THE DIET OF FERAL CATS: WHAT CAN WE LEARN FROM IT?

W. H. HENDRIKS

Animal Nutrition Group, Wageningen University, Wageningen and Faculty of Veterinary Medicine, Utrecht University, Utrecht, The Netherlands

Introduction

The domestic cats' wild ancestors are known to be obligatory carnivores, consuming predominantly prey. Cats were domesticated approximately 9,000-10,000 years ago in the Near East and are thought to originate from at least five distinctive subspecies of *F. silvestris* from across the Near East region, namely *F.s. silvestris*, *F.s. lybica*, *F.s. ornate*, *F.s. cafra* and *F.s. bieti* (Driscoll et al. 2007). After domestication, descendants spread across the world with human settlements, resulting in the modern-day domestic cat. A small subset of these domesticated cats has undergone intensive selection directed at specific aesthetic traits, leading to the development of so-called pedigree cats. Nowadays, 41 breeds are recognized by the Cat Fanciers' Association, including 16 "natural breeds" which are thought to be regional variants originating from domesticated *F. silvestris* subspecies. The remaining breeds were developed over the past 50 years and are simple single gene variants originating from these natural breeds (Lipinski et al. 2008).

The consumption of a diet composed of animal tissues throughout evolution has led to unique digestive and metabolic adaptations (often referred to as idiosyncrasies) (MacDonald et al. 1984; Morris, 2002; Zoran 2002) in domestic cats. Reduction of redundant enzymes and modification of enzyme activities will have had specific advantages in terms of energy expenditure increasing survival of individuals. Examples of these adaptations include: a) the high dietary protein requirement as a consequence of a limited ability to decrease the enzyme activity of amino acid catabolising enzymes below a certain threshold in response to a lowered protein intake, b) an inability for *de novo* arginine synthesis, c) a lack of taurine synthesis making this sulfonic acid an essential dietary nutrient for cats, d) unability to use carotenoids to synthesise retinol, e) an obligatory dietary requirement for cholecalciferol, f) unability to synthesize niacin from tryptophan, g) a limited ability to synthesize arachidonic acid from linoleic acid, h) adaptations in the metabolism of starch and glucose, and several other unique but general carnivorous physiological and metabolic adaptations.

Nutrient requirement determination

Several methods are available for determining the nutrient requirements of growing and adult animals. Each of these methods can be criticised and depending on the method yield different estimates of the nutrient requirements. Appreciation of the advantages and limitation of each of these methods is important in nutrition in order to optimise production, health, longevity and vitality. The dose-response method involves the administration of various doses of a nutrient to animals and the measurement of a particular response or particular responses. This method has been almost exclusively used to determine the minimum physiological requirement of nutrients by growing and adult cats and dogs (NRC (2006) and from it the allowance estimates published the NRC (2006), AAFCO (2010) and FEDIAF (2011).

Response variables often used in the determination of requirements are weight gain, nitrogen (N) balance, urinary urea excretion, plasma urea concentration, plasma amino acid concentration and amino acid oxidation, etc. The value obtained for the requirement of a nutrient in a given experiment may depend on the response variable measured as not all response variables result in the same estimate of requirement, and on the pattern of the response curve. In cases where the response curve shows no obvious maximum, the adequate dietary inclusion level of the nutrient may be difficult to determine. Response data have been examined and an arbitrary decision about an adequate dietary level of the nutrient has been made by investigators. This latter method is rather subjective and a more appropriate technique to determine the adequate dietary inclusion level of the nutrient is to fit a statistical model to the data. Statistical models used to describe response curves and determine an animal's requirement for a nutrient include the "broken line model", the "nutrient-response or Reading model" and the "saturation kinetics model".

The factorial method has also been used to derive nutrient requirement estimates for cats and dogs (Greaves 1965; Kienzle 1998). This method consists of the summation of nutrients lost in normal physiological functions such as nutrients lost directly or indirectly through metabolism in the faeces, urine, skin and other minor routes e.g. nails and sweat.

The epidemiological approach to determining nutrient requirements involves measuring the intake of a given nutrient by a population of normal healthy individuals. The assumption is made that the individuals in this population consume food according to their requirements. In growing animals, the intake of milk from the mother can serve as a basis for estimating the requirement of a particular nutrient. This method has been used extensively in humans. In adult animals, a detailed account of food intake by adult animals in the wild and of the digestibility of consumed food can be used to determine the requirement of a particular nutrient during this stage of life (Hendriks et al. 2000; Schley and Roper 2003; Cottam et al., 2006; Potter et al. 2010; Brightsmith et al. 2010).

