THE CAT AND CARBOHYDRATE CONUNDRUM - WHAT HAVE WE LEARNED FROM SCIENCE AND RESEARCH?

Andrea J. Fascetti, VMD, Ph.D., DACVIM (SA), DACVN
Department of Molecular Biosciences, School of Veterinary Medicine
University of California, Davis, CA

Nitrogen, amino acids, fatty acids, vitamins and minerals are all essential nutrients for the dog and cat. However, once the concentrations of the essential nutrients are met, energy is often still required. Additional energy may come from one of three dietary macronutrients, protein, fat or carbohydrates. Protein supplied in amounts that exceed requirements will be used for energy and fat will be stored and used as energy. Carbohydrates are often included as an energy source that will spare protein to some extent. They can also help with the technological aspects of food formulation and production. However the role of carbohydrates has come under intense scrutiny in recent years, particularly in the cat, an animal considered to be a strict carnivore.

WHAT ARE DIETARY CARBOHYDRATES?

Dietary carbohydrates include low and high molecular weight sugars, starches, and various cell wall and storage non-starch polysaccharides or dietary fibers.[1,2] The National Research Council (NRC) separates carbohydrates into four functional groups based on their degree of polymerization and digestibility.[2] The four categories are absorbable (monosaccharides such as glucose and fructose), digestible (disaccharides such as lactose, sucrose, some oligosaccharides, and nonstructural polysaccharides starches), fermentable (lactose, some oligosaccharides, dietary fiber and resistant starch), and non-fermentable (certain dietary fibers). This proceeding will focus primarily on the absorbable and digestible carbohydrates, rather than the latter two categories, as these are the focus of the current controversy. However, fermentable and non-fermentable carbohydrates will be mentioned when indicated to underscore discussion of the former two.

The guaranteed analysis on the pet food label in the United States requires that the minimum concentrations for crude protein and fat, as well as maximum concentrations for moisture and crude fiber be reported.[3] The digestible carbohydrate content of the diet (nitrogen-free extract) is calculated by difference (100-crude protein + crude fat + crude fiber + moisture + ash). Given that the minimum and maximum values are not generally reflective of the actual macronutrient distribution of the diet, this calculation is an estimate at best. Furthermore, crude fiber only reflects a portion of the total dietary fiber and does not include soluble fiber; thereby compounding any calculated estimates of digestible carbohydrate, and energy content of a diet.[4,5]

DOES THE CAT HAVE A DIETARY CARBOHYDRATE REQUIREMENT?

Carbohydrate provides energy and glucose, which is metabolically essential, and can be either obtained by dietary carbohydrate or synthesized in the body from amino acids or glycerol through gluconeogenesis.[6] Glucose is an energy source for cells and a precursor for many important biological substances. The NRC does not suggest a minimal requirement (MR) or recommended allowance (RA) for this macronutrient. Nor are there any recommendations or guidelines from two major feed organizations, the Association of American Feed Control Officials and The European Pet Food Industry Federation.[3,7] Several veterinary organizations have categorized diets based on carbohydrate content. The American Animal Hospital Association (AAHA) Diabetes Management Guidelines provide medical and nutritional management recommendations that include limiting carbohydrate intake.[60] Carbohydrate concentrations in diets are defined as 'ultralow' if the diet provides less than 5% carbohydrate on a metabolizable energy (ME) basis and 'low' if the diet provides 5-25% carbohydrate on a ME basis. The American College of Veterinary Internal Medicine (ACVIM) organized a work-group several years ago to develop a consensus statement on the topic of carbohydrate intake in cats; at the time of this writing this statement is still in process. Carbohydrate content in commercial diets in the United States ranges from approximately 0% (some canned and raw diets) to 45-50% of the ME (informal market survey, Fascetti).

Cats lack salivary amylase and have lower amounts of pancreatic amylase compared to dogs.[8,9] Regardless, they can digest starch well, especially when processed and cooked.[10,11] One study reported that there is no adaptation to varying concentrations of dietary carbohydrate intake with respect to the intestinal transport of sugar to enterocytes in cats.[12] Vomiting and diarrhea has been reported in cats fed high amounts of sugar and starch,[13,14] however not all studies report similar findings.[8,15,16] These observations may be driven, in part, based on differences in the basal diets used in these studies, as different studies used plant[15] or meat-based diets.[17] However, these findings have lead some to conclude that the cat cannot cope with high concentrations of dietary carbohydrates.[18]

Cats have low glucokinase activity in their liver, an enzyme that has a low binding affinity (high Km) for glucose.[19,20] They instead have hexokinase, an enzyme that is present in multiple tissues and has a high binding affinity (low Km) for glucose. It phosphorylates glucose even at low concentrations and results in an overall slower rate of glucose utilization. Hexokinase is inhibited by glucose-6-phosphate, thereby limiting uptake of glucose in the liver. This may contribute to urinary losses of monosaccharides when consumed at high concentrations.[15] Practically this is not a problem, as simple sugars are not routinely used in commercial diets.

