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Dietary Impact on Canine Behaviour

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Dietens påverkan på hundens beteende

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Abstract

Currently there has been a lot of interest in nutritional effects on behaviour, but the connection between diet and behaviour is still quite unestablished in dogs. This literature review presents connections between nutrition, physiology and canine behaviour, and whether canine behaviour can be regulated by altering the diet, based on current scientific literature in this field. By altering the diet, availability of precursors for hormones and neurotransmitters that controls behaviour may be regulated. Activity level is found to be affected by the fermentability of dietary fibre, energy restriction and indirectly by energy surplus. Aggressive behaviour may be decreased by low protein content and tryptophan supplement. Undesirable behaviour caused by lack of satiety is affected by dietary fibre and their fermentability. Taken together, the studies presented in this review points towards that there is a connection between nutrition, physiology and behaviour in dogs, as well as that canine behaviour can be regulated to some extent by altering the diet. However, further research is required to draw more specific conclusion on how nutrition affect canine behaviour.

Sammanfattning

Hur diet påverkar beteendet är ett aktuellt intresseområde, men sambandet mellan foderintag och beteende är fortfarande till stor del okänt hos hund. Denna litteraturöversikt är baserad på vetenskaplig litteratur och presenterar studier där samband mellan diet, fysiologi och beteende hos hund har undersökts. Hundens beteende kan påverkas genom tillförsel av utgångsämnen för beteendereglerande hormoner och signalsubstanser. Förekomst av aggressiva beteenden kan reduceras med lägre proteininnehåll och tryptofantillsatts. Hundens aktivitetsnivå har visats kunna påverkas av mängden kostfiber och energitillgång. Kostfiber och dess fermentabilitet påverkar också hundens mättnadskänsla, vilket i sin tur inverkar på oönskade beteende som uppstår vid hunger. Studierna i denna litteraturöversikt tyder på att hundens beteende till en viss grad kan regleras med förändringar i dieten. För att kunna dra mer specifika slutsatser krävs ytterligare forskning inom ämnesområdet.

Introduction

In Sweden, there is around 784 000 dogs in 572 000 households (SCB, 2012). Dogs are popular pets and people all around the country are in close contact with dogs every day. The dog was domesticated 13 000-17 000 years ago from the Grey wolf (Driscoll *et al.*, 2009) and has since then adapted remarkably to the human life style. Still, the dog is a predator that prefers to live in packs and have natural behavioural needs, such as digging, using their senses and exercise. An environment that does not fulfil these needs can cause the dog to become stressed, anxious or aggressive, which compromises its wellbeing. A dog's behaviour is not only controlled by the environment, but also by genetic, cognitive and physiological factors (Miklosi, 2014). Physiological factors, in turn, can be effected by nutrition (Bosch *et al.*, 2007) which will be explored further in this thesis.

There are significant evidence that nutrition can affect behaviour in mammals, through increasing or decreasing the substances that are precursors for behavioural regulating hormones and neurotransmitters (Bosch *et al.*, 2007). The connection between feed intake, physiology and behaviour in dogs, however, is not well established. Many factors, such as, breed and individual must be considered before applying this knowledge in dogs.

The aim of this literature review is to get an overview of connections between nutrition, physiology and behaviour in adult dogs reported in current literature and to find out if canine behaviour can be affected by altering the diet. The focus of nutrition will be on the major nutrient and energy content of diets. Physiology will include differences in physiological measures, such as plasma concentration of acting substances, between dogs expressing problematic behaviour and normal dogs, and the physiological mechanisms relevant for the connection between nutrition and behaviour. Since the definition of behaviour is wide, focus will be on common behaviours that have been studied and are considered problematic by dog owners, e.g. aggression, behaviours caused by lack of satiety and increased/decreased level of activity, or are indicators of poor animal welfare, e.g. stress. Presently, there is an insufficient amount of research on dogs, so some findings in other mammals with similar physiological traits e.g. human, monkey and rat, are also included. As diet may alter the availability of precursors for behaviour-regulating neurotransmitters and hormones, the hypothesis is that canine behaviour can be affected by dietary adjustment.

Literature research

This literature review is based mainly on peer-reviewed scientific literature, which were found mainly using databases such as Web of Knowledge, PubMed and Google Scholar. General articles were found using following search terms; ”dog* or canine” and ”nutrition or feed or diet” and ”behavio*”. Search terms such as ”aggression or satiety or activity”, ”protein or tryptophan”, ”fibre or carbohydrates”, ”PUFA or fatty acid”, ”seroton*”, ”cholesterol” were used to find more specialized articles. Besides databases, literature was also found from references of other articles.