Practical nutrient requirement recommendations

Current nutrient requirement estimates for dogs and cats for different physiological life stages (growth, maintenance and gestation/lactation) have been published by the NRC (2006), AAFCO (2010) and FEDIAF (2011). The NRC (2006), AAFCO (2010) and FEDIAF (2011) use the physiological minimum nutrient requirement estimates of the NRC (2006) to derive recommended dietary nutrient allowances using a factor in order to account for a lower nutrient bioavailability in practical/commercial diets compared to the diets that were used for the determination of the physiological minimum nutrient requirements. The many studies determining the latter requirement often used highly purified ingredients and mineral sources and as such estimates cannot be translated to practical/commercial diets using less purified ingredients and applying heat in their manufacture. The factors used by the NRC (2006), AAFCO (2010) and FEDIAF (2011) for crude protein and amino acids for adult maintenance of dogs is provided as an example in Table 1. As can be seen, the NRC (2006) estimates are corrected using a standard factor of 80% to derive recommended allowance estimates to account for an average apparent faecal crude protein digestibility of practical diets of 80% (NRC 2006). AAFCO (2010) values range from a 44 to >100% while FEDIAF values range from 44 to 84%. Interestingly, these factors to account for digestibility have not been critically reviewed or experimentally validated. In light of the often highly accurate determination of the minimum nutrient requirements, validation of the factor used to ensure adequate nutrient supply by commercial/practical diets has not been the focus of any studies. Hervera (2011), showed that the apparent faecal crude protein digestibility of 100 commercial dry dogs foods was on average 82.0 % with a range of 71.0 to 92.0%. Assuming an average apparent faecal crude protein and amino acid digestibility of 80% would already underestimate the digestibility of a number of commercially available dry dog foods. Whether this leads to a nutrient supply below the dogs requirement depends on the dietary concentration of amino acids. The number of diets which could be potentially deficient in protein and amino acids would increase if the large intestinal N metabolism in dogs is taken into account. Recently, Hendriks et. (2012) compared the difference between apparent ileal and faecal N digestibility in a number of monogastric species including adult dogs. As amino acids are predominantly absorbed in the small intestine, with large intestinal amino acid absorption not significantly contributing to overall protein metabolism, digestibility estimates determined at the end of the small intestine are more representative of the amino acids utilised by the animal. Taking into account large intestinal N metabolism, more accurate estimates of the dietary protein/amino acids absorbed in the studies of Hervera (2011) would be on average 71.5%, ranging from 49 to 92%. These simple calculations show that the factors used by NRC (2006) are yielding allowance estimates which when followed would potentially result in diets which are deficient in crude protein. However, also the estimates provided by AAFCO (2010) and FEDIAF (2011) although for crude protein being sufficient, require to be investigated. Whether the digestibility of individual dietary amino acids are similar to dietary N digestibility remains to be determined. Several studies have shown for example lysine to be less bioavailable than other amino acids due to involvement in the Maillard reaction (Williams et al 2006; Rutherfurd et al. 2007; Lankhorst et al. 2008). The recommended dietary nutrient content to meet the nutrient requirements of cats and dogs as published by the NRC (2006), AAFCO (2010) and FEDIAF (2011) should therefore be considered estimates and more validation work needs to be conducted to ensure that diets containing these concentration of nutrient do not result in deficiencies.

Table 1: Factors used by the NRC (2006), AAFCO (2004) and FEDIAF 2011) to derive recommended nutrient allowances for protein and amino acids of adult dogs from minimum nutrient requirement estimates (NRC 2006).

Nutrient	Minimum	Recommended allowance			Invers factor (x100)		
	NRC (2006)	NRC (2006)	FEDIAF (2011)	AAFCO (2010)	NRC (2006)	FEDIAF (2011)	AAFCO (2010)
Protein	8	10	18	18	80.0	44.4	44.4
Arginine	0.28	0.35	0.52	0.51	80.0	53.8	54.9
Histidine	0.15	0.19	0.23	0.18	78.9	65.2	83.3
Isoleuscine	0.3	0.38	0.46	0.37	78.9	65.2	81.1
Methionine	0.26	0.33	0.31	-	78.8	83.9	-
Met+cys	0.52	0.65	0.62	0.43	80.0	83.9	>100.0
Leucine	0.54	0.68	0.82	0.59	79.4	65.9	91.5
Lysine	0.28	0.35	0.42	0.63	80.0	66.7	44.4
Phenylalanine	0.36	0.45	0.54	0.54	80.0	66.7	66.7
Phe+tyr	0.59	0.74	0.89	0.73	79.7	66.3	80.8
Threonine	0.34	0.43	0.52	-	79.1	65.4	-
Tryptophan	0.11	0.14	0.17	0.16	78.6	64.7	68.8
Valine	0.39	0.49	0.59	0.39	79.6	66.1	100.0

Providing minimum dietary nutrient requirements for cats and dogs is not necessarily synonymous with the provision of nutrients to optimise health, longevity or vitality. In human nutrition, knowledge about the feeding strategies, food items consumed and composition of the natural diet has provided valuable insights for the formulation and selection of appropriate diets to maintain health. Paleolithic nutrition of humans has received much attention over the past decades (Eaton and Konner 1985; Eaton et al. 1997; Raitin et al. 1998; Mann 2000; Cordain et al. 2005; Eaton 2006; Frassetto et al. 2009) and has provided new information regarding the nutritional composition of the evolutionary diet of humans. Today's food consumption patterns by humans appear to go hand in hand with a shift in disease patterns. These so called "diseases of civilisation" are advocated to be caused by a discordance between the contemporary human diet and the natural diet to which evolutionary forces adapted the core metabolism and physiology over a period of millions of years (Eaton and Konner 1985; Mann 2000; Cordain et al. 2005). Frassetto et al. (2009) investigated whether a paleolithic diet confers health benefits in humans and found that even short-term consumption of a paleolithic type diet had proven health benefits for glucose metabolism and the cardiovascular system. In addition, the composition of breast milk has provided valuable information about the dietary nutrient profile to meet the nutrient requirement for optimal health and development of human infants (Raiton et al. 1998). For many captive, endangered and domesticated animal species, the study of the natural diet has yielded data to successfully improve their nutrition (Hendriks et al. 2000; Schley and Roper 2003; Cottam et al. 2006; Brightsmith et al. 2010; Potter et al. 2010).