It has been hypothesized that these idiosyncracies in carbohydrate metabolism are the result of a teleological adaptation to eating a prey-based diet that is inherently low in carbohydrates.[21] However, cats can digest, absorb and use carbohydrates in the amounts commonly contained in commercial feline foods, particularly if they are cooked.[8,13] Cats typically consume

multiple, small meals throughout the day, a pattern that favors a reduced, but regular intake of carbohydrates and may compliment their enzyme physiology.[22]

While not providing a MR or RA due to an absence of data, the NRC does suggest safe upper limits (SUL) for several carbohydrates in cats.[2] A range of 50-150 g/kg diet (DM, dry matter) has been recommended for glucose and sucrose;[15,17] 50 mg/kg diet (DM) for lactose,[15,17] and 250 mg/kg diet for cooked corn starch.[17] There are also recommended SULs for fructooligosaccarides, 7.5 mg/kg diet (DM)[23]; cellulose, 100 mg/kg diet (DM)[24]; wheat bran, 100 mg/kg (DM)[25] and fiber blends, 80 mg/kg (DM).[24]

WHAT IS THE NATURAL DIET OF THE CAT AND WHAT DOES IT TELL US ABOUT FELINE CARBOHYDRATE INTAKE?

A recent report summarized data from 27 studies providing body composition information from a variety of species (primarily mammals and birds) consumed by feral domestic cats.[26] Most of the data came from wild-caught prey. Since this was a meta-analysis, there was tremendous variation in methodologies between the studies and how data were reported. They estimated that the average caloric distribution of the prey species was 52% protein, 46% fat and 2% carbohydrate on a metabolizable energy basis (ME). A second study, focusing on feline prey species in Northern California, reported that wild caught animals were usually leaner and had a higher mineral content.[27] This study reported the estimated average caloric distribution to be 63% protein, 25% fat and 12% carbohydrate on a ME basis. The discrepancies between these two studies likely reflect both the use of different physiological fuel values for crude fat and the leaner animals analyzed in the latter report.

These two studies have been used to underscore the findings of recent work evaluating the macronutrient preferences of the cat. Hewson-Hughes et al.[28] evaluated the preferences of cats for various combinations of different foods using the same ingredients and textures with macronutrient content as the only variable. The cats in this study chose a diet providing a caloric distribution of 52% protein, 36% fat and 12% carbohydrate on a ME basis. The authors did not report any concerns or complications with carbohydrate digestion in their study, but regardless went as far as to suggest there is a 'carbohydrate ceiling' of 70 kcal/day that a cat will not willingly exceed. This suggests that when a diet contains a high concentration of carbohydrate, cats may only have a marginal intake of energy and protein. They justify this hypothesis based on the cat's limited ability to digest and metabolize carbohydrates.

Taken together, these three studies support the idea that the natural diet of the cat is low in carbohydrates and high in protein. However, it is important to note that preference studies can be complicated by other confounding factors such as texture, ingredient choice and processing method. Furthermore, there is no evidence that feral cats live longer, healthier lives or that one macronutrient profile is optimal.

WHAT ARE THE CONSEQUENCES OF CARBOHYDRATE CONSUMPTION IN CATS CONSUMING COMMERCIAL DIETS?

There has been a trend recently amongst some veterinarians, animal professionals and pet owners to malign carbohydrates as an unhealthful food source for dogs and cats. As an obligate carnivore, much of the focus and controversy has centered on the cat. The basis for the argument is that since starch and related carbohydrates were not part of the cat's natural diet, it is unhealthy for such products to be consumed. The simultaneous increase in the use of carbohydrates in many commercial pet foods and the increasing rates of obesity and diabetes mellitus in cats is frequently cited as evidence for this theory. However, the totality of scientific evidence summarized below counters these claims.