Nutrient requirements of dogs

Energy

Chemical energy is found in proteins, fats and carbohydrates. It is not a nutrient per se but has a large impact on the physiological activity in all living organisms and is therefore important to consider in diets. In the body, energy is converted into adenosine triphosphate (ATP) which is utilized for most energy-requiring processes why a sufficient dietary energy supply is required to maintain homeostasis (Sjaastad *et al.*, 2010).

Adult dogs have a maintenance metabolic energy requirement of 552 kJ/ kg $BW^{0.75}$, but this estimation is just indicative since the energy requirement is effected by multiple factors. The requirements can either increase or decrease by factors such as breed, lean body mass percentage, age, stress level, activity, illness or trauma. It is also important to acknowledge that the individual variation between dogs and environmental factors, such as temperature, also effect the energy requirements. (NRC, 2006)

Protein

Amino acids are divided into essential and non-essential. Ten amino acids are essential for dogs; arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine. Essential amino acids are mainly used for protein synthesis. Whereas, dispensable amino acids are mainly required for maintenance, growth, lactation and gestation. Amino acids contain nitrogen, carbon and structural components that are used for making essential components like enzymes, purines, pyrimidines, heme, neurotransmitters, neuromodulators and hormones. The carbon can be used for energy or glucose production through gluconeogenesis. (NRC, 2006)

Adult dogs have a maintenance minimum crude protein requirement of 5.90 g/ kg $BW^{0.75}$ (AAFCO, 2014), however the National Research Council (NRC, 2006) presents 2.62g/ kg $BW^{0.75}$ to be the minimal requirement. The protein requirement is increased for dogs that are active, growing, geriatric, gestational, lactating and sick (NRC, 2006). There is no safe upper limit for proteins as excess protein is excreted through urine why it is assumed that dogs can handle high protein intakes without negative effects on homeostasis (NRC, 2006).

Fat

In addition to fats, there are other lipids with nutritional value e.g. glycolipids, phospholipids, lipoproteins, steroids and terpenes (McDonald *et al*., 2002). Fat is a macronutrient that provides energy and can be stored in both plants and animals. Fats are a form of glycerol based lipids where an alcohol glycerol is esterified with three fatty acids resulting in triglycerides (McDonald *et al.*, 2002). The fatty acid composition varies between fats. In dogs, two fatty acids are essential; linoleic and α-linolenic acid, also known as omega-6 and omega-3, respectively (NRC, 2006). These have both structural and physiological functions that are vital for the wellbeing of animals (McDonald *et al.*, 2002). The essential fatty acids are also sources of other important fatty acids, such as eicosapentaenoic (EPA) and docosahexaenoic (DHA) acids (McDonald *et al*., 2002).

For adult dogs at maintenance, the recommended allowance for total fat intake is 1.8g/ kg $BW^{0.75}$ (NRC, 2006). The recommended allowance of linoleic and α-linolenic acid is 0.36g/ kg $BW^{0.75}$ and 0.014g/ kg $BW^{0.75}$ of DM, respectively (NRC, 2006).

Although triglycerides are the main dietary lipids there are other important dietary lipids, such as cholesterol which is utilized for the structure of cell membranes and other cellular functions. Animals can synthesize cholesterol in most of their cells, but not in sufficient amounts to meet the demand and therefore dietary cholesterol is required. (Sjaastad *et al*., 2010)

Carbohydrates and dietary fibre

Dogs do not have a specific requirement for carbohydrates in their diet, but carbohydrates are used in dog feeds for energy, structure, texture, palatability and beneficial fibre (NRC, 2006). As a facultative carnivore, the dog is able to utilize starch to a larger extent compared with the carnivorous wolf (Axelsson *et al*., 2013). Axelsson *et al*. (2013) found that the wolf has two copies of a gene coding for amylase (AMY2B), whereas the dog has 4-30 copies, and that the gene expression is 28 times higher in dogs. They also presented evidence that two other genes (MGAM an SGLTI), which are important for starch digestion, have gone through selection during the domestication process.

