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The effects of raw-meat diets on the gastrointestinal microbiota of the cat and dog: a review

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ABSTRACT

The aim of this review is to summarise the available literature on the effects of consuming raw, red meat diets on the gastrointestinal microbiome of the cat and dog. In recent years, feeding raw meat diets to cats and dogs has increased, in part associated with trends in human nutrition for “natural” and “species-appropriate” diets. These diets range from home-prepared unprocessed, nutritionally incomplete diets to complete and balanced diets with sterilisation steps in their manufacturing process. Feeding some formats of raw meat diets has been associated with nutritional inadequacies and zoonotic transfer of pathogens. The feeding of raw meat diets has been shown to alter the gastrointestinal microbiome of the cat and dog, increasing the relative abundances of bacteria associated with protein and fat utilisation, including members of the genera *Fusobacterium* and *Clostridium*. While in humans, these genera are more commonly known for members that are associated with disease, they are a diverse group that also contains harmless commensals that are a normal component of the gastrointestinal microbiota. Moreover, members of these genera are known to produce butyrate from protein and amino acid fermentation and contribute to intestinal homeostasis in raw meat-fed dogs and cats. Currently, only a limited number of studies have examined the impacts of raw meat diets on the cat and dog microbiota, with many of these being descriptive. Additional controlled and systems-based studies are required to functionally characterise the roles of key microbial groups in the metabolism of raw meat diets, and determine their impacts on the health and nutrition of the host.

Abbreviations: AAFCO: American Association of Feed Control Officials; BARF: Bone and raw food; FEDIAF: The European Pet Food Industry.

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Introduction

Due to its role in host health and nutrition, there is increasing interest in the gastrointestinal microbiome of mammalian species, including the cat and dog. Diet is one of the major drivers of the composition and function of the microbiome (Alessandri *et al.* 2020). Studies investigating the associations between diet, disease, and the gastrointestinal microbiome in the domestic cat (Suchodolski *et al.* 2015; Pallotto *et al.* 2018; Summers *et al.* 2019) and dog (Suchodolski *et al.* 2012; Honnuffer *et al.* 2014; Guard *et al.* 2015) have been undertaken. However, our understanding of the consequences of these changes in microbial composition is limited.

The feeding of minimally processed diets, high in animal protein and fat, has increased in recent years (Davies *et al.* 2019; Stogdale 2019). As noted in Stogdale (2019), raw meat diets encompass a wide variety of dietary formats ranging from incomplete, unprocessed (i.e. no sterilisation steps) to complete and balanced diets including sterilisation steps. The purpose of this review is to outline current knowledge

relating to the impacts of feeding raw meat diets on the microbiome of the cat and dog.

Nutritional requirements of the domestic cat and dog

The domestic cat is an obligate carnivore and, therefore, derives energy from animal protein consumption. Analysis of highly conserved regions of Felidae genomes and assessment of orthologous genes for dietary adaption has revealed a loss of gene families in the starch and sucrose metabolism pathways (Kim *et al.* 2016), reflecting their carnivorous nature. In contrast, dogs are classed as facultative carnivores and are often regarded nutritionally as omnivores as they consume and utilise both plant and animal material (Pilla and Suchodolski 2019). Through their domestication, dogs have retained many ancestral traits, although adaptations to diets with a higher carbohydrate content in conjunction with human civilisation have been observed (Axelsson *et al.* 2013).

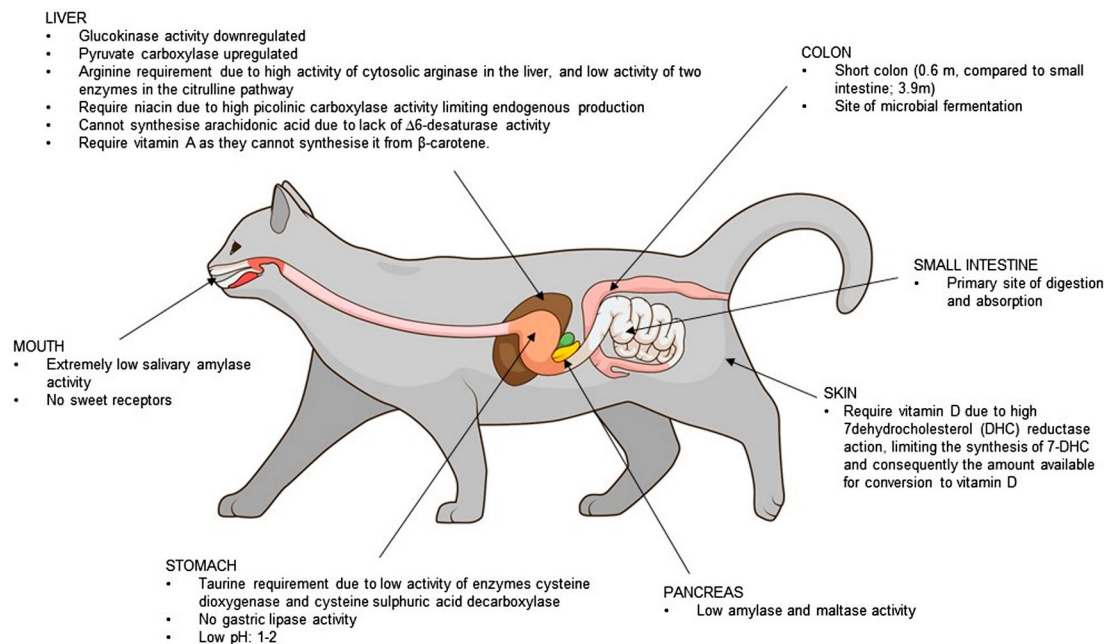


Figure 1. Metabolic and physiological characteristics specific to the domestic cat (from McGeachin and Akin 1979; Kienzle 1993; Pawlosky *et al.* 1994; Knosp and Plendl 1997; Washizu *et al.* 1999; Brosey *et al.* 2000; Schweigert *et al.* 2002; Li *et al.* 2005; Hiskett *et al.* 2009).