Glucose is one of the most important secretagogues of insulin in healthy subjects. The composition and quantity of carbohydrates in foods for the management of diabetes mellitus in dogs and cats is controversial. In humans, a diet that minimizes the glycemic response is desirable because this provides better control of blood glucose and its associated complications. The term "glycemic index" refers to a ranking system for food based on its effects on blood glucose levels. In general, complex carbohydrates have a lower glycemic index (such as barley) than simple carbohydrates (such as potatoes) because they are more slowly digested and absorbed. Existing data in cats is still inconclusive regarding the effect of starch consumption on insulin and post-prandial glucose response as large variation is reported.[29] A recent study examined six different starch sources (cassava flour, brewers rice, corn, sorghum, peas or lentils) in extruded feline diets.[10] When compared to the other five starch sources, only corn stimulated an increase in the glucose response at 4 and 10 hours following a meal. Plasma insulin concentrations increased not only when the cats were fed the diet containing corn, but also those containing sorghum, peas and brewers rice. The authors concluded, that similar to previous studies[30,31], dietary starch intake has little impact on glucose and insulin response in the cat. In one of these studies, high intake of glucose (up to 40% of DM) did not result in average plasma concentrations greater than 100 mg/dL.[31] The authors base their conclusions on the cat's metabolic preference for amino acids for energy and reduced enzymatic ability to metabolize dietary starch that slow and prolong digestion and absorption.[8,13] They underscore their conclusions based on studies reporting prolonged oral or intravenous glucose elimination times in cats compared to dogs or humans.[29,30,31,32]

Additional, recent studies support these conclusions. Feeding starch concentrations at approximately 35% DM resulted in maximum glucose concentrations within the normal range several hours post food consumption.[33] In another study, both healthy obese and lean cats demonstrated little variation in blood glucose concentrations when fed a diet containing carbohydrate at 47% of the DM under normal daily conditions.[34]

Do dietary carbohydrates cause obesity?

The association between obesity in cats and the development of diabetes mellitus has been well documented.[35,36,37,38,39] Given the high prevalence of obesity in the pet feline population and the link between obesity and diabetes in the cat, focus naturally turned to what dietary factors may predispose cats to obesity.

Due in part, to epidemiologic reports, it has been proposed that 'premium', high fat dry foods may cause obesity in cats, launching the hypothesis that the high carbohydrate content of these diets may be driving weight gain.[36,40] Many have challenged that the high carbohydrate content of dry cat foods may be the cause of feline obesity based on several points. The term 'premium' has no legal definition so varying opinions on what constitutes a premium diet exist amongst researchers and nutritionists. Other macronutrient characteristics of these diets may play a role in the development of obesity and should have been considered. Furthermore, the initial studies supporting this hypothesis were retrospective in nature and did not quantify other meaningful variables such as food intake.

Epidemiological studies report that feline obesity is associated with high fat foods and not high carbohydrate foods.[36,41] In fact there are some studies that suggest that high carbohydrate, low fat diets have an obesity-protective effect.[42,43] Exchanging dietary carbohydrate for protein may be helpful for weight loss and managing diabetes in some cats[44]; however, a similar macronutrient exchange does not appear to prevent weight gain in post-ovariohysterectomized cats.[44,45]

Additional retrospective and prospective studies have emerged to challenge this initial hypothesis. In one study, colony cats were fed semi-purified diets *ad libitum* for 13 weeks before and 17 weeks following gonadectomy. Only cats consuming the highest fat dietary treatment gained weight prior to gonadectomy. All cats gained weight post-castration, but the magnitude of weight gain was positively correlated to fat inclusion in the diet.[43] Another study reported that feeding a moderate carbohydrate diet (23% ME) or a higher carbohydrate diet (51% ME), both with equal concentrations of dietary fat, resulted in weight gain when fed *ad libitum* for 8 weeks.[14] Finally, a recently published prospective survey study from New Zealand specifically tested the hypothesis that an increase in feeding energy dense, premium diets to cats was associated with a change in the prevalence of obesity in that population since it was last surveyed 15 years before.[40] Despite an increased proportion of owners feeding dry food daily since the last survey, the lack of association with dry food feeding and the absence of an increase in obesity over the study period did not support the hypothesis that energy dense dry food feeding increases the risk of feline obesity in New Zealand. Together, these results suggest that high carbohydrate diets are not associated with weight gain and obesity in cats, but that other factors (such as energy density (high fat), and feeding method) may play a more important role.

Do dietary carbohydrates cause diabetes mellitus?