Dietary fibre is structural remains of plant cells that are resistant to digestion and absorption by enzymes in the gastrointestinal tract, instead they are to a various extent fermented by microorganisms in the large intestine. Short-chain fatty acids (SCFA), such as acetate, propionate and butyrate, are product yield from the microbial fermentation of fibre and can be utilized as energy, thereby contributing to a small part of the energy intake (McDonald *et al.*, 2002). Even though dogs have the capacity to ferment dietary fibre, it is limited and an overconsumption of fibre will decrease availability and digestibility of other nutrients (NRC, 2006).

Dietary impact on canine behaviour

There are widespread disagreements about the definition of behaviour. These are reviewed in Levitis *et al*. (2009) and behaviour is concluded as: "… the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes" (Levitis *et al*., 2009, p. 10).

Activity

Activity is not per se a behaviour, but is connected to behaviours such as laziness and hyperactivity which can indicate poor welfare. Different activity levels are desirable in different context, e.g. therapy dogs need to be calm and patient with a low activity level whereas working dogs often need to be fast and vigorous with a high activity level.

Energy restriction effect on activity

The energy content in feed may affect activity level of the dog (Crowell-Davis *et al.*, 1995a;1995b). To investigate this relationship, Crowell-Davis *et al.* (1995a) studied the change in behaviour and activity of 39 overweight dogs of different breeds of both sexes that were put on restricted diets. Same feed was used in all parts of the study and the measurements were done individually. In a pre-study, the dogs were fed ad libitum for 15 minutes twice a day and the activity and behaviours were measured to create a baseline level for the studies. During the restriction period dogs were divided into groups with diets containing different degree of restriction; 0, 25, 40 or 50 % from calculated maintenance energy intake. Different behaviours, such as barking, movement and object manipulation, was recorded 4 times a day during days 1-2, 8-9 and 15-16 of calorie restriction. An activity index was measured to estimate the activity levels of individual dogs. The study ended when the dogs reached target weight or ultimately after 16 weeks. Data presented in the study showed that lower energy intake resulted in a lower activity level, except pre-feeding which was thought to be due to increased arousal during food anticipation (Crowell-Davis *et al.*, 1995a). A negative correlation between degree of restriction and activity index was seen, which was thought by the authors to be due to calorie-conserving behaviour (Crowell-Davis *et al.*, 1995a). Further, restricting energy intake can also cause frustration in dogs which can be seen as different behaviours such as increased object manipulation including chewing, pawing, licking and holding in mouth (Crowell-Davis *et al.*, 1995a). In a continuous study, Crowell-Davis *et al.* (1995b) studied the changes in activity when dogs were taken off the restricted diets and the difference in activity between baseline and 10 months after restriction for the same 39 dogs directly after the previous study ended. The dogs were transferred to either the same diet as in the pre-study or on maintenance requirement diet (Crowell-Davis *et al*., 1995b). Same feed and methods as in Crowell-Davis *et al*. (1995a) were used. The continuous study reported only minimal or non-substantial changes in activity when dogs were taken off the restricted diets, as well as between baseline and 10 months after restriction (Crowell-Davis *et al.*, 1995b).

Energy surplus effect on activity

Excess energy intake is stored in the body as fat and glycogen, therefore a constant excess energy intake will lead to weight gain in dogs. Obesity is a major health and welfare issue for pet dogs. In humans, there is a bidirectional relationship between obesity and physical activity i.e. obesity reduces physical activity and low physical activity is a risk factor for obesity (Hughes *et al.*, 2006; Ekelund *et al*., 2008). A similar bidirectional relationship has been presented in studies of dogs. In a study by Morrison *et al*. (2013) total activity and the time spent on behaviours requiring different activity levels for dogs in various body conditions were registered. The obese dogs performed less of vigorous activities than the ideal weight dogs. Further, an epidemiological study which investigated factors associated with obesity using a cross-sectional questionnaire for dogs attending veterinary practices, has found lack of exercise to be a risk factor associated with canine obesity (Courcier *et al.*, 2010).

Dietary fibre effect on activity

Bosch *et al.* (2009b) compared the effect of a low-fermentable fibre (LFF) diet containing 8.5 % cellulose and a high-fermentable fibre (HFF) diet containing 8.5 % sugar beet pulp and 2% inulin on behaviour in dogs, by continuous recording of different behaviours and several behavioural tests. They found that dogs fed HFF were more inactive than those fed LFF, probably due to prolongation of postprandial satiety. Dogs on LFF diet seemed to have increased arousal before feeding, seen as increased tail wagging, whereas dogs on HFF diet were more relaxed (Bosch *et al.*, 2009b).