Cats and dogs obtain the essential nutrients that cannot be endogenously synthesised from animal proteins and fats (Figures 1 and 2). For example, cats do not endogenously synthesise niacin (Çatak 2019), but animal tissues such as liver and muscle provide high levels of dietary niacin. Such dependencies may explain the high drive to consume protein and fat in both the cat and dog. Studies have shown that when cats are given free access to diets with different macronutrient profiles they will select a diet with a macronutrient profile of 48–53% protein, 36–41% fat, and 11% carbohydrate (on a total energy intake per

macronutrient basis) (Hewson-Hughes *et al.* 2013a; Salaun *et al.* 2017). Similarly, dogs select a diet of 30–45% protein, 51–63% fat and 4–7% carbohydrate (Hewson-Hughes *et al.* 2013b; Roberts *et al.* 2018).

The way cats and dogs have been fed has drastically changed over the last 60 years with the modernisation and globalisation of the pet food industry (see Guy 2016). Typically, pet foods are sold in various formats, although extruded/kibble and cans/pouches predominate. Kibble diets typically contain a large amount of carbohydrate ($\geq 35\%$ DM), while canned diets contain $< 5\%$ carbohydrate on a DM basis (Davies *et al.* 2017).

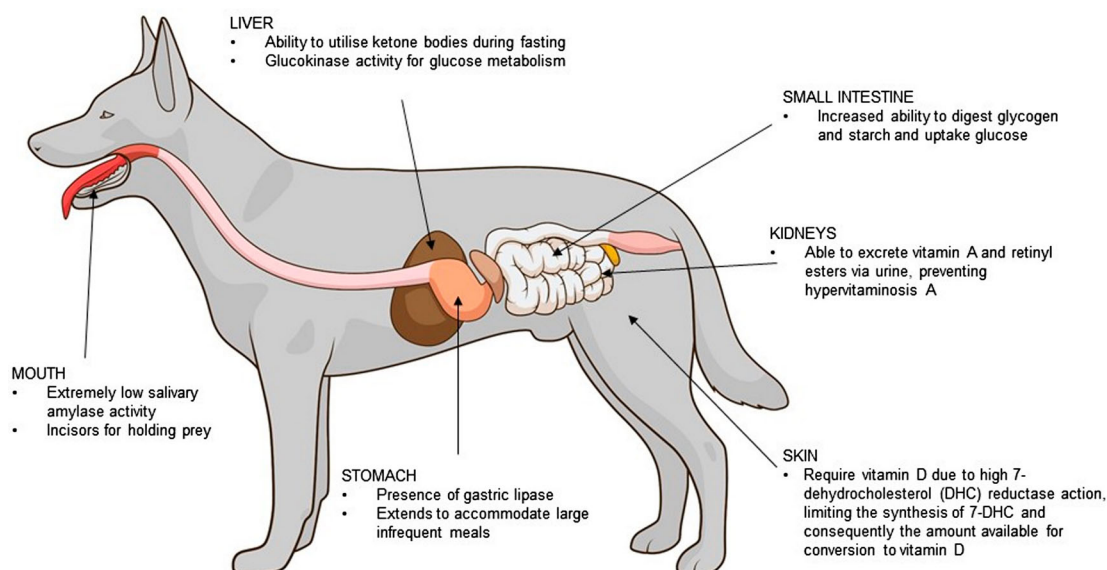


Figure 2. Metabolic and physiological characteristics specific to the domestic dog (from de Bruijne and van den Brom 1986; Carriere *et al.* 1992; How *et al.* 1994; Raila *et al.* 2000; Bosch *et al.* 2015).

Recently, minimally processed, or raw, high animal protein (meat) diets have become increasingly popular (see recent review by Davies *et al.* 2019), mirroring trends in human nutrition (e.g. “Paleo” diets and intuitive eating) and have resulted in demand for less processed, more “natural” pet foods that reflect the animals’ carnivorous nature. These pet foods are typically sold in raw (fresh or frozen), air- or freeze-dried formats (Stogdale 2019). These high meat diets are typically high in crude protein (>50% DM) and contain moderate–high levels of crude fat (20–25% DM) with minimal carbohydrate content. From a nutritional adequacy perspective (according to the American Association of Feed Control Officials (AAFCO 2020) or the European Pet Food Industry (FEDIAF 2020) guidelines) raw meat diets can range from incomplete, homemade bone and raw food (BARF) diets to manufactured complete and balanced diets (Stogdale 2019).

Nutritional impacts and risks associated with feeding raw meat diets

Despite the classification of both the cat and dog as carnivores, there is a shortage of knowledge on the nutritional impacts on our pets of feeding raw meat diets. Raw meat diets are known to decrease faecal output and improve consistency (Bermingham *et al.* 2017; Butowski *et al.* 2019), likely seen as beneficial to pet owners, but the effects on the pet’s general health has yet to be understood. However, a recent blinded study has shown that dogs fed raw meat diets had an improved composite clinical health score (dental score + otitis score + integument score) when compared to dogs fed a high quality kibble, suggesting a “modest improvement in dog health” (Hiney *et al.* 2021). The authors also noted an increased lymphocyte count in the dogs fed raw meat but were unable to differentiate between inflammatory or anti-inflammatory functions. However, in a pilot study, dogs fed a high quality kibble had changes in gene expression that suggested a pro-inflammatory response compared to dogs fed a raw meat diet (Anderson *et al.* 2018). Certainly, the impacts of diet on inflammation warrant further investigation.

Raw meat diets have a higher apparent macronutrient digestibility compared to extruded diets (Bermingham *et al.* 2017; Butowski *et al.* 2019) and this may indicate increased bioavailability of the macro and micronutrients present in the diet. The nutritional requirements of domestic cats and dogs have primarily been determined using commercial or experimental, purified, extruded or canned diets (National Research Council 2006). Therefore, the highly digestible nature and the higher nutritional content of raw/minimally processed diets may indicate that the AAFCO and

FEDIAF nutrient guidelines for minimally processed diets may not be appropriate. However, further research is required to substantiate this hypothesis.

Due to the relatively small body of scientific literature on the nutritional impacts of feeding raw, high meat diets to pets, coupled with the wide range of diets covered in this format, there are concerns regarding their nutritional adequacy (Stockman *et al.* 2013). This is especially relevant in the context of home-prepared diets, which may lack the correct balance of macro- and micro-nutrients required to achieve a complete and balanced diet. For example, Laflamme *et al.* (2008) found that only 15% of owners who fed home-prepared diets used a recipe obtained from a veterinarian for feeding. More recently, a survey undertaken by Morelli *et al.* (2019) identified that only 8% of respondents relied on veterinarians for formulating the raw meat-based diets fed to their pets. This may contribute to the high occurrence of vitamin and mineral deficiencies observed with feeding home-prepared diets (Remillard 2008; Dillitzer *et al.* 2011). However, ensuring the diet is complete and balanced (i.e. adherence to National Research Council (2006), AAFCO or FEDIAF guidelines), significantly reduces this concern. Furthermore, the inclusion of veterinary practitioners in the owner’s decision to feed raw meat diets can help ensure the safe feeding of these diets, for both the owners and the pets (Stogdale 2019).

