Toward Optimizing Feline Nutrition: Insights from the Dietary Nutrient Profile of Feral Cats

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Abstract

A recent review of the nutrient profile of feral cats, using the rates of ingestion of various prey items, expectedly demonstrated the carnivorous nature of cats, with a high daily energy intake from protein and fat and a low intake of carbohydrate. The abbreviated nutrient profile can be considered a profile to which the cat's metabolic system has adapted. The question remains to what extent can this nutrient profile be considered optimal for today's domestic cat and to what extent can the characteristics of the natural diet be used to further optimize commercial feline foods.

Glossary of Abbreviations
CP: Crude Protein
DM: Dry Matter
EE: Ethereal Extract
GFR: Glomerular Filtration Rate
ME: Metabolizable Energy
NFE: N-Free Extract
PUFA: Polyunsaturated Fatty Acid

Introduction

The domestic cat (*F. silvestris catus*) can be considered as one of the most popular pet animals worldwide. The cat relatively recently derived from the wildcat of the Near East (*F. silvestris lybica*)[1] in a process that caused only minor alterations to the animal's morphology and behavioral repertoire.

As for nutrition, the domestic cat's wild ancestor is known to be an obligatory carnivore, consuming prey high in protein and moderate in fat and carbohydrate. This consumption pattern has led to unique metabolic idiosyncrasies that are generally accepted as the direct result of an evolutionary adaptation to a diet strictly composed of animal tissue. Of these nutritional idiosyncrasies, the cat's limited ability to decrease the activity of amino-acid catabolizing enzymes most markedly shows the cat's carnivorous nature. Other nutritional idiosyncrasies include requirements for arginine, taurine, niacin, arachidonic acid, and vitamins A and D.[2]

The carnivorous nature of the domestic cat has led to a popular trend in feline nutrition, in which a feeding strategy is adopted that more closely resembles the cat's "natural" food intake, namely feeding a diet high (>45% metabolizable energy [ME]) in animal protein and low (5-25% ME) in carbohydrate. The rationale behind this strategy is the fact that the cat's metabolism has evolved on an animal-based, high-protein diet and, as such, is physiologically and metabolically adapted to it. Besides that, feeding a high-carbohydrate content is thought by some to induce certain health disorders, such as obesity and diabetes mellitus, though data supporting a cause-and-effect relationship is lacking.

The concept of "natural" foods that may better match the physiological and metabolic makeup of cats is comparable to the paradigm that the Palaeolithic hunter-gatherer diet would better fit modern man than current human nutrition. The discordance hypothesis originally described by Eaton and Konner[3,4] states that the human genome evolved to adapt to conditions that no longer exist. The change from Palaeolithic to current nutrition may have occurred too rapidly for adequate genetic adaptation, and the resulting mismatch helps to cause some common diseases of civilization, such as diabetes mellitus, obesity and dental disease.

To what extent the discordance hypothesis may also apply for cats and to what extent the nutrient profile of the feral cat's diet is optimal for domestic cats are subjects for debate. It needs to be noted, however, that the natural nutrient profile originates from feral cats living under severe physiological and climatic conditions and in which nutrition is a precondition for species survival and procreation. In general, our domestic cats have a much more sedentary lifestyle, regular meals and a longer life span, which may have significant effects on nutrient requirements and handling.

Natural Nutrient Profile Versus Nutrient Requirements

Knowledge about the feeding strategies and features of the natural diet of a species may provide valuable insights for the formulation and selection of appropriate diets to maintain and support health. For that reason, the nutrient profile of feral cats was recently reviewed using the rates of ingestion of various prey items in the literature.[5] The main items consumed by feral cats were mammals (78%), followed by birds (16%), reptiles and amphibians (3.7%), and invertebrates (1.2%). Consumption of plant material was reported but was considered a minor component of the diet and likely to occur incidentally while foraging for

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invertebrates. There existed a large variation in types of prey items that were consumed by feral cats in different regions and climates, with a higher consumption of reptiles, amphibians and invertebrates in warmer climates. These differences clearly show that cats are opportunistic predators, thriving on a wide range of prey.