Aggression

Aggression is a behaviour causing serious problems and can be a public health risk. Each year approximately 12 500 people in Sweden visit hospitals due to dog related injuries (SKK, 2012). Aggression is therefore a contributing factor for people to give up or euthanize their dog. There are several forms of aggression, for example dominant and territorial aggression. Territorial aggression can further be divided into fear or defensively induced.

Effect of energy restriction on aggression

Crowell-Davis *et al*. (1995a; 1995b) reported that dogs given energy restricted diets, i.e. energy deficient diets, can show aggressive behaviour such as snaps, bites, focused barking and fighting. The authors also found correlations between level of energy restriction and the amount of aggressive behaviours, but the direction of the correlation depended on how long the diet had proceeded as well as individual differences (Crowell-Davis *et al.*, 1995a). In Crowell-Davis *et al.* (1995a) study, where overweight dogs were put on caloric restricted diets, the overall aggression depended on how long the dogs had been on the restricted diet. Measures at day 1 showed a significant positive correlation i.e. the more restrictive the diet was, the more aggressive behaviours occurred. Whereas, by the second week on the diet the correlation became negative. The significant aggressive behavioural changes were however due to few dogs which indicates that there are individual differences that affect the aggressive behaviours. Overall, the aggressive behaviours that occurred initially decreased when the calorie restricted diet was prolonged. In the continuous study by Crowell-Davis *et al.* (1995b) the aggression decreased significantly from the time before restriction until 5-9 months after the restriction diet.

Fatty acids effect on aggression

Serum concentration of triglyceride is connected with dominance aggression in dogs. According to Pentürk & Yalcin (2003), who analysed blood samples of both aggressive and non-aggressive dogs, dominant aggressive dogs have significantly lower serum concentration of triglycerides than non-aggressive dogs.

Plasma α-linolenic acid concentration is found to be associated with aggression in dogs. This was concluded from a pilot study by Re *et al.* (2008) that analysed blood samples of both aggressive and non-aggressive dogs. The results demonstrated that the plasma concentrations of docosahexaenoic acid (DHA) was lower and the ratio between linoleic and α-linolenic acid was higher in aggressive than non-aggressive German Shepherds (Re *et al.*, 2008).

Cholesterol effect on aggression

Both total cholesterol and high-density lipoprotein cholesterol levels in serum have been found to be lower in aggressive than non-aggressive dogs (Pentürk & Yalcin, 2003), which agrees with Re *et* al. (2008) that showed lower plasma cholesterol in aggressive than non-aggressive dogs. These findings are also in line with the results of several studies made on humans and rats (Hillbrand & Spitz, 1999). The reason may be that serotonergic activity is found to be positively correlated with serum cholesterol levels in studies made on humans and monkeys (Buydens-Branchey *et al.*, 2000; Kaplan *et al*., 1994). There are no studies on how dietary levels of cholesterol affects behaviour in dogs, but Kaplan *et al*., (1994) found that monkeys in low-cholesterol diet were more aggressive than those on high-cholesterol diets.

The serotonergic system

Serotonin is a neurotransmitter in the serotonergic system, which affects a variety of physiological functions. Among these, serotonin modulates physiological function and is associated with both well-being and elevated mood (Mann, 1999; Young, 2007). Dysfunction in the serotonergic system is associated with increased aggression and decreased impulse control in dogs (Reisner *et al*., 1996), as well as in humans and rats (Mann, 1999). Reisner *et al*. (1996) found that aggressive and impulsive dogs had less serotonin metabolites in their cerebrospinal fluid than nonaggressive dogs. This agrees with findings by Rosado *et al*. (2010) who reported that aggressive, especially defensively aggressive, dogs had significantly lower serotonin concentration in serum than nonaggressive dogs.