Risks associated with the feeding of raw meat diets include pathogenic contamination of the diet, which has been reviewed recently (Davies *et al.* 2019). Briefly, various species of bacteria such as *Salmonella* spp. (Finley *et al.* 2006), *Campylobacter* spp. and *Escherichia coli* (Nüesch-Inderbilen *et al.* 2019) as well as the parasites *Toxoplasma gondii* and *Sarcocystis* spp. pose a potential zoonotic risk to humans (van Bree *et al.* 2018). While clinical signs of pathogenicity from these organisms have been reported in pets consuming raw diets (Fauth *et al.* 2015; Jones *et al.* 2019; O’Halloran *et al.* 2020), some pets may shed pathogens with no clinical symptoms (Finley *et al.* 2007) suggesting that pets may act as carriers and pose zoonotic risks to their owners (Baede *et al.* 2017).

There is a scarcity of knowledge as to the risks associated with consuming raw meat diets. For example, on the American Veterinary Medical Association website (AVMA 2020), of the 29 commercial pet food recalls issued to November 2020, three were recalled due to microbial contamination, and one of those was a kibbled product. In fact, most of the recalls issued were due to the presence of aflatoxin, a mould toxin associated with grain (Bischoff and Rumbelha 2018). Nonetheless, the shedding of pathogenic bacteria in dogs fed raw, red meat appears to occur to a greater extent than dogs fed a kibbled diet (Oikkola *et al.* 2015; Runesvärd *et al.* 2020). The levels of pathogens in faeces that can be directly attributed to dietary

contamination are of interest due to other feeding (e.g. scavenging, coprophagia, etc) and grooming behaviours that occur in dogs and cats. However, *Mycobacterium bovis* infection in cats was linked to a contaminated raw venison pet food and it was suspected that this was the cause of latent tuberculosis infection in five people related to the outbreak (O'Halloran *et al.* 2020). A recent study showed that 0.2% of households ($n=16,475$) who feed raw pet food reported transmission of pathogens from pets to humans (Anturaniemi *et al.* 2019). Therefore, it appears further research is required to quantify the extent of zoonotic transfer of pathogens from pets to their owners. Moreover, there is a need for increased education on the appropriate hygiene practises for the handling of pets and their food in relation to zoonoses, especially given less than 33% of pet owners wash their hands after handling their pets (Thomas and Feng 2020).

Raw pet foods and the gut microbiome

The dog and cat gastrointestinal tract harbour complex and diverse communities of microorganisms, where the microbes that reside in the intestines are commonly referred to as the gut microbiota. These microbes are natural symbionts that have co-evolved with their hosts and can influence host health and wellbeing. The microbiota contributes to host nutrition as they are able to synthesise vitamins, protect against pathogenic organisms, provide energy substrates for gut epithelial cells, and contribute to gut metabolic and immune homeostasis (see Flint *et al.* 2012 for review).

Studies of gut microorganisms have traditionally been challenging as many of these are strictly anaerobic, which hampers their isolation and characterisation using standard microbiology methods. Moreover, many gut microbes are “as-yet-uncultured.” However, recent efforts to bring diverse microbial groups from the human gut into cultivation have been successful through high-scale cultivation efforts that employ multiple culture conditions in parallel in an attempt to meet specific growth requirements for diverse microbial groups (Lagier *et al.* 2018; Diakite *et al.* 2020). The advent of high-throughput DNA sequencing technologies (such as 16S rRNA amplicon and whole metagenome shotgun sequencing) have greatly accelerated culture-independent investigations of the gut microbiota. Typically, DNA is extracted directly from faecal samples, sequenced, then reads are aligned to reference databases and microbial taxonomy and predicted functions assigned. Such studies have provided important insights into “who is there” and “what are they doing” with regard to gut microbiota composition and function.

The dominant bacterial groups present in the dog and cat microbiota at the phylum level are generally the Firmicutes, Bacteroidetes, and Fusobacteria, followed by the Proteobacteria and Actinobacteria (Garcia-Mazcorro and Minamoto 2013; Moon *et al.* 2018) and members of these have been shown to represent a commonly found “core microbiota” in gut environments (Alessandri *et al.* 2019). In healthy animals, host diet is a major driver of microbiome composition and function. A growing number of studies have begun to provide new insights into the influence of raw meat-based diets on the composition of the gut microbiota, of the cat (Kerr *et al.* 2014; Butowski *et al.* 2019) and dog (Beloshapka *et al.* 2013; Bermingham *et al.* 2017; Alessandri *et al.* 2019) and its impact on the host. However, within these studies, there are inconsistencies in the characterisation of the diets consumed in terms of macronutrients (i.e. crude protein ranging from 25 to 74% DM) or dietary format (e.g. BARF). Similarly, much of the literature is presently descriptive and has characterised microbiota composition independent to, or in the absence of, host physiological data which could provide insights into the implication of the changes. Faecal samples, which can be collected non-invasively, are typically used and widely accepted as a proxy for assessing the colonic microbiota composition; however, they are not entirely representative of the colonic microbiome. Microbial functions are also generally interpreted in the context of model omnivore microbiota (e.g. from human and rodent) derived data. Together, these approaches have limited the ability to determine the relationships and impacts of dietary macronutrients on the microbiome composition (see review by Pilla and Suchodolski 2019).

Microbiome diversity

The diversity of microbes in complex communities is commonly reported in the literature. Different metrics of diversity can be employed to take into account the number of species present, their relative abundances and their relatedness to each other. Alpha diversity refers to the richness and evenness of microbial taxa (e.g. genera, species, operational taxonomic units) within a given sample, commonly using the Shannon, Simpson's or Chao1 index. In contrast, beta diversity measures similarities between samples (e.g. Euclidean distance or Bray–Curtis dissimilarity).