The above-mentioned adaptations in cats are thought to have evolved from nutrition solely based on animal tissues and highlight the carnivore connection of cats. Although the latter is well recognised by many researchers (MacDonald et al. 1984; Zoran 2002; Morris 2002; NRC 2006), there is a paucity of information on the precise dietary nutrient profile responsible for these physiologic and metabolic adaptations of the domestic cat. Determining the epidemiological nutrient intake provides a nutrient profile which may be considered to be a metabolic more optimal nutrient profile, reflecting the nutrient intake to which the cats' metabolic system has adapted. The current minimum requirement estimates represent the limits of the adaptation capacity of domestic cats in relation to dietary nutrient concentrations as determination of the requirements using the dose-response approach yield maximum adaptation of metabolism to the provided dietary nutrient. Whether it may be considered "optimal" for today's nutritional goals for domesticated cats remains however to be determined. In addition, knowledge of possible non-nutritive aspects of a natural diet of whole prey for cats will provide novel ways to optimise feline diets to potentially increase health and longevity.

Epidemiologically determine nutrient intake of cats

Recently, the feeding habits of feral cats (a free-ranging representatives of the domesticated house cat) were reviewed (Plantinga et al. 2012) and a dietary nutrient profile (dry matter, crude protein, crude fat, nitrogen free extractables, ash, minerals and energy) of the diet of feral cats was derived. Fifty-five studies reporting feeding strategy data of cats in the wild were found and analysed. After specific exclusion criteria, twenty seven studies were used to derive thirty individual dietary nutrient profiles of a total of 6666 feral cats. Figure 1 shows the calculated macronutrient and mineral composition of the natural diet of free-ranging feral cats (Plantinga et al. 2012). The mean (± SEM) energy content of the natural diet was 1770 (± 13) kJ/100g DM with a dry matter content of 30.5% (± 0.4). The calculated mean macronutrient composition on a DM basis was 62.7% (± 0.30) crude protein, 22.8% (± 0.5) ether extractables, 11.8% (± 0.1) ash, and 2.8% (± 0.3) nitrogen free extract. A mean mineral content (in g/100g DM) of 2.64 (± 0.04) was found for calcium, 1.76 (± 0.03) for phosphorus, 0.50 (± 0.01) for sodium, and 0.93 (± 0.01) for potassium. The mean calcium to phosphorus ratio was 1.51 (± 0.02). The mean trace-element content (in mg/100g DM) was 130 (± 4) for magnesium, 29.6 (± 1.1) for iron, 1.67 (± 0.12) for copper, and 9.77 (± 0.19) for zinc.