Insufficient insulin secretion and impaired insulin sensitivity are the major abnormalities of feline diabetes.[44] The "Carnivore Connection" paradigm hypothesizes that these abnormalities are the result of long-term feeding of dietary carbohydrates.[46] While it is true that experimentally induced hyperglycemia is detrimental to feline beta-pancreatic cells, the same is true in omnivores.[10,47] Furthermore, the amount of carbohydrates present in commercial diets has not been shown to induce hyperglycemia.[44] Three recent population studies further refute the hypothesis that feeding dry-type extruded diets long-term are the cause of diabetes in cats.[48,49,50]

Several studies feeding carbohydrate concentrations ranging from 32-51% of the calories (ME) can raise glucose and insulin concentrations in healthy cats.[14,51,52] A recent study reported that a high carbohydrate diet (compared to high protein or fat) increased the glucose response but not the insulin response.[53] Another study reported that a high fat diet (compared to a high carbohydrate diet) resulted in reduced clearance of glucose.[54]

A recent review concludes that existing evidence does not support that carbohydrate consumption is a risk factor for developing diabetes in cats.[6]

Are dietary carbohydrates (including dietary fiber) helpful in managing diabetes mellitus in cats?

When it comes to using dietary carbohydrates to manage diabetes mellitus in cats, there are essentially two approaches; fiber-enhanced diets and low carbohydrate diets. Diets reduced in carbohydrates have received more attention recently from a clinical and research perspective, but studies suggest we should not be ignoring the former approach because the latter is receiving more press.

The amount and type of dietary fiber has been the subject of extensive investigation in the management of diabetic patients. For the purposes of this section, dietary fiber will be classified into two broad categories, insoluble and soluble fiber. Soluble fibers (pectins, gums, mucilages, FOS and some hemicelluloses) have a high water-holding capacity, delay gastric emptying, slow the rate of nutrient absorption across the intestinal surface and are highly fermentable by intestinal bacteria. Insoluble fibers (cellulose, lignin and most hemicelluloses) have less initial water-holding capacity, decrease gastrointestinal transit time and are less efficiently fermented by gastrointestinal bacteria. Fiber is proposed to promote slowed digestion and absorption of dietary carbohydrate, reducing insulin peaks after meals. Soluble fibers are also believed to form gels in aqueous solutions, thereby binding glucose and water and preventing their transfer to the absorptive surface of the intestine.

There are currently few studies evaluating the effects of dietary fiber on naturally occurring diabetes in cats.[55] Cats in this randomized cross-over study were fed either a diet containing 12% cellulose (insoluble fiber, DM) (19% of total dietary fiber) or low insoluble fiber (4.1% total dietary fiber) for 24 weeks. Mean pre-prandial glucose concentrations, most post-prandial glucose concentrations and 12-hour mean glucose concentrations were significantly lower in the cats eating the high fiber diet. The carbohydrate content was higher in the low fiber diet. The authors do not rule out the possibility that the higher corn starch content in the low fiber diet may have impacted glycemic control in the cats in this study.

A more recent study looked at the effects of a low carbohydrate/low fiber diet compared to a moderate carbohydrate/high fiber diet in cats with diabetes mellitus.[56] Sixty-eight percent of the cats consuming the low carbohydrate/low fiber diet and 41% of the cats eating the moderate carbohydrate/high fiber diet were able to discontinue insulin and reverted to a non-diabetic state during the sixteen-week trial. While these findings suggest that cats are more likely to not need insulin and have their diabetes resolve when consuming a low carbohydrate/low fiber diet perhaps it was not only the amount of carbohydrate and fiber that was responsible for this finding but also the type of digestible carbohydrate. The low carbohydrate/low fiber diet contained soybean meal and corn gluten meal whereas the moderate carbohydrate/high fiber diet contained ground corn. Corn gluten meal is a high protein product of corn with most of the soluble carbohydrates extracted and therefore will have a lower glycemic index compared to whole ground corn. Soybean meal has a low glycemic index as well. The use of carbohydrates with a lower glycemic index in the low carbohydrate/low fiber diet may have influenced the overall findings of the study.

Recent investigations into obesity and the pathogenesis of diabetes mellitus in cats have lead to the hypothesis that feline diabetics might have improved glycemic control, or in some cases even revert to a non-diabetic state when dietary carbohydrate is restricted. One study in healthy cats demonstrated that lower post-prandial glucose concentrations were measured in cats consuming 46% of their calories from protein compared to the same amount provided by fat or carbohydrates.[51] Caloric intake was not determined in these cats, nor were differences in the composition of the diets addressed.

