (D1, D2, D3 and D4) and diets with palatability enhancer (D1PE, D2PE, D3PE and D4PE). Values are adjusted means ± 1 SEM, $n = 10$. Letters a, b, c and d indicate statistically homogeneous groups ($p = 0.05$), texture of diets with the same letter is not significantly different.

only because the food compositions in Plantinga study precluded the possibility of 2% of ME intake as carbohydrate. Our results support the contention that this macronutrient composition approaches the ideal food chosen by cats. When this ideal food is chosen, the protein intake is close to 6 g/kg BW/d, which is consistent with Laflamme and Hannah (2013) recommendations of 5.2 g/kg BW/d as a minimum for cats to maintain their lean body mass. When offered a pair of foods that did not allow the cats to reach their intake, the food closest to the targeted protein content was chosen. Protein intake recommendations by the Association of American Feed Control Officials (AAFCO 2012) are around 3.5 g/kg BW/d. National Research Council recommends ~3 g/kg BW as a daily protein allowance and a minimal requirement of 2.5 g/kg BW (National Research Council, 2006). As previously stated by Laflamme and Hannah (2013), these recommendations are far below our results and may not cover daily protein requirements, especially if bioavailability of amino acids in commercial diets is low compared to bioavailability of amino acids-enriched model diets used to determine requirements.

The preference of cats for high-protein/low-carbohydrate diets is not surprising. Cats have particularly high-protein requirements – approximately two to three times higher than non-carnivorous mammals (MacDonald et al., 1984; Morris, 2002; Russell et al., 2002). Cats cannot decrease protein oxidation or urea cycle activity when fed a diet with less protein than their minimum requirement (Rogers et al., 1977; Green et al., 2008). Cats preferentially use amino acids for gluconeogenesis to maintain the glucose needs of their relatively large brain as reviewed in Eisert (2011). Like other carnivores including mink (Mayntz et al., 2009), feral cats (Plantinga et al., 2011) and domestic dogs (Félix et al., 2012; Hewson-Hughes et al., 2012), domestic cats can regulate their intake to a specific target.

Cats offered low-protein/high-carbohydrate foods did not increase their food intake to compensate, but rather decreased their food intake. This observation supports the existence of a carbohydrate ceiling as proposed by Hewson-Hughes et al. (2011). Alternatively, this observation might simply reflect that cats will not eat foods that differ from their metabolic needs. Cats exhibit multiple metabolic and functional traits that appear to be adaptations to a high protein intake and low carbohydrate intake. For example, cats lack of a functional sweet taste receptor (Bradshaw et al., 1996; Li et al., 2005) and salivary amylase responsible for the initiation of carbohydrate digestion (Kienzle, 1993a). Intestinal amylases, pancreatic amylases and intestinal disaccharidases have low activities in cats, which limits the digestion of carbohydrate in the small intestine even if properly cooked starch can be digested (Morris et al., 1977; Kienzle, 1993a; Kienzle, 1993b; de Oliveira et al., 2008). Whereas glycogen significantly contribute to endogeneous glucose production (Hoenig et al., 2011), Zoran (2002) reported that cats have a limited capacity to store glycogen in the liver due to very low hepatic glycogen synthetase activity. Carbohydrate intake that exceeds glycogen storage capacity is not directed to *de novo* lipogenesis in cats (Richard et al., 1989; Hewson-Hughes et al., 2011). Finally, cats are able to use gluconeogenic amino acids, fat or carbohydrate to provide energy depending on their food consumption (Zoran, 2002; Green et al., 2008; Gooding et al., 2014). To our knowledge, the mechanism whereby cats limit their carbohydrate intake is not known and requires further elucidation.

Palatability enhancers are used in most commercial diets to make foods more attractive to companion animals and to ensure consistent food intake from one manufacturing batch to the other. The inclusion of palatability enhancers in diets significantly increased the food intake and thereby carbohydrate, protein and energy intakes. Low-protein/high-carbohydrate diets probably have impaired palatability due to their high amounts of carbohydrate. This is strengthened by human olfactory sensorial analysis that showed a marked effect of protein and carbohydrate contents on the odour of diets. As obligate carnivores, cats often prefer diets with meat flavours and many amino acids or nitrogen compounds present in animal tissues

are stimuli for taste receptors in the tongue (White and Boudreau, 1975; Beauchamp et al., 1977; Boudreau and White, 1978). Such flavours are reinforced by the use of palatability enhancers, regardless of the macronutrient composition of the diet. The palatability enhancer respects carnivore's nature of cats. However, the regulation in carbohydrate intake was almost identical for diets with and without palatability enhancer; the same carbohydrate ceiling of ~3 g carbohydrate/kg BW/d was observed. We conclude that cats retain the ability to discriminate between high- and low-protein diets regardless of the presence of palatability enhancer.

One of the limitations of this study is that macronutrient composition was confounded by food texture. We chose not to adapt the quantity of texturizers in each formula but instead changed only the quantities of meat and flour. Foods with low protein/high carbohydrate content were softer than high-protein/low-carbohydrate diets. It is possible that macronutrient intake might not be the only criterion for cats' food selection and that texture might have an influence on food intake. Moisture content of diets also changed throughout the 16-h period of time for the meal. As this study is based on a comparison between diets and as we assumed that drying between offerings and collections is similar in all diets, our conclusions remain valid. Furthermore, Hewson-Hughes et al. (2013) demonstrated that cats regulate their macronutrient intake even when they are fed with diets that combine different macronutrient compositions and physical characteristics (texture and water content).

The daily carbohydrate intake ceiling in our study is lower than the ceiling observed previously : 50 kcal (210 kJ) for a 5 kg-cat compared with 72 kcal (300 kJ) (Hewson-Hughes et al., 2011). Some of this difference might be accounted for by differences in body weight or energy calculation methodology. The body weights of cats included in the Hewson-Hughes studies were not reported. The Atwater coefficients used in the studies by Hewson-Hughes et al. were those reported by Kendall et al. (1985) (Hewson-Hughes, personal communication), whereas we used modified Atwater coefficients. Energy intake was almost stable around 40 kcal/kg BW/d (170 kJ/kg BW/d) for diets D1, D2, D1PE and D2PE. This value is in accordance with published reports in low-activity, neutered cats (Laflamme, 2001; Appleton et al., 2004; Nguyen et al., 2004; Kienzle et al., 2006; National Research Council, 2006; Bermingham et al., 2010; Hewson-Hughes et al., 2013; Thes et al., 2015).

Conclusion

This study confirms that cats prefer protein over carbohydrate as the major macronutrient and select foods to maintain adequate protein intake, but limit food consumption to avoid excessive carbohydrate intake. The addition of palatants widely used in the pet food industry increases food consumption but does not compromise the ability of cats to discriminate between high-protein/low-carbohydrate and low-protein/high-carbohydrate foods. Commercial foods containing high levels of carbohydrate might not satisfy the metabolic needs of obligate carnivores cats.

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