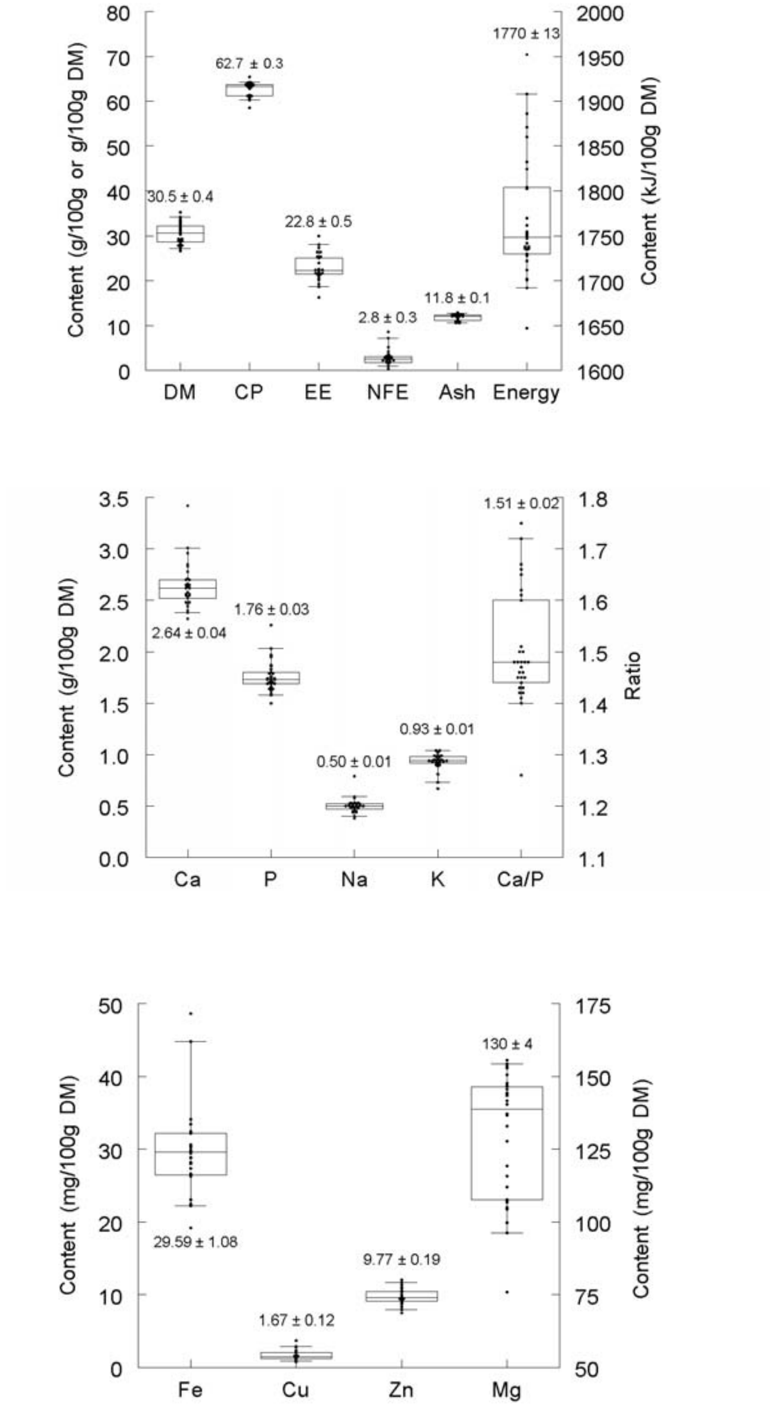

Figure 1: Calculated macronutrient and mineral composition of the natural diet of free-ranging feral cats (from Plantinga et al. 2012). DM, dry matter; CP, crude protein; EE, ethereal extract; NFE, nitrogen-free extract. Above the box-plots the calculated mean +/-

Twenty-one of the 27 studies reported small amounts of plant material being found in the scats, stomach and gut content of feral cats and ingestion is likely to have occurred incidentally while foraging for invertebrates. The NFE fraction of feral cats is likely to consist of components such as sugars, starches, mono- and disaccharides, but also water soluble vitamins. Animal tissue do not contain starch but other carbohydrates such as small amounts of glucose, glycogen, glycoproteins, glycolipid, and pentose. Some starch may have been ingested by feral cats as the digesta of prey items may contain some starch. Plantinga et al (2012) calculated that the maximum starch content of prey items consumed by feral cats would not exceed 0.2% of the bodyweight of the prey and starch intake can therefore be expected to have been very low throughout evolution. These above mentioned intake of carbohydrate sources may be the reason why domestic cats cats have retained a limited ability to digest starch/glycogen.

These results show clearly that feral cats are obligatory carnivores, with their daily energy intake from crude protein being 52%, from crude fat 46% and from N-free extract only 2%. Minerals and trace elements are consumed in relatively high concentrations compared with recommended allowances determined using empirical methods. These data are highly similar to data obtained in recent feeding studies on adult domestic cats designed to determine interactions among dietary protein, fat and carbohydrate by Hewson-Hughes et al. 2011). The latter authors reported that cats closely regulate macronutrient intake and found that the voluntary diet consumed by adult cats consists of 52% protein, 36% fat and 12% carbohydrate, results similar to the estimates of Plantinga et al. (2012). In addition, Hewson-Hughes et al. (2011) showed that cats appear to have a ceiling for carbohydrate intake limiting ingestion and constrains them to deficits in protein and fat intake on high-carbohydrate foods. These new insights into the nutrition of feral and domestic cats can have major implications for designing feeding regimens for companion animals in practise.

Table 2: Recommended composition of selected nutrients according to NRC (2006) and FEDIAF (2011) vs. assessed nutrient composition of the “natural” diet of feral cats.

Nutrient (/MJ ME)	Growth			Maintenance		Late Gestation / Peak Lactation		
	Unit	NRC (2006)	FEDIAF (2011)	NRC (2006)	FEDIAF (2011)	NRC (2006)	FEDIAF (2011)	Natural diet
Protein	g	10.5/13.5[1]	17.9	9.6/12.0	14.9	10.3/12.7	17.9	35.4
Fat	g	-/5.4	5.4	-/5.4	5.37	-/5.4	5.4	12.9
Calcium	g	0.31/0.48	0.60	0.10/0.17	0.35	0/0.65	0.60	1.5
Phosphorus	g	0.29/0.43	0.50	0.08/0.15	0.30	0.29/0.45	0.50	1.0
Potassium	g	0.16/0.24	0.36	-/0.31	0.36	-/0.31	0.36	0.53
Sodium	g	0.07/0.08	0.10	0.04/0.04	0.05	0/0.16	0.10	0.28
Magnesium	mg	9.6/23.9	31.0	12.0/23.9	23.9	24.9/29.9	31.0	73.4
Iron	mg	4.1/4.8	4.8	-/4.8	4.8	-/4.8	4.8	16.7
Copper	mg	0.26/0.50	0.60	-/0.29	0.30	-/0.53	0.60	0.9
Zinc	mg	3.0/4.4	4.49	0/4.42	4.49	2.51/3.59	4.49	5.5

MJ, megajoule; ME, metabolisable energy.