Protein and amino acid effect on aggression

Tryptophan is an amino acid mainly utilized to produce nicotinamide adenine dinucleotide (NAD+), but is also a precursor for serotonin. Excess serotonin is not synthesized directly as a result of increased tryptophan intake, but if there is an increased amount of tryptophan available when the enzyme tryptophan hydroxylase that synthesizes serotonin synthesis is activated, the serotonin synthesis could increase up to double (Bosch *et al*., 2007). However, plasma tryptophan concentrations are regulated by tryptophan deoxygenate and therefore a continuous supply of dietary tryptophan is required (NRC, 2006)

A prospective study by Dodman *et al.* (1996) indicated that a diet with high protein concentration (32 %) increased fear induced territorial aggression in dogs compared to low (17 %) and medium (25 %) protein concentrations. However, protein concentration in the diet did not affect dominance aggression or hyperactivity. Another study compared if dominance aggression, territorial aggression and hyperactivity in dogs was effected by high (30 %) and low (18 %) protein diets with or without tryptophan supplementation (DeNapoli *et al*., 2000). Both low protein and tryptophan supplement reduced these behaviours. One reason for this could be the fact that tryptophan is generally found in lower concentration compared to other large neutral amino acids (LNAA), which all use the same transport carriers across the blood-brain barrier (Bosch *et al*., 2007). Low protein diet as well as tryptophan supplement will increase the ratio of tryptophan to other LNAA in the plasma, increasing the transport of tryptophan to the brain causing a higher serotonin synthesis (Bosch *et al*., 2007).

Carbohydrates effect on serotonin

The brain concentration of tryptophan is positively correlated with the synthesis of serotonin in the brain. Tryptophan competes with other LNAA for transport to the brain. In rats, ingestion of a carbohydrate rich diet increased plasma and brain tryptophan, which led to an increased serotonin synthesis in the brain (Fernstrom & Wurtman, 1971; Madras *et al.,* 1973). This is due to the fact that carbohydrates activate insulin secretion which increases plasma tryptophan, while decreasing the plasma concentration of other LNAA, which in turn leads to elevated brain tryptophan concentration that increases brain serotonin synthesis (Madras *et al.,* 1973). There has not been any research in dogs on how carbohydrates effect serotonin synthesis and thereby behaviour.

Satiety

Studies from different countries reported that 22-44% of the dogs are overweight (McGreevy *et al.,* 2005) and a small exploratory study reported the corresponding number to be 29% in Sweden (Björk, 2015). A critical factor for decreasing overweight is to reduce the energy intake and increase the energy expenditure. When decreasing the feed intake, most dogs do not feel satiated which can result in poor mental welfare and behavioural problems. Different undesirable behaviours, such as begging and scavenging, might occur due to feeling of hunger (Weber *et al*., 2007). The effectiveness of maintaining satiety after a meal varies between diets, indicating that dietary content affects satiety (Bosch *et al*., 2009a; Weber *et al*., 2007).

Dietary fibre effect on satiety

In humans and rats, SCFA activates the production and secretion of satiety-increasing hormones, like peptide tyrosine tyrosine (PYY) and glucagon-like peptide-1 (GLP-1), while decreasing the production and secretion of ghrelin which is a hunger-stimulating hormone (Batterham *et al*., 2002; Massimino *et al*., 1998; Wren *et al*., 2001). In a study by Bosch *et al.* (2009a) dogs fed a HFF diet had higher fermentation and SCFA production as well as lower voluntary feed intake than dogs fed a LFF diet. The authors concluded that the dogs felt more satiated on HFF diet. However, in the same study they did not find any effects of SCFA on PYY, GLP-1 or ghrelin responses (Bosch *et al.,* 2009a), so further studies are required to understand these mechanisms in dogs. In turn, Massimino *et al.* (1998) found that HFF increased GLP-1 secretion compared to LFF. There are additional studies presenting evidence that dietary fibre increases satiety and satiety duration in dogs (Weber *et al.,* 2007). However, conflicting results have been presented by other studies (Butterwick *et al*., 1994; Butterwick & Markwell, 1997) in dogs.

Stress

Stress can be an indicator of poor welfare in dogs and can be indicated by several different behaviours, such as snout licking, paw lifting, panting and a lowered posture (Beerda *et al.,* 1997).

Tyrosine effect on stress

Tyrosine is not an essential amino acid because it can be synthesized from phenylalanine. Tyrosine is a precursor to catecholamines, including dopamine, norepinephrine and epinephrine, which have many physiological functions but is especially important for coping with stress (Sjaastad *et al*., 2010). There are presently no reports on how tyrosine influences canine behaviour, but several on rats. Exposing an animal to uncontrollable stress increases the norepinephrine (NE) turnover in the brain which leads to a negative balance when more NE is used than synthesized (Rauch & Lehnert, 1990; Reinstein *et al*., 1984). Both Rauch & Lehnert (1990) and Reinstein *et al.* (1984) reported that this led to both neurochemical and behavioural deficits, such as depression and exploratory behaviours in rats. However, in both studies it was found that the symptoms could be prevented by pre-treatment of dietary tyrosine. Tyrosine rich diets does not increase catecholamine synthesis directly, but could be thought to improve coping with stress in dogs by increasing the amounts of the tyrosine available during stressful situation (Bosch *et al.*, 2007).