The nutrient profile that was derived from the ingested prey items expectedly showed that cats are true carnivores, with 52% of the daily energy intake being derived from protein, 46% from fat and only 2% from N-free extract (NFE). The feral cat's natural dietary nutrient profile differs in several aspects from the nutrient guidelines and characteristics of commercial feline foods. Table 1 provides the average dietary nutrient profile for feral cats (units/MJ ME), based on 27 dietary prey profiles of feral cats,[5] compared to the minimum and recommended nutrient requirement of cats during growth and maintenance as provided by the National Research Council.[6]

The physiological nutrient requirements have been accurately determined for several nutrients and can be considered to represent the limit of the adaptation capacity of domestic cats in relation to dietary nutrient concentrations. Contents of crude protein (CP), Ca, P, Zn, Fe, Cu, and Mg in the average feral cat diet are well above the minimal nutrient requirement for these nutrients, though the bioavailability of these nutrients in the natural diet is unknown. Recent studies on apparent macronutrient and energy digestibility of raw meat diets in felids have shown that CP digestibility ranges from 91 to 96.7% according to the species studied and meat sources applied.[7,8] Data concerning the bioavailability of micronutrients and trace elements in felids consuming whole prey items are lacking. However, it may be that absorption of minerals such as Ca and P are much lower in prey items compared with the forms used to supplement commercial feline diets because of the complexity of bone matrix.

The average nutrient composition of commercial high-quality dry extruded (n=252) feline foods[9] also are displayed in Table 1. The average dietary NFE content of cats fed dry commercial foods is substantially higher (17.2 g/MJ ME), and the CP and phosphorus content is substantially lower (20.0 g/MJ and 0.53 g/MJ ME, respectively) than the dietary NFE, CP and phosphorus content of the feral cat diet (1.6, 35.5 and 1.0 g/MJ ME, respectively).

Dietary NFE

The NFE content in feline commercial foods mainly originates from starch of cereal grains. These starches are cooked during processing and are, therefore, generally well-digested by cats, with apparent digestibility reaching values of above 90% for starches in dry extruded diets.[10] For feral cats, NFE intake is considered to be low, and it is not likely that they are exposed to a daily glycemic load that pet cats fed commercial foods may experience. The question remains to what extent a long-term high-carbohydrate intake could potentially lead to unwanted health effects throughout the cat's life.

Recently, Kirk[11] wrote an excellent overview regarding current literature status on carbohydrate intake and metabolism in cats. It was concluded that although the cat's metabolic adaptations suggest poor carbohydrate utilization, cats do seem able to readily digest, absorb and utilize carbohydrate up to a level of at least 6.7 g/kg BW/day, depending on the source of carbohydrate and type of processing. Cats do, however, seem to have a rate-limiting capacity to digest and utilize large amounts of simple sugars. Dietary carbohydrate intake and the relationship to disease were also thoroughly discussed. It was concluded that although an increased carbohydrate intake may lead to altered metabolic responses, the magnitude of these alterations generally falls well within the normal limits of adaptation. Although diabetic cats may benefit from feeding a high-protein and low-carbohydrate

Table 1. Approximated dietary nutrient profiles reported in literature of feral cats,[5] minimal and recommended allowances for feline growth and maintenance,[6] and average nutrient profile of commercial feline dry diets.

Item	Unit	Feral Cat[5]	National Research Council[6]				Commercial[9]
			Growth		Maintenance		Dry
			Minimum	RA	Minimum	RA	
ME	kJ/100g DM	1770					1790
CP	g/MJ ME	35.4	10.8	13.5	9.6	12.0	20.0
EE	g/MJ ME	12.9		5.4		5.4	9.1
NFE	g/MJ ME	1.6					17.2
Ca	g/MJ ME	1.5	0.31	0.48	0.10	0.17	0.60
P	g/MJ ME	1.0	0.29	0.43	0.08	0.15	0.53
Na	g/MJ ME	0.28	0.07	0.08	0.04	0.04	0.36
K	g/MJ ME	0.53	0.16	0.24		0.31	NA
Cu	mg/MJ ME	0.90	0.26	0.50		0.29	NA
Zn	mg/MJ ME	5.5	3.0	4.4		4.4	NA
Fe	mg/MJ ME	16.7	4.1	4.8		4.8	NA
Mg	mg/MJ ME	73.4	9.6	23.9	12.0	23.9	NA

RA, recommended allowance; ME, metabolizable energy; DM, dry matter; CP, crude protein, EE, ethereal extract; NFE, N-free extract.