There have been four clinical trials in diabetic cats investigating the potential benefits of feeding low carbohydrate, high protein diets. The first study only evaluated 18 cats fed a high protein diet and a hypoglycemic agent, acarbose.[57] Cats were classified as responders (insulin discontinued) and non-responders (continued to require insulin or glipizide). Eleven of eighteen cats were discontinued from insulin by the end of the 4 month study. Overall, responders lost weight during the study and non-responders had significantly less body fat than cats that did respond. Both responders and non-responders had similar decreases in serum glucose and fructosamine concentrations.

A second paper (discussed in more detail above) compared cats fed either a moderate carbohydrate/high fiber diet (Hill's feline w/d) or a low carbohydrate/low fiber diet (Hill's feline p/d) for 4 months.[56] More cats fed the low carbohydrate diet (12/13) had reduced fructosamine and glucose concentrations compared to the cats (3/9) eating the high fiber diet. However, the cats consuming the high protein, low carbohydrate diet lost weight during the study. Food intake data was not collected, so it is difficult to determine if they were not meeting their caloric requirements, or were losing weight because they were taken off insulin or their insulin dosages were reduced. As mentioned above, the use of carbohydrates with a lower glycemic index in the low carbohydrate/low fiber diet may have influenced the overall findings of the study.

The third, clinical trial examined the use of a high protein canned diet in 9 cats for 3 months (Purina D/M).[58] All of the cats were initially adapted to a high-fiber, moderate fat canned diet (Hill's w/d) for a standardization period of one month prior to the study. The cats remained stable on the high protein canned diet and most owners thought their cats were slightly more active. In 3 cats, insulin was discontinued all together, although serum fructosamine concentrations increased in these cats. There was no diet effect on serum glucose concentrations. There were a small number of cats in this study, and it was unknown what type of diabetes the cats had. Furthermore, the study was conducted for only 3 months, with no follow up on the cats.

A fourth study found no difference in improvement rates between the groups of cats fed lower carbohydrate diets and those fed maintenance diets.[59] It is interesting to note that this study also reported a median body weight gain in both diet groups.

It is difficult to discern from the above research what nutrient modifications are having a positive impact. Most published studies are testing products, not particular nutrients. There appears to be some clear evidence that supplementation with insoluble fiber helps to reduce the glycemic response and assists in managing diabetic cats. However is this effect from the fiber or the caloric dilution that occurs secondary to the addition of the fiber? Alternatively, could it be related to the amount of soluble carbohydrate in the diet?

The results of carbohydrate restriction or protein augmentation are less clear. With respect to the research in cats, the amount of protein fed in some of the studies is no higher than many other diets on the market. In the studies reported here, the carbohydrate concentration in the test diets ranges from 5-12% ME. However, no dose-response studies on increasing carbohydrates in cats with diabetes exist.

One additional challenge is that dietary fiber is not reported in many of studies looking at carbohydrate restriction, or only reported as crude fiber, not total dietary fiber. Depending upon the diet, crude fiber may only be a small representation of total dietary fiber content.[4] An in press publication looking at dietary fiber content of feline diets used for managing obesity and diabetes mellitus looked for a correlation between low carbohydrate diets and fiber content.[5] Defining diets as "low-carbohydrate" using either company marketing or American Animal Hospital Association (AAHA) guidelines resulted in no differences in any fiber type or proportion between groups using AAHA guidelines, and only limited differences based on marketing categorization, despite a wide range of fiber concentrations among individual diets. It is often assumed that fiber and carbohydrate are bound variables; however, the results from this study indicate these are not entirely dependent factors.

One finding that does recur throughout the studies is that overweight or obese diabetic patients that lose weight develop better control, or in some cases revert to a non-diabetic state. This finding suggests that in obese or overweight cats, weight loss to achieve an ideal body condition may be the most effective modification toward achieving better glycemic control or in cats reverting to a non-diabetic state.

SUMMARY

Carbohydrate provides energy and glucose, which is metabolically essential, and can be either obtained by dietary carbohydrate or synthesized in the body from amino acids or glycerol through gluconeogenesis.

Currently there is no NRC minimal requirement (MR) or recommended allowance (RA) for carbohydrates in cats, although the NRC does suggest safe upper limits (SUL) for a few specific digestible carbohydrates and fiber. The NRC specifically mentions that more research is needed in this area.