It is commonly thought that greater gut microbiota alpha diversity is associated with greater functional resilience (through redundancies in functional groups of microbes), whilst lower diversities are thought to be inferior, largely due to their associations with dysbiosis, a term which is generally used to describe an imbalance in the gut microbial community composition that is associated with disease states. However,

many factors contribute to diversity (including diet, body mass, and gut morphology), and interpretation of the drivers and consequences of diversity are particularly complex for microbial ecosystems (Reese and Dunn 2018). In fact, some of the most beneficial host-microbiota relationships exhibit exceedingly low diversity as a result of co-evolution between the host and its microbiota (Pacheco *et al.* 2015). For example, the faecal microbiota diversity of breast-fed infants is lower than that of formula-fed infants (Ma *et al.* 2020) and is underpinned by a specialist community dominated by beneficial *Bifidobacterium* sp. which can utilise milk oligosaccharides and protect the infant from gastrointestinal disease. Microbial diversity may reflect the type (and complexity) of dietary nutrients consumed by the host and that subsequently become available for bacterial fermentation in the gut. For example, most obligate carnivores have an inherently lower microbial diversity than omnivores and herbivores, as they are monogastric and consume a diet based on only a relatively narrow range of prey species which requires a select community of microbes (Reese and Dunn 2018).

Studies in healthy dogs have shown that raw meat-based diets have variously resulted in no difference (Schmidt *et al.* 2018), greater (Kim *et al.* 2017; Sandri *et al.* 2017), or reduced (Bermingham *et al.* 2017; Alessandri *et al.* 2019) gut microbial diversity to those from commercial diets to which they were compared. The apparent inconsistencies in microbial diversity between these different studies likely reflect finer differences in the compositions of the diets used. However, differences in alpha diversity metrics, which may be based on community richness, evenness or both, may also contribute to the differing outcomes reported, as may the relatively small sample sizes used in many of the studies. In a comprehensive study, which included 169 dogs of various breeds and six wolves consuming a wide range of diets, Alessandri *et al.* (2019) reported that the microbial diversity of those fed BARF diets was significantly lower than those fed commercial diets containing high proportions of fibre and carbohydrate. Increased proportions of vegetables in the diet are likely to contribute to higher microbial diversity as plant-based fibres are complex polysaccharides that are generally fermented by a consortium of microbes in the colon. In some studies, the raw meat-based diets contained a considerable amount of vegetable matter (Kim *et al.* 2017) or added flours and fibre (Sandri *et al.* 2017), which likely contributed to the greater diversity observed on the raw dietary treatments.

Few studies have examined the microbiota of cats fed raw meat diets. In a study comparing kibble, raw meat, and raw meat and fibre diets, a trend towards greater gut microbial diversity in the raw meat compared to the kibble-fed cats was observed (Butowski

et al. 2019). The raw meat diet in this study contained a range of animal products including muscle, various offals and bone (Butowski *et al.* 2019), that are likely to have contributed to the higher diversity of gut microbiota observed in the raw meat-fed cats. However, to date the relationship between the taxonomic diversity of the microbiota and the diversity of their functional potential has not been examined.

Microbiota composition

The composition of the gut microbiota from dogs and cats fed raw meat-based diets is distinct from those fed kibble diets. In our previous studies where raw diets containing only animal products (supplemented with vitamins and minerals) were compared to commercial kibble diets, the faecal microbiota of dogs fed the raw meat diet were dominated by *Peptostreptococcus* spp., *Fusobacterium* spp., *Blautia* spp., *Clostridium* spp. and *Lactobacillus* spp., which together comprised nearly 55% of the total sequence reads on average (Bermingham *et al.* 2017). This contrasted with the dominant microbial taxa from the kibble-fed dogs, where *Peptostreptococcus* spp., *Bacteroides* spp., *Prevotella* spp., *Faecalibacterium* spp. and *Blautia* spp., comprised nearly 60% of sequence reads (Bermingham *et al.* 2017). Many of these groups are able to utilise dietary glycans and are associated with fibre and carbohydrate utilisation. Significant enrichment of *Fusobacterium* spp. and *Clostridium* spp. from feeding the raw meat diet was also observed in the cat, where the microbiota was dominated by *Clostridium* spp., and unclassified members of *Peptostreptococcaceae*, *Fusobacterium*, *Prevotellaceae* and *Clostridiales* (comprising nearly 70% of the total 16S rRNA gene sequence reads on average) (Butowski *et al.* 2019). *Fusobacterium* (16S rRNA) and *Clostridium* (16S rRNA and quantitative PCR) were also the two most discriminatory genera in faecal samples of dogs fed BARF and commercial canned and kibbled diets (Schmidt *et al.* 2018), the most relatively abundant genera in dogs fed raw beef and raw chicken diets (Beloshapka *et al.* 2013), and dogs fed a raw-beef based diet compared to a commercial kibbled diet (Sandri *et al.* 2017). In the cat, *Fusobacterium* spp. and *Clostridium* spp. appeared to have greater relative abundances when fed raw whole chicks than an extruded chicken diet (Kerr *et al.* 2014). Overall, *Fusobacterium* spp. and *Clostridium* spp. appear to be very strongly associated with feeding raw meat-based diets to cats and dogs.

Fusobacterium spp. and *Clostridium* spp. are perhaps more widely known for their pathogenicity in humans, where *Fusobacterium nucleatum* is one of the most studied organisms implicated in periodontal disease (Signat *et al.*, 2011), and more recently has been identified as a facilitator of colorectal cancer (Rubinstein *et al.*, 2019). The genus *Clostridium* also contains a

number of pathogenic strains, such as *C. difficile* and *C. perfringens*, which have been associated with severe enteric disease in dogs (Schlegel *et al.* 2012; Andrés-Lasheras *et al.* 2018). In cats, both of these *Clostridium* species are commonly observed in faeces, however, unlike dogs, there is, as yet, no association between *C. perfringens* enterotoxins and enteric disease (Sabshin *et al.* 2012).