[1]Minimum nutrient requirement/nutrient allowance.

The physiological nutrient requirements (minimum and maximum) of cats for growth, maintenance and late gestation/peak lactation have been accurately determined and can be considered to represent the limits of the adaptation capacity of domestic cats in relation to dietary nutrient concentrations. Table 2 provides the minimum nutrient requirements and the recommended allowance of cats as provided by the NRC (2006) and FEDIAF (2011) expressed per units/megajoule (MJ) ME. As previously stated the recommended allowance provides the amount of a nutrient in the diets which supports a given physiological state and is based on empirically determined minimum requirement estimates to which a safety margin has been added. Both the minimum nutrient requirement and recommended allowance estimates therefore can be considered to represent the maximum or near maximum adaptation limit of cats to (semi) purified and commercially prepared diets, respectively for a specified live stage. As can be seen from Table 2, there is a large difference between the recommended nutrient allowance and the nutrients consumed by free-roaming feral cats with the exception of Zn and Cu. These data on the evolutionary diet of cats however, does not included the digestibility and bio-availability estimates of the different nutrients, making direct comparison with the recommended allowance more difficult. Estimates of macronutrient digestibility of whole prey items can be extrapolated from literature on whole prey assimilation by bobcats and ocelots. In the study with bobcats, Powers et al. (1989) evaluated the nutritive and energy value of winter diets of bobcats. Amongst others, a diet comprising of four species of rodents (mice and voles) was fed to four bobcats of wild origin. The apparent digestibility of crude protein and ether extractables was 82.0 and 92.3%, respectively. In the recent study by Bennett et al. (2010), six diets (a commercial processed diet and five species of whole prey) were fed to a total of six ocelots to evaluate nutrient digestibility. The diets had similar digestibility values, with crude protein digestibility ranging from 85 to 91%, and ether extractable digestibility ranging from 96 to 99%. The outcome of these studies make the use of modified Atwater coefficients (in which protein and fat digestibility are estimated as 79 and 90% respectively) for energy prediction of whole prey defendable but also the comparison of the recommended crude protein requirements of cats and the evolutionary crude protein intake. Data on bio-availability of micronutrients and trace-elements in felids consuming whole prey items are lacking. Further research is therefore needed to determine the precise nutrient digestibility of the evolutionary diet especially with respect to minerals such as Ca, P, Mg and Fe, which are consumed in relatively high concentrations compared to recommended allowance determined using empirical methods. It is likely that the absorption of minerals such as Ca and P is much lower in prey items compared to the forms used to supplement commercial feline diets.

Table 3: Long-chain fatty acid composition in wild or free-range animals and captive or feedlot animals.

Fatty acid (g/100g FA)	Wild/ Free-range							Captive/ Feedlot				
	Brown lemming[1]	Rabbit[2]	Hare[2]	Wood thrush[3]	Duck[4]	Bison[5]	Beef[5]	Brown lemming[1]	Hare[6]	Bison[5]	Beef[5]	Chicken[5]
	White adipose tissue n=13	Muscle + perirenal fat n=5	Muscle + perirenal fat n=5	Carcass n=21	Muscle + liver n=5	Muscle n=10	Muscle n=10	White adipose tissue n=15	Muscle n=32	Muscle n=10	Muscle n=10	Muscle n=10
14:0	0.98	1.49	3.10	NP	0.36	1.53	1.95	0.43	1.33	1.41	2.50	0.48
16:0	20.74	24.94	29.11	18.13	19.87	16.77	20.57	16.80	19.83	17.27	24.40	21.80
16:1	1.32	1.47	2.99	3.17	1.19	2.77	3.61	1.78	1.24	3.47	3.69	5.30
18:0	6.56	9.02	7.30	9.67	16.60	16.60	13.20	3.19	11.05	11.78	12.83	8.83
18:1	21.24	26.04	17.77	52.53	24.27	30.47	33.93	43.96	14.58	44.33	41.83	28.10
18:2 (n-6)	24.80	16.17	20.87	9.07	19.13	7.98	5.25	27.42	34.65	6.70	3.69	17.00
18:3 (n-3)	16.17	12.08	11.30	2.17	0.76	2.87	1.71	2.35	1.36	0.41	0.28	0.45
20:4 (n-6)	1.76	7.10	7.03	2.63	14.10	2.71	2.12	0.31	8.37	1.97	1.03	4.69
20:5 (n-3)	0.29	1.25	0.87	NP	0.48	1.17	0.85	0.04	2.13	0.39	0.17	0.18
22:5	NP	3.53	2.26	1.90	NP	NP	NP	NP	NP	NP	NP	NP
22:5 (n-6)	0.54	NP	NP	NP	NP	NP	NP	0.08	NP	NP	NP	NP
22:5 (n-3)	NP	NP	NP	NP	0.77	1.44	0.94	NP	1.33	0.53	0.34	0.31
22:6 (n-3)	0.25	NP	NP	0.70	2.24	0.23	0.11	0.02	0.27	0.20	0.05	0.26
PUFA (n-6)	27.76	23.27	27.90	11.70	33.24	10.76	7.43	28.92	43.60	8.74	4.74	21.89
PUFA (n-3)	17.08	13.33	12.17	4.77	4.25	5.68	3.61	3.00	5.09	1.53	0.84	1.19
(n-6)/(n-3)	1.63	1.25	1.67	2.45	7.82	1.92	2.10	9.63	8.57	5.79	5.85	18.50

[1]West and Coady 1974; [2]Cobos et al. 1995; [3]Conway et al. 1994; [4]Cobos et al. 2000; [5]Rule et al. 2002; [6]Vicenti et al. 2003. NP, not provided.