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diet, a cause-and-effect relationship between chronic high-carbohydrate intake and development of obesity and diabetes mellitus is lacking.

Dietary Protein and Phosphorus

The natural nutrient profile contains an excess of dietary protein and phosphorus compared to the physiological minimum requirement for the domestic cat and to the CP and phosphorus content of feline dry foods (Table 1). An excess in protein and phosphorus may pose a risk for the elderly cat as a significant decline in renal function is a common finding. It is estimated that one in three cats older than 12 years of age has some form of renal insufficiency.[12] A prospective longitudinal study by Jepson et al.[13] demonstrated that 30.5% of apparently healthy and biochemically normal geriatric cats (>9 years) developed biochemical evidence of azotemia within 12 months.

Although there is no direct scientific evidence that a chronic high intake of protein and phosphorus will induce glomerular injury in cats, it can be debated that a high-protein and phosphorus intake may have some negative effects on an already impaired kidney. Ross et al.[14] in a model of induced kidney failure in cats demonstrated that a high dietary phosphorus intake (1.56% dry matter [DM]) for up to 11 months was associated with renal mineralization, fibrosis and mononuclear cell infiltration. In comparison, a low-phosphorus intake (0.42% DM) was not associated with these abnormalities. Adams et al.[15] showed that in cats with surgically reduced renal mass feeding a high-caloric, animal-based, high-protein diet (51.7% protein as is and 38% ME from protein) for up to one year resulted in significant renal morphologic injury, which was largely prevented by dietary protein and calorie restriction. However, Finco et al.[16] failed to demonstrate a protein or calorie effect in a one-year study on the progression of surgically induced renal failure in cats.

The discrepancy between these two studies was ascribed to differences in the absolute potassium, protein and fat intake and the sources of protein. Adams et al.[15] mainly used animal-based protein sources, whereas in the study of Finco et al.[16] a larger part of the protein was derived from plant-based raw materials. Animal protein is thought to alter renal hemodynamics more markedly compared to vegetable protein, which may, in part, explain the found differences.[17] Another explanation may be the fact that in the Adams study some of the cats on the high-protein diet developed hypokalemia. Dow et al.[18] demonstrated that hypokalemia was associated with a transient reduction in glomerular filtration rate (GFR) in clinically normal cats. Whether hypokalemia may also cause or enhance renal damage is not yet established.

As a large part of the feline population may suffer from an impairment in renal function as age is progressing, one could argue there is a lack of suitability of a natural dietary nutrient profile with high dietary protein (>45% ME) and phosphorus intake (>0.75 g/MJ) in support of health and longevity.

Dietary Lipids and Lipid Profile

The average content of fat (assayed as ethereal extract [EE]) of the feral cats' diet is slightly higher than the average content normally observed in commercial feline foods (Table 1). The origin of lipids in both diets, however, can be expected to be different, resulting in consumption of a different fatty acid profile. Feline foods may contain lipids from vegetable oil (e.g., soybean, sunflower, corn) and/or animal origin (e.g., pork fat, beef tallow, poultry fat, fish oil). Lipids from vegetable origin are typically higher in ω-6 polyunsaturated fatty acids (PUFAs) than ω-3 PUFAs. The PUFA profile of lipids derived from animals is significantly influenced by nutritional fatty acid intake during rearing. The ω-6:ω-3 ratios in fat tissue and muscle lipids of captive and feedlot animals ranges between 6:1 to 19:1, whereas a diet based on wild animal species contains a ratio of approximately 2:1.[5]

The vegetable and animal lipid sources commonly used in commercial foods consequently result in a higher ω-6:ω-3 ratio than that of lipids ingested when wild prey are consumed. For instance, the typical ω-6:ω-3 ratio of commercial dog foods (n=12) showed an average of 8:1, ranging from 5:1 to 17:1.[19] It is expected that feline commercial foods fall within the same range. Considering the involvement of ω-3 PUFAs in numerous physiological processes, including the mediation of inflammatory and immune responses, renal functioning, cardiovascular health, and neurologic development,[20-23] the fatty acid profiles of our feline foods deserve careful (re)consideration.