Discussion

Dietary impacts on dog behaviour is a relatively unexplored field, but in this literature review, the main studies that I have found within the area have been presented. Taken together, these indicate that a link between nutrition, physiology and behaviour exists in dogs and that canine behaviour can be regulated to some extent by altering the diet.

Activity

In some context it is desirable to be able to control the activity level of a dog. Present studies present evidence that a dog's activity level can be reduced by energy restriction (Crowell-Davis *et al.*, 1995a; b) or a diet containing HFF (Bosch *et al.*, 2009b), but whether these are good methods is arguable. Decreasing a dog's long term energy intake below maintenance would lead to a deficiency that disturbs the body's homeostasis and cause underweight, which both have negative health impact. Dogs fed HFF had a lower activity level than dogs fed LFF, which could be due to prolongation of postprandial satiety or just be due to a variation in individual activity levels since the experimental dogs were not fed both diets. Indirectly, a long term energy surplus can decrease activity level by causing overweight which in Morrison *et al.* (2013) was correlated to lower activity level. However, due to health reasons, this is not a desirable method and should not be practiced. Just before feeding, activity level can be increased, either by an energy deficient (Crowell-Davis *et al.*, 1995a; b) or LFF (Bosch *et al.*, 2009b) diet in dogs. So in practice, performing high activity requiring work before feeding might cause the dog to be more active. The higher activity level might although be due to frustration as a result of not feeling satiated, which the increased object manipulation in Crowell-Davis *et al.* (1995a) suggests. If frustration is a good type of high activity for working dog is arguable since frustration can lead to less thinking and more spontaneous reactions.

Aggression

Canine aggression is a severe problem for many dog owners. Low aggression is often desired as it may increase the life quality of both the animal and its owner. Energy restriction may affect aggressive behaviour in dogs but depends on the duration of the diet (Crowell-Davis *et al.*, 1995a). In the beginning of the energy restricted diet, dogs on more restricted diets showed a greater number of aggressive behaviours than dogs on less restricted diets, which may be due to frustration. Whereas by the second week on the diet, the number of aggressive behaviours decreased. This may be due to decreased energy intake which causes decreased activity (Crowell-Davis *et al.*, 1995a) or decreased protein intake which also causes decreased aggression (Dodman *et al.*, 1996; DeNapoli *et al.*, 2000).

Serotonin plays a significant role in aggression control. DeNapoli *et al.* (2000) discovered that tryptophan supplement also decreased aggression by increasing the precursor to serotonin. For animals it is important for the diet to have a good amino acid balance. Supplementing specific amino acids might disturb this balance because these amino acid would compete with the other amino acids for absorption which might lead to a deficiency of essential amino acids causing negative health impacts such as lowered immune response. Increased carbohydrate intake may also reduce aggression since increased carbohydrate intake led to increased serotonin synthesis in the brain in rats (Fernstrom & Wurtman, 1971; Madras *et al.,* 1973) and serotonin is associated with decreased aggression. Whether dietary carbohydrate can decrease aggression in dogs requires further research.

Also, a diet with high content of cholesterol, triglycerides, DHA and a low linoleic:α-linolenic ratio might decrease aggression (Pentürk & Yalcin, 2003; Re *et al.,* 2008) but this area requires further research.

Satiety

Unsatiated dogs that feel hungry may perform undesirable behaviours such as scavenging and begging (Weber *et al.,* 2007). This can lead to the owner giving the dog food to get rid of the behaviour, which is especially problematic for overweight dogs. A better solution may be to feed the dog a diet that increases satiety, such supplementation of HFF, which increases the fermentation product SCFA (Bosch *et al.*, 1995a). Dogs fed HFF diet in Bosch *et al.* (1995a) also showed lower voluntary feed intake, which suggest that these dog felt more satiated than dogs fed LFF. The mechanism behind SCFA and increased satiety in dogs is still uncertain, but might be similar to humans and rats where SCFA activates secretion of satiety increasing hormones PYY and GLP-1 while decreasing secretion of the hunger increasing hormone ghrelin (Batterham et al., 2002; Massimino et al., 1998; Wren et al., 2001). Studies on how dietary fibre effect satiety and feed intake have shown conflicting results. One reason for this might be that the studies used different types of fibres and inclusion levels, which effect the impact on stimulation and prolongation of satiety. Also, both studies by Butterwick *et al.* (1994) and Butterwick & Markwell (1997) only included 6 dogs on an energy restricted diet, which makes the result debatable since energy restriction, in addition to the dietary fibre, affect the voluntary feed intake.