Other dietary properties

Plantinga et al. (2012) reported that the fatty acid composition, especially the polyunsaturated fatty acids (PUFAs) content and the n6:n3 ratio differed considerably between wild or free-ranging animals and captive or feedlot animals. Table 3 provides the unpublished data of Plantinga et al. (2012). The n6:n3 ratios in captive or feedlot animals ranges between 6:1 to 19:1 while it can be calculated that a diet based on wild animal species would contain a much lower ratio around 2:1. Domestic cats fed commercially prepared foods containing lipids from captive domestic animal species and thus will consume a different fatty acid pattern compared to feral cats. The typical n6:n3 ratio's in petfoods ranges between 5:1 to 17:1 yet from the teleological determined nutrient intake, a much lower ratio is indicated. The importance of this finding in light of the helath of cats remains to be determined.

Besides insights into the dietary nutrient intake, non-nutritive properties, like food consistency, texture, taste, temperature and behaviour may play an important role in maintaining optimal health and integrity of physiological functions. Bond and Lindberg (1990) investigated the effect of feeding whole carcasses to captive cheetahs compared to feeding a commercial diet and showed that cheetahs receiving whole carcasses fed longer, spent more time smelling their food, chewed their food more and used their molars to slice their food more often than cheetahs receiving a commercial diet. The authors concluded that feeding a more naturalistic diet may better meet a cheetahs physical, physiological and nutritional needs by taking into account such factors as diet consistency, texture, temperature, palatability and variability. In addition, feed consistency and texture have been shown to be important in maintaining a balanced microbial population in the gastro-intestinal tract in different animal species (Mikkelsen et al. 2004;Huang et al. 2006;. In addition, consumption of whole prey provides for a relatively high intake of animal derived fermentative substances, like cartilage, collagen, glycosaminoglycans, which may enhance gut health, stimulate growth of a different subset of microbial commensals, and optimise immune function in a different way compared to consuming foods which are for a large part derived from plant origin. Recently, Depauw et al. (2012) showed that components derived from animals when used as a substrates for in vitro fermentation showed a shorter time for maximal gas production rate compared to vegetable fiber and non-pure sources of glycosaminoglycans. Collagen was found to be moderately fermentable, whereas rabbit hair, skin, and bone were poorly fermentable substrates. Collagen induced an acetate production comparable to fructo-oligosaccharides and a markedly high acetate-to-propionate ratio (8.41:1) compared to other substrates (1.67:1 to 2.97:1). The study provides the first insight into the potential of animal tissues to influence large intestinal fermentation in a strict carnivore, and suggests that animal tissues have potentially similar functions as soluble or insoluble plant fibers. However, products derived from fermentation by microbiota may be different between substrates and more research is required to determine potential health benefits of animal derived fermentation substrates.

Epilogue

Similar to the study of Plantinga et al. (2012), the nutrient intake of wolves, the direct ancestor of our domesticated dogs can be determined. Although this approach is more difficult compared to feral cats due to several assumptions related to preferred organ consumption of prey, prey availability throughout the year, hierarchal structure of the wolf pack, etc, first estimates of the nutrient intake of wolves indicate a diet composed of 39.8 % dry matter, and 69.4% crude protein, 26.8% ether extractables, 6.5% ash and 0.8% nitrogen free extractables in the dry matter. Although variation in this composition is larger compared to the diet composition of feral cats due to the above-mentioned factors influencing intake, the diet is similar to those of feral cats, low in carbohydrates, high in crude protein and fat.

Acknowledgement

The author would like to acknowledge the work conducted by Drs Plantinga-Hagen (Utrecht University) and G Bosch (Wageningen University) in calculating the nutrient compositions of the diet of feral cats and wolves.

References

AAFCO (2010) Official publication of the Association of the American Feed Control Officials.

Bennett CL, Booth-Binczik SD & Steele SRE (2010) Nutritional composition and digestibility by Ocelots (*Leopardus pardalis*) of whole animals and a commercial diet. *Zoo Biol* .

Bond JC & Lindberg DG (1990) Carcass feeding of captive cheetahs (Acinonyx jubatus): the effects of a naturalistic feeding program on oral health and psychological well-being. *Appl Anim Behav Sci* **26**, 373-382.

Brightsmith DJ, McDonald D, Matsafuji D *et al.* (2010) Nutritional Content of the Diets of Free-living Scarlet Macaw Chicks in South Eastern Peru. *J Avian Med Surg* **24**, 9-23.

Cobos A, Delahoz L, Cambero MI *et al.* (1995) Chemical and Fatty-Acid Composition of Meat from Spanish Wild Rabbits and Hares. *Zeitschrift fur Lebensmittel-Untersuchung Und-Forschung* **200**, 182-185.