The genera *Fusobacterium* and *Clostridium* also contain harmless commensals that are normal components of the gastrointestinal microbiota (Citron 2002; Cruz-Morales *et al.* 2019). *Fusobacterium* was found to be the most abundant bacterial genus (25% average relative abundance) across the 175 healthy dogs' faeces and wolves' scats (independent of diet), making it an important member of the canine core gut microbiota (Alessandri *et al.* 2019). Given its abundance and prevalence in the dog and wolf, it has been suggested that there has been extensive co-evolution between *Fusobacterium* spp. and the canine gastrointestinal environment (Alessandri *et al.* 2019). *Clostridium* spp. was present in over 99% of samples in the same study and is also part of the core microbiota (Alessandri *et al.* 2019). We have found that relative abundances of *Clostridiaceae* and *Fusobacteriaceae* in the dog were positively correlated with protein digestibility and dietary crude protein concentration and strongly negatively correlated with dietary carbohydrate content (Birmingham *et al.* 2017). Members of the *Clostridium* genus are widely known for their roles in protein metabolism and amino acid fermentation in the gut (Oliphant and Allen-Vercoe 2019), a feature shared with *Fusobacterium* spp. for which amino acids are important carbon and energy sources (Bakken *et al.* 1989; Ramezani *et al.* 1999). Moreover, members of each genus are known to produce butyrate from protein and amino acid fermentation (Potrykus *et al.* 2007; Vital *et al.* 2015). Thus, they may be major suppliers of energy to the gut epithelium, contributing to gut homeostasis in raw meat-fed dogs and cats. These functions, together with their high relative abundances, suggest that *Fusobacterium* spp. and *Clostridium* spp. play key roles in protein utilisation in healthy dogs and cats fed raw meat diets. Additionally, *C. hiranonis* is also responsible for the conversion of bile acids in dogs (Ziese and Suchodolski 2021).

Many of the dominant gut microbial taxa in the dog and cat cannot be classified to known genera or species by 16S rRNA gene sequences and have not been isolated and characterised (Birmingham *et al.* 2017; Alessandri *et al.* 2019; Butowski *et al.* 2019). This suggests that they differ from the main characterised and classified reference species in databases that are typical of those of human origin. Moreover, it has been shown that general microbiome functions, such as butyrate production, can be performed by

different functional guilds of microbes in a diet-dependent manner (Vital *et al.* 2015). Thus, it cannot be assumed that the functions of microbes are conserved between the dog and cat and humans, despite apparent taxonomic similarities. Therefore, much work is required to isolate and characterise dog- and cat-derived gut microbes to determine differences in their functional capacity and impact on host health compared to current human-derived references.

Metabolic function of the microbiome

The functions of gut microbiota of cats and dogs when feeding raw diets are poorly understood. Initial insights into the metabolic functions of gut microbiota from a single dog fed an unspecified BARF diet, compared to one fed an unspecified commercial diet high in carbohydrate content, were generated through metagenome shotgun sequencing of faecal DNA (Alessandri *et al.* 2019). Consistent with the greater intake of vegetable-based carbohydrates and fibre in the unspecified commercial diet, the faecal microbiota from the dog on this diet had a greater abundance of genes classified as glycosyl hydrolase genes involved in the degradation of complex plant polysaccharides. In contrast, the dog fed the unspecified BARF diet had a greater abundance of genes involved in amino acid degradation and fatty acid and lipid degradation. These data support the view that diets high in animal protein and fats promote microbial communities enriched for functions that contribute to amino acid and lipid degradation (Alessandri *et al.* 2019). However, additional studies are required to gain more detailed insights into the microbiome function.

Conclusions

Several major themes arise from the literature surrounding the impacts of feeding raw meat diets to cats and dogs. Firstly, the lack of standardisation of what "raw-feeding" is (diets can vary from incomplete, unprocessed to balanced and processed) impairs the interpretation of the microbial and nutritional effects of these diets. The nutritional and zoonotic risks associated with incomplete, unprocessed diets (both with nutritional adequacy and zoonotic transfer of pathogens) are perceived to be higher compared to commercial, processed diets; however, there is a lack of published information to support this. Secondly, although studies have shown that raw meat diets promote gut microbial communities dominated by *Fusobacterium* spp. and *Clostridium* spp., the metabolic and physiological impacts of these bacterial strains on the host are unclear. In this vein, microbiome data have generally been interpreted in the context of omnivore-derived references, which may not be applicable to the carnivore microbiome. Moreover, most

studies provide little dietary information (macro- and micro-nutrient composition) or data on physiological impacts (e.g. faecal metabolites, faecal health score) to allow deeper conclusions into the consequences of these diets on the carnivore host. Thus, there is still significant scope to better understand the interactions between raw meat diets, cats and dogs and their gastrointestinal microbiota to promote better nutrition in carnivorous companion animals.