Stress

If nutrition has any effect on stress in dogs is still unknown and requires further research, but in rat's, tyrosine is found to increase the ability to cope with stress thorough increased precursor for catecholamine's (Rauch & Lehnert, 1990; Reinstein *et al*., 1984).

General discussion

The results of Crowell-Davis *et al.* both studies indicate that dogs are able to adapt their activity level, i.e. energy output, to the energy intake level. This, as well as the fact that increased satiety decreases activity (Bosch *et al.*, 2009b), may be counter-productive for weight loss purposes. Overweight dogs require a higher energy expenditure than energy intake in order to lose weight. Therefore, energy restricted diets are supplemented with dietary fibre for its ability to reduce voluntary food intake (Bosch *et al*., 2009a; Weber *et al.*, 2007). Both reduced energy intake and increased satiety leads to a lower spontaneous activity in dogs, thus decreasing energy expenditure. This may lead to an overestimation of the energy expenditure and therefore decreased rate of weight loss. The increased object manipulation measured in Crowell-Davis *et al*. (1995a), indicate the need to offer dogs on restricted calorie diets objects so that they have an allowed object to focus the object manipulative behaviour on.

Whether it is possible or recommended to apply nutrition as a regulator of behaviour in practical recommendations is still unknown since there are several aspects to consider. As baseline it is important to make sure that the nutritional requirements are fulfilled and that no safe upper limits are crossed. Health aspect, i.e. can the dietary alteration harm the dog, needs to be considered and studied. For example, high fibre intake decreases protein digestibility (Weber *et al.*, 2007) which could cause a protein deficiency that can result in several negative physiological effects, such as impaired reproduction and weakened immune system. Also, the ethical aspect, such as whether an energy-deficient diet with low protein and high carbohydrate content is suitable to a carnivorous animal just to decrease aggression, where several other methods are available. The fact that dogs are able to digest starch (Axelsson *et al.*, 2013) is not equal to that high amounts of starch is beneficial for maintaining a good health.

The dog feed companies compose a large industry and differs a lot from e.g. livestock feed companies. Dog owners have generally less knowledge about nutrition and are willing to pay a lot more for feed than farmers, which affects the production of feed. Dietary alteration has to be profitable and sustainable for both owners and feed producers, therefore specialized feed for treatment of behavioural problems need to have a significant and verified effect. Palatability of dog feed is another important factor that has to be considered. A dog feed with low palatability will decrease consumption and would be pointless to produce, therefore aspects such as fibre content that has reported to decrease palatability (Weber *et al.,* 2007) has to be considered. The dog feed industry is run by large companies and many studies on canine nutrition are sponsored by these. This requires extra critical assessment of the results and conclusions in the articles since they might not have a complete objective standpoint. Also, areas in canine nutrition that are not beneficial for these companies lack in research which makes the science of canine nutrition unbalanced and specialized to their products.

Behaviours may be hard to register and can be influenced by multiple factors, such as environment, genetics, cognition and physiology, which makes behavioural research in dogs difficult. It is therefore important to acknowledge breed differences in both phenotype, temperament, genetics and behavioural traits. Therefore, conclusions made in one breed cannot always be directly applied on another. However, using a single breed in a study, as Re *et al.* (2008) did, will reduce the effect genetics has on behaviour.

Although there is evidence that diet may have an impact on canine behaviour, nutrition might not be the most effective treatment of problematic behaviours. Nutrition might, however, be a good additional treatment to more conventional ways.

Conclusion

There are documented connections between nutrition, physiology and behaviour indicating that canine behaviour could be regulated to some extent by altering the diet. Activity may be affected by the fermentability of dietary fibre, energy restriction and indirectly by energy surplus. Aggression may be affected by energy restriction, protein content and tryptophan supplement. Undesirable behaviour caused by lack of satiety may be affected by dietary fibre and their fermentability. Further research is required before it will be possible to make more specific conclusions and perhaps present possible practical recommendations for how to affect canine behaviour.

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