Cats lack salivary amylase and have lower amounts of pancreatic amylase compared to dogs, but they can digest starch well, especially when processed and cooked. Cats have low glucokinase activity in their liver; they instead have hexokinase. This enzyme phosphorylates glucose at a slower rate, limiting glucose uptake by the liver.

Several studies support that the natural diet of the cat is high in protein and low in carbohydrate. However there is no evidence that this feeding approach supports a longer healthier life.

Research studies support the maintenance of blood glucose concentrations within the normal range in healthy cats consuming diets containing approximately 40% DM as carbohydrate.

Research studies support that diets containing high dietary fat, not high carbohydrates, are associated with weight gain and the development of obesity in the cat. Current studies also do not support the hypothesis that carbohydrate consumption is a risk factor for the development of diabetes.

When nutritionally managing diabetic cats there are essentially two approaches; fiber-enhanced diets and low carbohydrate diets. Research supports that both diets can be successful in managing diabetic patients. More compelling is the finding that overweight or obese diabetic cats that lose weight develop better control or revert to a non-diabetic state. In this author's opinion, weight loss is most important in controlling or reverting diabetic patients and either diet type can be used to achieve that goal.

REFERENCES

1. Bach-Knudsen KE. Carbohydrate and lignin contents of plant materials used in animal feeding. Anim Feed Sci Technol 1997;67:319-338.
2. National Research Council. Nutrient Requirements of Dogs and Cats. Washington DC: The National Academies Press; 2006.
3. AAFCO. Official Publication. Oxford (IN): Association of American Feed Control Officials; 2008.
4. Farcas AK, Larsen JA, Fascetti AJ. Evaluation of fiber concentration in dry and canned commercial diets formulated for adult maintenance or all life stages of dogs by use of crude fiber and total dietary fiber methods. J Am Vet Med Assoc 2013; 242: 936-940.
5. Owens TJ, Larsen JL, Farcas AK et al. Total Dietary Fiber Composition of Feline Diets for Obesity and Diabetes Mellitus. J Am Vet Med Assoc 2014;245:1413-1422 .
6. Verbrugghe A, Hesta M, Daminet S, et al. Nutritional modulation of insulin resistance in the true carnivorous cat: a review. Crit Rev Food Sci Nutr 2012;52:172–82.
7. FEDIAF The European Pet Food Industry Federation. Guidelines for Complete and Complementary Pet Foods for Cats and Dogs. 2013.
8. Morris JG, Trudell J, Pencovic T. Carbohydrate digestion by domestic cat (Felis Catus). Br J Nutr 1977;37:365–73.
9. McGeachin RL, Akin JR. Amylase levels in the tissues and body fluids of the domestic cat (Felis catus). Comp Biochem Physiol B 1979;63:437–9.
10. de-Oliveira LD, Carciofi AC, Oliveira MCC et al. (2008) Effects of six carbohydrate sources on diet digestibility and post-prandial glucose and insulin responses in cats. Journal of Animal Science 2008;86:2237–2246.
11. Kienzle E. Carbohydrate metabolism of the cat 1. Activity of amylase in the gastrointestinal tract of the cat. J Anim Physiol Anim Nutr 1993a;69:92–101.
12. Buddington RK, Chen JW, Diamond JM. Dietary regulation of intestinal brush-border sugar and amino acid transport in carnivores. Am J Physiol 1991;261:R793–801.
13. Kienzle E. Carbohydrate metabolism of the cat 2. Digestion of the starch. J Anim Physiol Anim Nutr 1993;69:102–14.
14. Coradini M, Rand JS, Morton JM, Rawlings JM. Effects of two commercially available feline diets on glucose and insulin concentrations, insulin sensitivity and energetic efficiency of weight gain. Br. J. Nutr. 2011;106 Suppl :S64–77.
15. Drochner W and Muller-Schlosser S. Digestibility and tolerance of various sugars in cats. In: Nutrition of the Dog and Cat. Ed. RS Anderson, 1980: 101-111: London, Pergamon Press.
16. Green AS, Ramsey JJ, Villaverde C, et al. cats are able to adapt protein oxidation to protein intake provided their requirement for dietary protein Is met. J Nutr 2008;138: 1053–60.
17. Meyer H and Kienzle E. Dietary protein and carbohydrates: Relationship to clinical disease. 1991: In Proc. Purina Int. Symposium, Orlando, FL.
18. Legrand-Defretin V. Differences between cats and dogs: A nutritional view. Proc Nutr Soc 1994;53:15-24.
19. Hiskett EK, Suwitheechon O-U, Lindbloom-Hawley S, et al. Lack of glucokinase regulatory protein expression may contribute to low glucokinase activity in feline liver. Vet Res Commun 2009;33:227–40.
20. Tanaka A, Inoue A, Takeguchi et al. Comparison of expression of glucokinase gene and activities of enzymes related to glucose metabolism in livers between dog and cat. Vet Res Commun 2005;29:477–85.
21. Morris JG. Idiosyncratic nutrient requirements of cats appear to be diet induced evolutionary adaptations. Nutr Res Rev 2002;15:153–68.