Non-Nutritive Properties of the Natural Diet

Although the suitability of the natural nutrient profile may to some respect be open for debate, the non-nutritive characteristics of the natural diet may provide valuable insights in optimizing today's feline diets. Feed consistency and texture have been shown to be important characteristics in maintaining a balanced microbial population in the gastrointestinal tract of different animal species.[24,25] Depauw et al.[26] recently researched the effect of food texture on fermentation in captive cheetahs. Both whole rabbit carcasses and beef chunks were fed to captive cheetahs for four weeks. It was demonstrated that the fermentation rate of whole rabbit carcass was much lower compared to the raw beef chunks. This was ascribed to the higher amount of indigestible and hardly fermentable materials, such as hair, in the hindgut. As a result, the formation of harmful products, such as indole and phenol, were lower, and the fecal bacterial protein content was increased when rabbit carcasses were fed.

Undigested dietary fractions provide substrate for the microbiota in the gut, and the type of substrate can be expected to differ between consumed prey items and commercial feline foods. Whole prey provide low digestible or indigestible substances like cartilage, collagens and glycosaminoglycans, with specific fermentative characteristics[27] other than fibers of vegetable origin and indigestible proteins in processed foods. Given the involvement

of the intestinal microbial community in host physiology and immune function and behavior,[28] the effect of these specific substances on the microbial composition in the feline gut and activity and on (intestinal) health warrants further investigation.

Conclusion

Although the natural diet may contain a nutrient profile to which the cat's metabolism is adapted, the question is to what extent does the natural nutrient profile optimally support health and longevity of domestic cats with a more sedentary lifestyle in a different environment. After all, the natural nutrient profile originates from feral cats living under severe physiological and climatic conditions and in which nutrition is a precondition for species' survival and procreation rather than long life.

On one hand, the nutritive characteristics of commercial foods, which differ markedly from the natural nutrient profile (a high-carbohydrate content being the most prominent), may pose physiological and metabolic challenges that cats need to cope with. On the other hand, the natural nutrient profile, with a significant excess in protein and phosphorus compared to minimal and recommended requirements, may pose a challenge for the elderly cat with impaired renal function.

Nevertheless, valuable insights may be gained by studying the natural diet of the domestic cat. Fatty-acid composition data and non-nutritive characteristics of the natural diet, for instance, may provide novel concepts for enhancing feline commercial diets in its purpose to further support health and longevity. Laboratory, clinical and epidemiological studies would be required to challenge these concepts in today's domestic cat.

References

1. Driscoll CA, Menotti-Raymond M, Roca AL, et al. The Near Eastern Origin of Cat Domestication. *Science*. 2007;317:519-523.

2. Morris JG. Idiosyncratic Nutrient Requirements of Cats Appear to be Diet-Induced Evolutionary Adaptations. *Nutr Res Rev*. 2002;15:153-168.

3. Eaton SB, Konner M. Paleolithic Nutrition: A Consideration of its Nature and Current Implications. *N Engl J Med*. 1985;312: 283-289.

4. Eaton SB, Konner M, Shostak M. Stone Agers in the Fast Lane: Chronic Degenerative Diseases in Evolutionary Perspective. *Am J Med*. 1988;84:739-749.

5. Plantinga EA, Bosch G, Hendriks WH. Estimation of the Dietary Nutrient Profile of Free-Roaming Feral Cats: Possible Implications for Nutrition of Domestic Cats. *Br J Nutr*. 2011; 106(Suppl 1):S35-S48.

6. Nutrient Requirements of Dogs and Cats. National Research Council. The National Academies Press, Washington, D.C. 2006.

7. Vester BM, Beloshapka AN, Middelbos IS, et al. Evaluation of Nutrient Digestibility and Fecal Characteristics of Exotic Felids Fed Horse- or Beef-Based Diets: Use of the Domestic Cat as a Model for Exotic Felids. *Zoo Biol*. 2010;29:432-448.

8. Kerr KR, Vester BM, Boler CL, et al. Apparent Total Tract Energy and Macronutrient Digestibility and Fecal Fermentative End-Product Concentrations of Domestic Cats Fed Extruded, Raw Beef-Based and Cooked Beef-Based diets. *J An Sci*. 2012;90:515-522.