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References

- *AAFCO. American Association of Feed Control Officials 2020 Official Publication. AAFCO Publications, Champaign, IL, USA, 2020
- Alessandri G, Argentini C, Milani C, Turroni F, Cristina Ossiprandi M, van Sinderen D, Ventura M.** Catching a glimpse of the bacterial gut community of companion animals: a canine and feline perspective. *Microbial Biotechnology* 13, 1708–32, 2020
- Alessandri G, Milani C, Mancabelli L, Mangifesta M, Lugli GA, Viappiani A, Duranti S, Turroni F, Ossiprandi MC, van Sinderen D, et al.** Metagenomic dissection of the canine gut microbiota: insights into taxonomic, metabolic and nutritional features. *Environmental Microbiology* 21, 1331–43, 2019
- Anderson RC, Armstrong KM, Young W, Maclean P, Thomas DG, Bermingham EN.** Effect of kibble and raw meat diets on peripheral blood mononuclear cell gene expression profile in dogs. *The Veterinary Journal* 234, 7–10, 2018
- Andrés-Lasheras S, Martín-Burriel I, Mainar-Jaime RC, Morales M, Kuijper E, Blanco JL, Chirino-Trejo M, Bolea R.** Preliminary studies on isolates of *Clostridium difficile* from dogs and exotic pets. *BMC Veterinary Research* 14, 77, 2018
- Anturaniemi J, Barrouin-Melo SM, Zaldivar-López S, Sinkko H, Hielm-Björkman A.** Owners' perception of acquiring infections through raw pet food: a comprehensive internet-based survey. *Veterinary Record* 185, 658, 2019
- AVMA.** *Recalls and Safety Alerts.* <https://www.avma.org/news/recalls-alerts> (accessed 22 December 2020) American Veterinary Medical Association, Schaumburg, IL, USA, 2020
- Axelsson E, Ratnakumar A, Arendt ML, Maqbool K, Webster MT, Perloski M, Liberg O, Arnemo JM, Hedhammar A, Lindblad-Toh K.** The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature* 495, 360–4, 2013
- Baede VO, Broens EM, Spaninks MP, Timmerman AJ, Graveland H, Wagenaar JA, Duim B, Hordijk J.** Raw pet food as a risk factor for shedding of extended-spectrum beta-lactamase-producing Enterobacteriaceae in household cats. *PLoS One* 12, e0187239, 2017
- Bakken V, Högh BT, Jensen HB.** Utilization of amino acids and peptides by *Fusobacterium nucleatum*. *European Journal of Oral Sciences* 97, 43–53, 1989
- Beloshapka AN, Dowd SE, Suchodolski JS, Steiner JM, Duclos L, Swanson KS.** Fecal microbial communities of healthy adult dogs fed raw meat-based diets with or without inulin or yeast cell wall extracts as assessed by 454 pyrosequencing. *FEMS Microbiology Ecology* 84, 532–41, 2013
- Bermingham EN, Maclean P, Thomas DG, Cave NJ, Young W.** Key bacterial families (Clostridiaceae, Erysipelotrichaceae and Bacteroidaceae) are related to the digestion of protein and energy in dogs. *PeerJ* 5, e3019, 2017
- Bischoff K, Rumberiha WK.** Pet food recalls and pet food contaminants in small animals: an update. *The Veterinary Clinics of North America: Small Animal Practice* 48, 917–31, 2018
- Bosch G, Hagen-Plantinga EA, Hendriks WH.** Dietary nutrient profiles of wild wolves: insights for optimal dog nutrition? *British Journal of Nutrition* 113(Suppl), S40–54, 2015.
- Brosey BP, Hill RC, Scott KC.** Gastrointestinal volatile fatty acid concentrations and pH in cats. *American Journal of Veterinary Research* 61, 359–61, 2000
- Butowski CF, Thomas DG, Young W, Cave NJ, McKenzie CM, Rosendale DI, Bermingham EN.** Addition of plant dietary fibre to a raw red meat high protein, high fat diet, alters the faecal bacteriome and organic acid profiles of the domestic cat (*Felis catus*). *PLoS One* 14, e0216072, 2019
- Carriere F, Raphel V, Moreau H, Bernadac A, Devaux MA, Grimaud R, Barrowman JA, Benicourt C, Junien JL, Laugier R, et al.** Dog gastric lipase: stimulation of its secretion *in vivo* and cytolocalization in mucous pit cells. *Gastroenterology* 102, 1535–45, 1992
- Çatak J.** Determination of niacin profiles in some animal and plant based foods by high performance liquid chromatography: association with healthy nutrition. *Journal of Animal Science and Technology* 61, 138–46, 2019
- Citron DM.** Update on the taxonomy and clinical aspects of the genus *Fusobacterium*. *Clinical Infectious Diseases* 35, S22–S7, 2002
- Cruz-Morales P, Orellana CA, Moutafis G, Moonen G, Rincon G, Nielsen LK, Marcellin E.** Revisiting the evolution and taxonomy of Clostridia, a phylogenomic update. *Genome Biology and Evolution* 11, 2035–44, 2019
- Davies M, Alborough R, Jones L, Davis C, Williams C, Gardner DS.** Mineral analysis of complete dog and cat foods in the UK and compliance with European guidelines. *Scientific Reports* 7, 17107, 2017
- Davies RH, Lawes JR, Wales AD.** Raw diets for dogs and cats: a review, with particular reference to microbiological hazards. *The Journal of Small Animal Practice* 60, 329–39, 2019
- de Bruijne JJ, van den Brom WE.** The effect of long-term fasting on ketone body metabolism in the dog. *Comparative Biochemistry and Physiology B* 83, 391–5, 1986
- Diakite A, Dubourg G, Dione N, Afouda P, Bellali S, Ngom II, Valles C, Tall MI, Lagier J-C, Raoult D.** Optimization and standardization of the culturomics technique for human microbiome exploration. *Scientific Reports* 10, 9674, 2020
- Dillitzer N, Becker N, Kienzle E.** Intake of minerals, trace elements and vitamins in bone and raw food rations in adult dogs. *British Journal of Nutrition* 106(Suppl 1), S53–6, 2011
- Fauth E, Freeman LM, Cornjeo L, Markovich JE, Janecko N, Weese JS.** *Salmonella* bacteriuria in a cat fed a *Salmonella*-contaminated diet. *Journal of the American Veterinary Medical Association* 247, 525–30, 2015