22. Kane E, Rogers Q, Morris J. Feeding behavior of the cat fed laboratory and commercial diets. Nutr Res 1981;1:499-507.
23. Sparkes AH, Papasoulitotis K, Sunvold G et al. Bacterial flora in the duodenum of healthy cats, and effects of dietary supplementation with fructooligosaccharides. Am J Vet Res 1998; 59: 431-435.
24. Sunvold, GD, Fahey GC, Merchen NR et al. Dietary fiber for cats: In vitro fertilization of selected fiber sources b cat fecal inoculum and in vivo digestion and metabolism of fiber-supplemented diets. J Anim Sci 1995;73:1099-1109.
25. Kienzle E, Meyer H, Schneider N. Investigation on palatability, digestibility, and tolerance of low digestible food components in cats. J Nutr 1991;121:S56-57
26. 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:S35–48.
27. Kremen NA, Calvert CC, Larsen JA, et al. Body composition and amino acid concentrations of select birds and mammals consumed by cats in northern and central California. J Anim Sci 2013;91:1270–6.
28. Hewson-Hughes AK, Hewson-Hughes VL, Miller AT, et al. Geometric analysis of macronutrient selection in the adult domestic cat, Felis catus. J Exp Biol 2011a;214:1039–51.
29. Appleton DJ, Rand JS, Priest J et al. Dietary carbohydrate source affects glucose concentrations, insulin secretion and food intake in overweight cats. Nutr Res 2004;24:447-467.
30. Bouchard GF and Sunvold GD. Effect of dietary carbohydrate source on postprandial plasma glucose and insulin concentration in cats. In Reinhart GA, Carey DP, eds. Recent Advances in canine and feline nutrition. Proceedings from the Iams Nutrition Symposium, 2000, pages 91-101.
31. Kienzle E. Blood sugar levels and renal sugar excretion after the intake of high carbohydrate diets in cats. J Nutr 1994;124(12 Suppl):2563S-2567S.
32. Farrow HA, Rand JS, Morton JM et al. Postprandial glycaemia in cats fed a moderate carbohydrate meal persists for a median of 12 hours – female cats have a higher peak glucose concentrations. J Feline Med Surg 2012: 14(10)706-715.
33. Hewson-Hughes AK, Gilham MS, Upton S et al. The effect of dietary starch level on postprandial glucose and insulin concentrations in cats and dogs. Br J Nutr 2011;106:S105-S109.
34. Hoenig M, Pach N, Thomaseth K et al. Evaluation of long-term glucose homeostasis in lean and obese cats using continuous glucose monitoring. Am J Vet Res 2012:73:1100-1106.
35. Rand JS, Fleeman LM, Farrow HA, et al. Canine and feline diabetes mellitus: nature or nurture? J of Nutr 2004;134;(8 Suppl):2072S-2080S.
36. Lund EM, Armstrong PJ, Kirk CA et al. Prevalence and risk factors for obesity in adult cats from private US veterinary practices. Int J App Vet Med Res 2005;3:88-96.
37. Prahl A, Guptill L, Glickman NW, et al. Time trends and risk factors for diabetes mellitus in cats presented to veterinary teaching hospitals. J Fel Med Surg 2007;9(5):351-8.
38. Laflamme DP. Letter to the editor: Cats and Carbohydrates. Topics Comp An Med 2008;23(4):159-60.
39. Laflamme DP. Cats and Carbohydrates: Implications for health and disease. Compendium for Continuing Education for Veterinarians. Jan 2010:E1-E3.
40. Cave NJ, Allan FJ, Schokkenbroek SL, Metekohy C a M, Pfeiffer DU. A cross-sectional study to compare changes in the prevalence and risk factors for feline obesity between 1993 and 2007 in New Zealand. Prev. Vet. Med. 2012;107(1-2):121–33.
41. Scarlett JM, and Donoghue S. Association between body condition and disease in cats. J Am Vet Med Assoc 1998;212:1725-1731.
42. Michel, K.E., Bader, A., Shofer, F.S., Barbera, C., Oakley, D.A., Giger, U. Impact of time-limited feeding and dietary carbohydrate content on weight loss in group-housed cats. J Fel Med Surg. 2005;7(6):349-55.