Conway CJ, Eddleman WR, Simpson KL (1994) Seasonal-Changes in Fatty-Acid Composition of the Wood-Thrush. *Condor* **96**, 791-794.Cordain L, Eaton SB, Sebastian A *et al.* (2005) Origins and evolution of the Western diet: health implications for the 21st century. *Am J Clin Nutr* **81**, 341-354.

Cottam Y, Merton D, Hendriks WH (2006) Nutrient composition of the diet of parent-raised Kakapo nestlings. *Notornis* **53**, 90-99.

Depauw S, Bosch, G, Hesta, M, Whitehouse-Tedd, K, Hendriks, WH, Kaandorp, J and Janssens, GPJ (2012) Fermentation of animal components in strict carnivores: a comparative study with cheetah fecal inoculum. *Journal of Animal Science* (accepted).

Driscoll CA, Menotti-Raymond M, Roca AL *et al.* (2007) The Near Eastern origin of cat domestication. *Science* **317**, 519-523.

Eaton SB & Konner M (1985) Paleolithic Nutrition - a Consideration of its Nature and Current Implications. *N Engl J Med* **312**, 283-289.

Eaton SB, Eaton SB, Konner MJ (1997) Paleolithic nutrition revisited: A twelve-year retrospective on its nature and implications. *Eur J Clin Nutr* **51**, 207-216.

Eaton SB (2006) The ancestral human diet: what was it and should it be a paradigm for contemporary nutrition? *Proc Nutr Soc* **65**, 1-6.

FEDIAF (2011) Nutritional Guideline for Complete and Complementary Pet Food for Cats and Dogs. European Pet Food Industry Federation, Brussels, Belgium.

Frassetto LA, Schloetter M, Mietus-Synder M *et al.* (2009) Metabolic and physiologic improvements from consuming a paleolithic, hunter-gatherer type diet. *Eur J Clin Nutr* **63**, 947-955.

Greaves, J. P. (1965) Protein and calorie requirements of the feline. In: Canine and Feline Nutritional Requirements. (Graham-Jones, O., editor), pp. 33-45, Pergamon Press, Oxford.

Hendriks WH, O'Conner S, Thomas DV *et al.* (2000) Nutrient composition of the crop contents of growing and adult grey-faced petrels (*Pterodroma macroptera):* A preliminary Kienzle 1998 Factorial calculation of the nutrient requirements of lactating queens. *J Nutr* 128: 2609-2614S.

Hendriks WH, van Baal J & Bosch G (2012) Ileal and faecal protein digestibility measurement in humans and other non-ruminants - a comparative species view. *Brit J Nutr* (accepted).

Hervera M (2011) Methods for predicting the energy values of dog foods. PhD Thesis, Universitat Autònoma de Barcelona, Barcelona, Spain.

Hewson-Hughes, A. K., Hewson-Hughes, V. L., Miller, A. T., Hall, S. R., Simpson, S. J. and Raubenheimer, D. (2011) Geometric analysis of macronutrient selection in the adult domestic cat, *Felis catus*. *J Exp Biol* **214**, 1039-1051.

Huang DS, Li DF, Xing JJ *et al.* (2006) Effects of feed particle size and feed form on survival of Salmonella typhimurium in the alimentary tract and cecal S. typhimurium reduction in growing broilers. *Poult Sci* **85**, 831-836.

Lankhorst, C., Tran , Q. D., Havenaar, R., Hendriks, W. H. and van der Poel, A. F. B. (2007) The effect of extrusion on the nutritional value of canine diets as assessed by key *in vitro* indicators. *Ani Feed Sci Technol* **138**, 285-297.

Lipinski MJ, Froenicke L, Baysac KC *et al.* (2008) The ascent of cat breeds: Genetic evaluations of breeds and worldwide random-bred populations. *Genomics* **91**, 12-21.

NRC (2006) Nutrient Requirement of Dogs and Cats. National Academy Press, Washington D.C.

Macdonald ML, Rogers QR, Morris JG (1984) Nutrition of the Domestic Cat, A Mammalian Carnivore. *Annu Rev Nutr* **4**, 521-562.

Morris JG (2002) Idiosyncratic nutrient requirements of cats appear to be diet-induced evolutionary adaptations. *Nutr Res Rev* **15**, 153-168.

Mann N (2000) Dietary lean red meat and human evolution. *Eur J Nutr* **39**, 71-79.

Mikkelsen LL, Naughton PJ, Hedemann MS *et al.* (2004) Effects of physical properties of feed on microbial ecology and survival of Salmonella enterica serovar Typhimurium in the pig gastrointestinal tract. *Appl Environ Microbiol* **70**, 3485-3492.

Powers JG, Mautz WW, Pekins PJ (1989) Nutrient and Energy Assimilation of Prey by Bobcats. *J Wildl Manage* **53**, 1004-1008.

Raiten DJ, Talbot JM, Waters JH (1998) Assessment of nutrient requirements for infant formulas. *J Nutr* **128**, 2059S-2293S.

Potter MA, Hendriks WH, Lentle RG *et al.* (2010) An Exploratory Analysis of the Suitability of Diets Fed to a Flightless Insectivore, the North Island Brown Kiwi (Apteryx mantelli), in New Zealand. *Zoo Biol* **29**, 537-550.