- ***FEDIAF**. *Nutritional Guidelines for Complete and Complementary Pet Food for Cats and Dogs*. http://www.fediaf.org/images/FEDIAF_Nutritional_Guidelines_2020_20200917.pdf (accessed 9 October 2020). European Pet Food Industry Federation, Brussels, Belgium, 2020
- Finley R, Reid-Smith R, Weese JS, Angulo FJ**. Human health implications of *Salmonella*-contaminated natural pet treats and raw pet food. *Clinical Infectious Diseases* 42, 686–91, 2006
- Finley R, Ribble C, Aramini J, Vandermeer M, Popa M, Litman M, Reid-Smith R**. The risk of salmonellae shedding by dogs fed *Salmonella*-contaminated commercial raw food diets. *Canadian Veterinary Journal* 48, 69–75, 2007
- Flint HJ, Scott KP, Louis P, Duncan SH**. The role of the gut microbiota in nutrition and health. *Nature Reviews in Gastroenterology and Hepatology* 9, 577–89, 2012
- Garcia-Mazcorro JF, Minamoto Y**. Gastrointestinal microorganisms in cats and dogs: a brief review. *Archivos de Medicina Veterinaria* 45, 111–24, 2013
- Guard BC, Barr JW, Reddivari L, Klemashevich C, Jayaraman A, Steiner JM, Vanamala J, Suchodolski JS**. Characterization of microbial dysbiosis and metabolic changes in dogs with acute diarrhea. *PLoS One* 10, e0127259, 2015
- ***Guy RCE**. Pet foods. In: *Reference Module in Food Science*. doi:10.1016/B978-0-08-100596-5.00140-2, Elsevier, Amsterdam, The Netherlands, 2016
- Hewson-Hughes AK, Hewson-Hughes VL, Colyer A, Miller AT, Hall SR, Raubenheimer D, Simpson SJ**. Consistent proportional macronutrient intake selected by adult domestic cats (*Felis catus*) despite variations in macronutrient and moisture content of foods offered. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 183, 525–36, 2013a
- Hewson-Hughes AK, Hewson-Hughes VL, Colyer A, Miller AT, McGrane SJ, Hall SR, Butterwick RF, Simpson SJ, Raubenheimer D**. Geometric analysis of macronutrient selection in breeds of the domestic dog, *Canis lupus familiaris*. *Behavioural Ecology* 24, 293–304, 2013b
- Hiney K, Sypniewski L, Rudra P, Pezeshki A, McFarlane D**. Clinical health markers in dogs fed raw meat based or commercial extruded kibble diets. *Journal of Animal Science* 99, skab133, 2021
- Hiskett EK, Suwitheechon O-u, Lindbloom-Hawley S, Boyle DL, Schermerhorn T**. Lack of glucokinase regulatory protein expression may contribute to low glucokinase activity in feline liver. *Veterinary Research Communications* 33, 227–40, 2009
- Honneffer JB, Minamoto Y, Suchodolski JS**. Microbiota alterations in acute and chronic gastrointestinal inflammation of cats and dogs. *World Journal of Gastroenterology* 20, 16489–97, 2014
- How KL, Hazewinkel HA, Mol JA**. Dietary vitamin D dependence of cat and dog due to inadequate cutaneous synthesis of vitamin D. *General and Comparative Endocrinology* 96, 12–8, 1994
- Jones JL, Wang L, Ceric O, Nemser SM, Rotstein DS, Jurkovic DA, Rosa Y, Byrum B, Cui J, Zhang Y, et al**. Whole genome sequencing confirms source of pathogens associated with bacterial foodborne illness in pets fed raw pet food. *The Journal of Veterinary Diagnostic Investigation* 31, 235–40, 2019
- Kerr KR, Dowd SE, Swanson KS**. Faecal microbiota of domestic cats fed raw whole chickens v. an extruded chicken-based diet. *Journal of Nutrition Science* 3, e22, 2014
- Kienzle E**. Carbohydrate metabolism of the cat 1. activity of amylase in the gastrointestinal tract of the cat1. *Journal of Animal Physiology and Animal Nutrition* 69, 92–101, 1993
- Kim J, An J-U, Kim W, Lee S, Cho S**. Differences in the gut microbiota of dogs (*Canis lupus familiaris*) fed a natural diet or a commercial feed revealed by the Illumina MiSeq platform. *Gut Pathogens* 9, 68, 2017
- Kim S, Cho YS, Kim H-M, Chung O, Kim H, Jho S, Seomun H, Kim J, Bang WY, Kim C, et al**. Comparison of carnivore, omnivore, and herbivore mammalian genomes with a new leopard assembly. *Genome Biology* 17, 211, 2016
- Knospe C, Plendl J**. Histochemical demonstration of lipase activity in the gastric mucosa of the cat. *Anatomia, Histologia, Embryologia* 26, 303–4, 1997
- Laflamme DP, Abood SK, Fascetti AJ, Fleeman LM, Freeman LM, Michel KE, Bauer C, Kemp BL, Doren JR, Willoughby KN**. Pet feeding practices of dog and cat owners in the United States and Australia. *Journal of the American Veterinary Medical Association* 232, 687–94, 2008
- Lagier J-C, Dubourg G, Million M, Cadoret F, Bilen M, Fenollar F, Lévassieur A, Rolain J-M, Fournier P-E, Raoult D**. Culturing the human microbiota and culturomics. *Nature Reviews Microbiology* 16, 540–50, 2018
- Li X, Li W, Wang H, Cao J, Maehashi K, Huang L, Bachmanov AA, Reed DR, Legrand-Defretin V, Beauchamp GK, et al**. Pseudogenization of a sweet-receptor gene accounts for cats' indifference toward sugar. *PLoS Genetics* 1, 27–35, 2005
- Ma J, Li Z, Zhang W, Zhang C, Zhang Y, Mei H, Zhuo N, Wang H, Wang L, Wu D**. Comparison of gut microbiota in exclusively breast-fed and formula-fed babies: a study of 91 term infants. *Scientific Reports* 10, 15792, 2020
- McGeachin RL, Akin JR**. Amylase levels in the tissues and body fluids of the domestic cat (*Felis catus*). *Comparative Biochemistry & Physiology B* 63, 437–9, 1979
- Moon CD, Young W, Maclean PH, Cookson AL, Bermingham EN**. Metagenomic insights into the roles of Proteobacteria in the gastrointestinal microbiomes of healthy dogs and cats. *Microbiologyopen* 7, e00677, 2018
- Morelli G, Bastianello S, Catellani P, Ricci R**. Raw meat-based diets for dogs: survey of owners' motivations, attitudes and practices. *BMC Veterinary Research* 15, 74, 2019
- National Research Council**. *Nutrient Requirements of Dogs and Cats*. National Academies Press, Washington DC, USA, 2006
- Nüesch-Inderbinen M, Treier A, Zurfluh K, Stephan R**. Raw meat-based diets for companion animals: a potential source of transmission of pathogenic and antimicrobial-resistant Enterobacteriaceae. *Royal Society Open Science* 6, 191170, 2019
- O'Halloran C, Tornqvist-Johnsen C, Woods G, Mitchell J, Reed N, Burr P, Gascoyne-Binzi D, Wegg M, Beardall S, Hope J, et al**. Feline tuberculosis caused by *Mycobacterium bovis* infection of domestic UK cats associated with feeding a commercial raw food diet. *Transboundary and Emerging Diseases* 68, 2308–20, 2020
- Oliphant K, Allen-Vercos E**. Macronutrient metabolism by the human gut microbiome: major fermentation by-products and their impact on host health. *Microbiome* 7, 91, 2019
- Olkkola S, Kovanen S, Roine J, Hänninen M-L, Hielm-Björkman A, Kivistö R**. Population genetics and antimicrobial susceptibility of canine *Campylobacter* isolates collected before and after a raw feeding experiment. *PLoS One* 10, e0132660, 2015
- Pacheco AR, Barile D, Underwood MA, Mills DA**. The impact of the milk glycobiome on the neonate gut microbiota. *Annual Review of Animal Biosciences* 3, 419–45, 2015