43. Backus RC, Cave NJ, Ganjam VK, et al. (2007b) Age and body weight variations in plasma glucose and insulin responses to intravenous glucose and insulin in colony cats maintained since weaning on high or low carbohydrate diets. ACVIM Forum Proceedings (abstract), Seattle, Washington, June 6-9, 2007.
44. Backus RC. Controversy over carbohydrate in diets for cats. ACVIM Forum Proceedings (abstract), Montreal, Canada, June 3-6, 2009.
45. Vester BM, Sutter SM, Keel TL, et al. Ovariohysterectomy alters body composition and adipose and skeletal muscle gene expression in cats fed a high-protein or moderate-protein diet. Animal 2009;3:1287–98.
46. Miller J, and Colaquiri S. The carnivore connection: dietary carbohydrate in the evolution of NIDDM. Diabetologica 1994;37:1280-1286.
47. Zini E, Osto M, Franchini M, et al. Hyperglycaemia but not hyperlipidaemia causes beta cell dysfunction and beta cell loss in the domestic cat. Diabetologica 2009;52(2):336-46.
48. Backus RC, Cave NJ, Keisler DH. Gonadectomy and high dietary fat but not high dietary carbohydrate induce gains in body weight and fat of domestic cats. British Journal of Nutrition 2007(a);98(3):641-50.
49. McCann TM, Simpson KE, Shaw DJ et al. Feline diabetes mellitus in the UK: the prevalence within an insured cat population and a questionnaire-based putative risk factor analysis. J Fel Med Surg 2007;9:289-299.
50. Slingerland LI, Fazilova VV, Plantinga EA, Kooistra HS, Beynen AC. Indoor confinement and physical inactivity rather than the proportion of dry food are risk factors in the development of feline type 2 diabetes mellitus. Vet J 2009;179(2):247-53.
51. Farrow HA, Rand JS, Morton JM, O'Leary CA, Sunvold GD. The effect of dietary carbohydrate, fat and protein on postprandial glycemia and energy intake in cats. J Vet Int Med 2013;27: 1121-1135.
52. Thiess S, Becskei C, Tomsa K, Lutz T, Wanner M. Effects of high carbohydrate and high fat diets on plasma mean glucose tolerance test in intact and neutered male cats. J Fel Med Surg 2004; 6(4): 207-218.
53. Deng P, Ridge TK, Graves TK, et al. Effects of dietary macronutrient composition and feeding frequency on fasting and postprandial hormone response in domestic cats. J Nutr Sci 2013;2:e36.
54. Hoenig M, Jordan ET, Glushka J, et al. Effect of macronutrients , age , and obesity on 6- and 24-h postprandial glucose metabolism in cats. Am J Physiol Regul Integr Comp Physiol 2011;301:R1798-807.
55. Nelson RW, Scott-Moncrieff C, Feldman EC et al. Effect of dietary insoluble fiber on control of glycemia in cats with naturally acquired diabetes mellitus. J Am Vet Med Assoc 2000;216:1082-1088.

56. Bennett N, Greco DS, Peterson ME, Kirk C, Mathes M, Fettman MJ. Comparison of a low carbohydrate-low fiber diet and a moderate carbohydrate-high fiber diet in the management of cats with diabetes mellitus. J Fel Med Surg 2006;8(2): 73-84.
57. Mazzaferro EM, Greco DS, Turner SJ, Fettman MJ. Treatment of feline diabetes mellitus using an α-glucosidase inhibitor and a low-carbohydrate diet. J Fel Med Surg 2003; 5:183-189.
58. Frank G, Anderson W, Pazak H et al. Use of a high-protein diet in the management of feline diabetes mellitus. Vet Therap 2001;2:238-246.
59. Hall TD, Mahony O, Rozanski EA, et al. Effects of diet on glucose control in cats with
diabetes mellitus treated with twice daily insulin glargine. J Feline Med Surg 2009;11(2):125-130.
60. Rucinsky R, Cook A, Haley S, et al. AAHA Diabetes Management Guidelines for Dogs and Cats. J Am Anim Hosp Assoc 2010; 46: 215-224.