The omnivorous dog dogma and carnivorous cat connection

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Introduction: Classification of animal species is commonly based on the diet they consume in nature. For domestic dogs and cats, however, classification has relied heavily on their (different) morphological, physiological and metabolic traits. Classification of dogs is even more challenging as dogs have been purposely bred by humans for many centuries starting with domestication of wolves (Driscoll et al., 2009; Coppinger and Coppinger, 2001). Domestic cats, however, still closely resemble their wild relatives as breeding between domestic and wild cats still yields viable offspring (Pierpaoli et al., 2003). Over the past decades, the realisation of the carnivorous nature of cats has been well-recognised. Many of the previously termed "metabolic idiosyncraties" are in fact normal metabolic adaptations similar to other carnivore species which cats have developed over evolution to deal with their specific food niche. Dogs on the other hand have lost this carnivorous connection in authoritive books (NRC, 2006; Hand et al., 2010) largely due to the lack of finding similar metabolic adaptations as seen in cats, as well as similarities of the dogs' metabolism to that of pigs, rats and humans. Aided by the use of the dog as a model for human physiology, metabolism and nutrition, this "omnivorous dog dogma" has found its way into these authoritative scientific reference books, nutritional concepts in pet nutrition and as a general view. The present contribution discusses some evolutionary aspects of the carnivore connection of cats and provides an explanation for the omnivorous-like metabolism of dogs by examining the diet and life-style of the dog's direct ancestor, the gray wolf (*Canis lupus*).

Carnivorous cat connection: There are a number of seminal papers (e.g. MacDonald et al., 1984; Morris, 2002; Zoran, 2002) where specific examples of the metabolic adaptations of cats to their carnivorous diet are discussed. Typical examples of these adaptations include a high dietary protein requirement, an inability for *de novo* arginine, taurine, retinol, cholecalciferol and niacin synthesis, a limited ability to synthesize arachidonic acid from linoleic acid, and adaptations in the metabolism of starch and glucose, including a lack of salivary amylase activity, low activity of pancreatic and intestinal amylases, low hepatic glucokinase activity, lack of hepatic fructokinase activity, and a non-functional Tas1R2 receptor resulting in an inability to taste sugar. A lesser known adaptation can be found in the spatial localisation of AGT1 which is species dependent. In cats, AGT1 (alanine:glyoxylate aminotransferase 1) is mainly present in mitochondria, while in the human liver an almost exclusive peroxisomal localisation of this enzyme has been reported (Dijcker et al., 2010). AGT1 is involved in the removal of glyoxylate to glycine and prevention of oxalate formation. These and other metabolic adaptations align with the dietary habits and feeding ecology of wild cats (*F. silvestris*) and feral/stray domestic cats. In a recently published literature-based study (Plantinga et al., 2011) free-roaming feral cats were shown to be predominantly solitary and hunt individually catching a variety of mainly rodents (e.g. mice, voles) but also lagomorphs, birds reptiles and insects can be part of their diet. Feral cats are obligatory carnivores, with their daily energy intake from crude protein being 52%, from crude fat 46% and from nitrogen-free extractables only 2%. These estimates align closely with detailed empirical studies into the selection and regulation of macronutrient intake by adult cats (Hewson-Hughes et al., 2011; 2013).

Omnivorous dog dogma: The scientific confirmation of the absence of identical or similar specialised metabolic pathways of dogs compared to cats has significantly contributed over the past 40 years to the development of an “omnivorous dog dogma”. Currently this dogma has established itself firmly into authoritative scientific reference books (NRC, 2006; Hand et al., 2010), nutritional concepts in pet nutrition, and as a general view. This, although there are a number of specific metabolic adaptations which can be classified as being typical carnivorous in nature. Among these are a limited ability to synthesise arginine, lack of cholecalciferol synthesis, a lack of salivary amylase, low activity of pancreatic and intestinal amylases, and a predominantly mitochondrial localisation of AGT1. In addition, adult dogs metabolically adapt to food deprivation by limiting the rate of body protein catabolism with endogenous urinary urea loss being intermediate (116 mg kg-0.75 d-1) compared to cats and rats (243 and 60 mg kg-0.75 d-1, respectively) (Hendriks et al., 1997).

The closest living relative of domestic dogs is the gray wolf. Breeding efforts during the last 3,000-4,000 years and in particular over the past two centuries have resulted in the remarkable morphological and behavioural diversity of dogs we see today (Driscoll et al., 2009; Driscoll and MacDonald, 2010). This remarkable diversity originates, from a simple genetic basis dominated by less than 4 quantitative trait loci. Recent evidence shows that three genes (AMY2B, MGAM and SGLT1) involved in starch digestion and glucose uptake were the target of selection during domestication (Axelsson et al., 2013). This recent study also shows that other metabolic traits observed in dogs, like capacity to down-regulate amino acid catabolism and the synthesis of sufficient amounts of essential nutrients such as niacin, taurine and arginine, were unaffected by domestication and remain present in dogs and gray wolves.

The scientific literature on the foraging ecology of free living gray wolves shows that wolves typically hunt in packs on large ungulates but also opportunistically scavenge a varied but essentially animal-based diet (Bosch et al., 2014). Consumption of vegetal matter is negligible with rumen contents not being consumed. Reconstruction of the diet of gray wolves shows a ratio of protein:fat:carbohydrate of 52:47:1% by energy making the direct ancestor of domestic dogs, true carnivores. Selection and regulation of macronutrient intake by adult dogs (Hewson-Hughes et al., 2011) showed a protein:fat:carbohydrate 30:63:7% by energy, which is also highly indicative of a true carnivorous ancestry of our modern-day dogs. The higher preference for carbohydrate may be explained by the genes involved in starch digestion (Axelsson et al., 2013). Explanation of the preference for fat may lay in the markedly changing nutrient intake of gray wolves throughout the year due to differences in prey availability. During periods of abundant prey availability (feast), wolves ingest large amounts of highly nutritious animal tissues, with meal weights of up to 22% of their body weight, and preferential consumption of internal organs such as liver. During prolonged periods of low prey availability (famine), wolves scavenge on low-nutritious left-overs like bones and hide or consume prey parts cached for later consumption. It is during these periods of famine that wolves require an ability to conserve body proteins and maintain a synthesis capacity for essential nutrients, hence the lack of similar metabolic adaptations as seen in cats. Selection and ingestion of fat during periods of famine would facilitate body protein conservation.

In rats and pigs, fluctuating nutrient intake is modulated by food availability but also food composition (vegetal and animal matter). The latter is far less in wolves where nutrient intake has been modulated predominantly by a “feast and famine” lifestyle. Therefore one can expect to see a metabolic specialisation in wolves (and therefore domestic dogs) which would be intermediate compared to rats, pigs and humans on the one side, and cats on the other side.

Conclusion: Both domestic cats and dogs are descendants of true carnivores with cats having a relatively highly non-adaptive metabolism while dogs have inherited a moderately adaptive metabolism due to the feast and famine lifestyle of its direct ancestor. The proposed classification of our domestic dogs as an adaptive carnivore and cats as an obligatory carnivore appear to be the most accurate. Knowledge regarding the ancestral diet of our domestic dogs and cats can provide important information and evidence to improve the nutrition of our modern-day domestic dogs and cats.

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