- Pallotto MR, de Godoy MRC, Holscher HD, Buff PR, Swanson KS.** Effects of weight loss with a moderate-protein, high-fiber diet on body composition, voluntary physical activity, and fecal microbiota of obese cats. *American Journal of Veterinary Research* 79, 181–90, 2018
- Pawlosky R, Barnes A, Salem N, Jr.** Essential fatty acid metabolism in the feline: relationship between liver and brain production of long-chain polyunsaturated fatty acids. *Journal of Lipid Research* 35, 2032–40, 1994
- Pilla R, Suchodolski JS.** The role of the canine gut microbiome and metabolome in health and gastrointestinal disease. *Frontiers in Veterinary Science* 6, 498, 2019
- Potrykus J, Mahaney B, White RL, Bearne SL.** Proteomic investigation of glucose metabolism in the butyrate-producing gut anaerobe *Fusobacterium varium*. *Proteomics* 7, 1839–53, 2007
- Raila J, Buchholz I, Aupperle H, Raila G, Schoon HA, Schweigert FJ.** The distribution of vitamin A and retinol-binding protein in the blood plasma, urine, liver and kidneys of carnivores. *Veterinary Research* 31, 541–51, 2000
- Ramezani M, MacIntosh SE, White RL.** Utilization of D-amino acids by *Fusobacterium nucleatum* and *Fusobacterium varium*. *Amino Acids* 17, 185–93, 1999
- Reese AT, Dunn RR.** Drivers of microbiome biodiversity: a review of general rules, feces, and ignorance. *MBio* 9, e01294–18, 2018
- Remillard RL.** Homemade diets: attributes, pitfalls, and a call for action. *Topics in Companion Animal Medicine* 23, 137–42, 2008
- Roberts MT, Bermingham EN, Cave NJ, Young W, McKenzie CM, Thomas DG.** Macronutrient intake of dogs, self-selecting diets varying in composition offered *ad libitum*. *Journal of Animal Physiology and Animal Nutrition* 102, 568–75, 2018
- Rubinstein MR, Baik JE, Lagana SM, Han RP, Raab WJ, Sahoo D, Dalerba P, Wang TC, Han YW.** *Fusobacterium nucleatum* promotes colorectal cancer by inducing Wnt/ β -catenin modulator Annexin A1. *EMBO Reports* 20, e47638, 2019
- Runesvård E, Wikström C, Fernström L-L, Hansson I.** Presence of pathogenic bacteria in faeces from dogs fed raw meat-based diets or dry kibble. *Veterinary Record* 187, e71, 2020
- Sabshin SJ, Levy JK, Tupler T, Tucker SJ, Greiner EC, Leutenegger CM.** Enteropathogens identified in cats entering a Florida animal shelter with normal feces or diarrhea. *Journal of the American Veterinary Medical Association* 241, 331–7, 2012
- Salaun F, Blanchard G, Le Paih L, Roberti F, Nicéron C.** Impact of macronutrient composition and palatability in wet diets on food selection in cats. *Journal of Animal Physiology and Animal Nutrition* 101, 320–8, 2017
- Sandri M, Dal Monego S, Conte G, Sgorlon S, Stefanon B.** Raw meat based diet influences faecal microbiome and end products of fermentation in healthy dogs. *BMC Veterinary Research* 13, 65, 2017
- Schlegel BJ, Van Dreumel T, Slavić D, Prescott JF.** *Clostridium perfringens* type A fatal acute hemorrhagic gastroenteritis in a dog. *The Canadian Veterinary Journal* 53, 555–7, 2012
- Schmidt M, Unterer S, Suchodolski JS, Honneffer JB, Guard BC, Lidbury JA, Steiner JM, Fritz J, Kolle P.** The fecal microbiome and metabolome differs between dogs fed bones and raw food (BARF) diets and dogs fed commercial diets. *PLoS One* 13, e0201279, 2018
- Schweigert FJ, Raila J, Wichert B, Kienzle E.** Cats absorb beta-carotene, but it is not converted to vitamin A. *The Journal of Nutrition* 132, 1610S–2S, 2002
- Signat B, Roques C, Poulet P, Duffaut D.** *Fusobacterium nucleatum* in periodontal health and disease. *Current Issues in Molecular Biology* 13, 25–36, 2011
- Stockman J, Fascetti AJ, Kass PH, Larsen JA.** Evaluation of recipes of home-prepared maintenance diets for dogs. *Journal of the American Veterinary Medical Association* 242, 1500–5, 2013
- Stogdale L.** One veterinarian's experience with owners who are feeding raw meat to their pets. *The Canadian Veterinary Journal* 60, 655–8, 2019
- Suchodolski JS, Foster ML, Sohail MU, Leutenegger C, Queen EV, Steiner JM, Marks SL.** The fecal microbiome in cats with diarrhea. *PLoS One* 10, e0127378, 2015
- Suchodolski JS, Markel ME, Garcia-Mazcorro JF, Unterer S, Heilmann RM, Dowd SE, Kachroo P, Ivanov I, Minamoto Y, Dillman EM, et al.** The fecal microbiome in dogs with acute diarrhea and idiopathic inflammatory bowel disease. *PLoS One* 7, e51907, 2012
- Summers SC, Quimby JM, Isaiah A, Suchodolski JS, Lunghofer PJ, Gustafson DL.** The fecal microbiome and serum concentrations of indoxyl sulfate and p-cresol sulfate in cats with chronic kidney disease. *Journal of Veterinary Internal Medicine* 33, 662–9, 2019
- Thomas M, Feng Y.** Risk of foodborne illness from pet food: assessing pet owners' knowledge, behavior, and risk perception. *Journal of Food Protection* 83, 1998–2007, 2020
- van Bree FPJ, Bokken GCAM, Mineur R, Franssen F, Opsteegh M, van der Giessen JWB, Lipman LJA, Overgaauw PAM.** Zoonotic bacteria and parasites found in raw meat-based diets for cats and dogs. *Veterinary Record* 182, 50, 2018
- Vital M, Gao J, Rizzo M, Harrison T, Tiedje JM.** Diet is a major factor governing the fecal butyrate-producing community structure across Mammalia, Aves and Reptilia. *International Society for Microbial Ecology Journal* 9, 832–43, 2015
- Washizu T, Tanaka A, Sako T, Washizu M, Arai T.** Comparison of the activities of enzymes related to glycolysis and gluconeogenesis in the liver of dogs and cats. *Research in Veterinary Science* 67, 205–6, 1999
- Ziese AL, Suchodolski JS.** Impact of changes in gastrointestinal microbiota in canine and feline digestive diseases. *Veterinary Clinics of North America: Small Animal Practice* 51, 155–69, 2021