Rule DC, Broughton KS, Shellito SM *et al.* (2002) Comparison of muscle fatty acid profiles and cholesterol concentrations of bison, beef cattle, elk, and chicken. *J Anim Sci* **80**, 1202-1211.

Rutherfurd SM,,Rutherfurd-Markwick KJ & Moughan PJ (2007) Available (ileal digestible reactive) lysine in selected pet foods. J Agric Food Chem **55**, 3517-3522.

Schley L & Roper TJ (2003) Diet of wild boar Sus scrofa in Western Europe, with particular reference to consumption of agricultural crops. *Mamm Rev* **33**, 43-56.

Strohle A & Hahn A (2006) Evolutionary nutrition science and dietary recommendations of the Stone Age - the ideal answer to present-day nutritional questions or reason for criticism? Part 1: Concept, arguments and paleoanthropological findings. *Ernahrungs-Umschau* **53**, 10-16.

Vicenti A, Ragni M, di Summa A *et al.* (2003) Influence of feeds and rearing system on the productive performances and the chemical and fatty acid composition of hare meat. *Food Sci Technol Int* **9**, 279-284.

West GC & Coady JW (1974) Fatty-acid composition of tissue lipids of captive and wild brown lemmings. *Comp Biochem Physiol* **47**, 353-368.

Williams PA, Hodgkinson SM, Rutherfurd SM & Hendriks, W. H. (2006) Lysine content in canine diets can be severely heat damaged· *J Nutr* 136, 1998S-2000S.

Zoran DL (2002) The carnivore connection to nutrition in cats. *J Am Vet Med Assoc* **221**, 1559-1567.

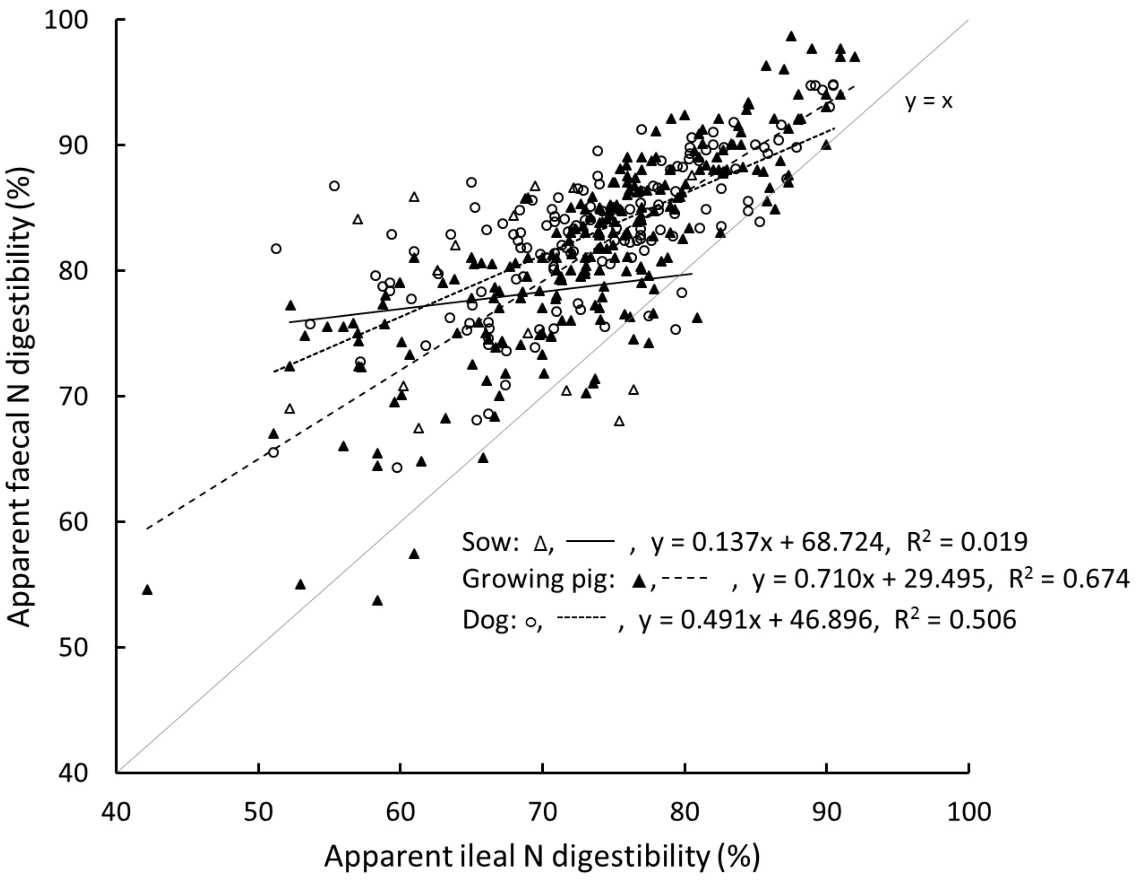

Figure 2: Ileal vs. faecal apparent N digestibility data for sows, growing pigs, and dogs with trend lines (from Hendriks et al. 2012).