9. Dijcker JC, Hagen-Plantinga EA, Everts H, et al. Factors Contributing to the Variation in Feline Urinary Oxalate Excretion Rate. *J An Sci*. 2014;epub (Ahead of print).

10. de-Oliveira LD, Carciofi AC, Oliveira MC, et al. Effects of Six Carbohydrate Sources on Diet Digestibility and Postprandial Glucose and Insulin Responses in Cats. *J An Sci*. 2008;86:2237-2246.

11. Kirk C. Feline Nutrition: What Is Excess Carbohydrate? Proceedings Nestlé Purina Companion Animal Nutrition Summit. 2013. Atlanta, GA.

12. Lulich JP, Osborne CA, O'Brien TD, et al. Feline Renal Failure: Questions, Answers, Questions. *Comp Cont Educ Pract Vet*. 1992;14:127-152.

13. Jepson RE, Brodbelt D, Vallance C, et al. Evaluation of Predictors of the Development of Azotemia in Cats. *J Vet Int Med*. 2009;23:806-813.

14. Ross LA, Finco DR, Crowell WA, et al. Effect of Dietary Phosphorus Restriction on the Kidneys of Cats with Reduced Renal Mass. *Am J Vet Res*. 1982;43:1023-1026.

15. Adams LG, Polzin DJ, Osborne CA, et al. Effects of Dietary Protein and Calorie Restriction in Clinically Normal Cats and in Cats with Surgically Induced Chronic Renal Failure. *Am J Vet Res*. 1993;54:1653-1662.

16. Finco DR, Brown SA, Brown CA, et al. Protein and Calorie Effects on Progression of Induced Chronic Renal Failure in Cats. *Am J Vet Res*. 1998;59:575-582.

17. Kontessis P, Jones S, Dodds R, et al. Renal, Metabolic and Hormonal Responses to Ingestion of Animal and Vegetable Proteins. *Kidney Int*. 1990;38:136-144.

18. Dow SW, Fettman MJ, Smith KR, et al. Effects of Dietary Acidification and Potassium Depletion on Acid-Base Balance, Mineral Metabolism and Renal Function in Adult Cats. *J Nutr*. 1990;120:569-578.

19. Ahlstrøm Ø, Krogdahl A, Vhile SG et al. Fatty-Acid Composition in Commercial Dog Foods. *J Nutr*. 2004;134:S2145-S2147.

20. Simopoulos AP. The Importance of the Ratio of Omega-6/Omega-3 Essential Fatty Acids. *Biomed Pharmacother*. 2002;56:365-379.

21. Bauer JE. Facilitative and Functional Fats in Diets of Cats and Dogs. *J Am Vet Med Assoc*. 2006;229:680-684.

22. Bauer JE. Responses of Dogs to Dietary Omega-3 Fatty Acids. *J Am Vet Med Assoc*. 2007;231:1657-1661.

23. Bosch G, Beerda B, Hendriks WH, et al. Impact of Nutrition on Canine Behavior: Current Status and Possible Mechanisms. *Nutr Res Rev*. 2007;20:180-194.

24. Huang DS, Li DF, Xing JJ, et al. Effects of Feed Particle Size and Feed Form on Survival of *Salmonella* Typhimurium in the Alimentary Tract and Fecal S. Typhimurium Reduction in Growing Broilers. *Poultry Sci*. 2006;85:831-836.

25. Mikkelsen LL, Naughton PJ, Hedemann MS, et al. Effects of Physical Properties of Feed on Microbial Ecology and Survival of *Salmonella Enterica* Serovar Typhimurium in the Pig Gastrointestinal Tract. *Appl Environ Microbiol*. 2004;70:3485-3492.

26. Depauw S, Hesta M, Vanhaecke L, et al. Impact of Diet Type on Fermentation Rate of Cheetahs in Captivity. Proceedings of the Sixth European Zoo Nutrition Conference. 2010. Barcelona, Spain.

27. Depauw S, Bosch G, Hesta M, et al. Fermentation of Animal Components in Strict Carnivores: A Comparative Study with Cheetah Fecal Inoculum. *J An Sci*. 2012;90:2540-2548.

28. Sekirov I, Russell SL, Caetano M Antunes L, et al. Gut Microbiota in Health and Disease. *Physiol Rev*. 2010;90:859-904.