Review

Do pets influence the quantity and choice of food offered to them by their owners: lessons from other animals and the pre-verbal human infant?

Jon E.L. Day[1,*], Sophie Kergoat[2] and Kurt Kotrschal[3]

Address: [1] WALTHAM Centre for Pet Nutrition, Freeby Lane, Waltham-on-the-Wolds, Melton Mowbray, Leicestershire LE14 4RT, UK. [2] Mars Catalyst, Kleine Kloosterstraat, B-1932 Sint Stevens Woluwe, Belgium. [3] Konrad Lorenz Research Station and Department of Behavioural Biology, University of Vienna, Althanstraße 14, 1090 Vienna, Austria.

*Correspondence: Jon E.L. Day. Fax: +44(0)1664 415440. Email: jon.day@eu.effem.com

The electronic version of this article is the definitive one. It is located here: http://www.cababstractsplus.org/cabreviews

Abstract

All social animals influence each other's behaviour. One area of particular interest is the social interaction that occurs between pets and their owners. Within pet–owner dyads, food and feeding are always part of the dyadic ritual. In this review, we hypothesize that feeding can be considered to be a push–pull relationship where pets are, at least in part, able to 'negotiate' with their owner to influence 'when', 'what' and 'how much' they are fed. We examine the evidence that supports this hypothesis by appraising similar studies of other animals and the pre-verbal human infant. First, we review the differences in approaches and methodologies that exist between disciplines within the behavioural sciences. Second, the feeding behaviour of neonatal wild animals and pre-verbal infants is examined in terms of its causation, ontogeny, phylogeny and adaptation. Finally, the resulting knowledge concerning begging as honest signals of need, scramble competition, re-conciliation and consolation is applied to domestic pets with the objective of understanding of how owners are influenced by the feeding behaviour of their pets.

Introduction

The macrostructure of foraging in wild and feral animals is based on quite simple choices such as 'when', 'what' and 'how much to eat' [1]. However, the microstructure of feeding behaviour can involve a rich diversity of behavioural elements. Feeding behaviour varies considerably between species, and the specific ethogram will have been shaped both by the ecological niche in which the species has evolved, and the nature of the food being consumed [2]. Altricial species also exhibit specific social behaviours to influence another individual that is involved in the acquisition and provision of food on their behalf [3]. Such strategies are most beneficial during the neonatal and early life period when developing animals are dependent on their parents and peers for nutritional support. In this paper, we review the evidence that exists in support of this assertion and apply the knowledge to domestic dogs and cats.

The social behaviours observed within a particular pet–owner dyad are a function of a number of factors that include the personalities of both the animal and the human. The thesis of our review is that pets are able to influence both the type and quantity of food offered to them by their owners, and that their degree of success will be determined by their owners' personality and attitudes. We will examine the evidence for such interactions in dogs and cats and make comparisons with the behaviour of other animals and pre-verbal human-infants where applicable. Such comparisons are valuable because

both animals and pre-verbal infants lack the linguistic ability to directly communicate their level of feeding enjoyment [4]. This comparative approach can reveal significant opportunities to transfer ideas and methodologies between disciplines and help to advance science at an elevated rate [5].

Our interest in acquiring such knowledge is rather more applied than fundamental in nature. There is currently great concern about the prevalence of obesity in pet cats and dogs because this has implications for their health and longevity [6–8]. The root cause of this problem is clearly that pets consume more energy than they expend. However, the aetiology of obesity is multifactorial and will be influenced by a number of animal characteristics such as genetics, life-style, life-stage and diet [9–12]. As the pet is ultimately dependent upon its owner to supply the food necessary to meet its nutrient requirements (and to a certain degree its level of energy expenditure), we believe that strategies to address this important concern should focus, first, on the pet–human interaction [13–16]. It is the psychological dimension of this dyadic relationship that determines 'when', 'what' and 'how much' food is offered to, or is demanded by, the pet. One aspect of the pet–human relationship that could be particularly important to understand relates to communication between pet and owner pre-, during and post-feeding. Therefore, the ultimate objective of this paper is to offer information that may be of help in addressing levels of obesity in companion animals by better understanding how owners are influenced by the feeding behaviour of their pets.

Framework for the Study of Non-verbal Communication During Feeding

When the benefits accrued by expressing social behaviours (e.g. helping, signalling, etc.) outweigh the costs, they are incorporated into the behavioural repertoire of a given species [17–19].

All social animals influence each other's behaviours. Such interactions can range from simple altruistic behaviours to much more complex forms of communication that involve signalling and language. The vast majority of published research that investigates the social behaviour of animals is conducted within species (intra-specific), but there is also a growing body of literature examining social behaviour between species (inter-specific). One of the theoretical foundations for such inter-specific studies lies in the field of socio-cognitive research. This area of science has its roots in the 'social brain hypothesis' [20, 21] and examines systems where complex cognitive and social mechanisms are reciprocally connected. The study of pet–human communication is a particularly dynamic example of such research.

Humans have the ability to engage in social relationships with other animals [22, 23]. It has been argued that this is possible because of the existence of homologous vertebrate brain structures for social behaviour [24] and emotions [25]. Furthermore, physiological mechanisms such as the hypothalamic–pituitary–adrenal and sympathico–adrenergic stress axes [26–28] are shared across all species from fish to humans.

Domesticated animals are among our closest social companions [23] because we have selected them for tameness and, over generations of breeding, they have become even more socially compatible with humans [15, 29–31]. Such social relationships may be characterized by (generally) harmonious collaboration under conditions of balanced interests where social partners provide support for each other. For example, having a pet as a social partner may yield measurable physiological and health benefits for the human partner [32, 33]. In general, intra- and inter-specific dyadic relationships in vertebrate species fit a model characterized by cycles of conflict and resolution [34] because interests between partners are never entirely stable or fully balanced. As a consequence, individual positions are dynamically negotiated over time [35]. Conflicts in long-term valuable relationships are either resolved by 'reconciliation' between former opponents or by 'consolation' between a target and the new partner [34]. Hence, similar hypotheses and predictions can be made both within and between species (i.e. human animal).

One of the most commonly studied forms of social communication during feeding is that associated with the parent–infant bond. In the pre-verbal human infant, the behaviours used to influence food choice and intake may be analogous to those used by pets. Anderson [36] commented that, 'dogs and, to a lesser extent, cats are dependent upon their owners for providing food which will support their health, reproduction, growth, work and maintenance' and that, in contrast to the infant–human bond, 'this dependency may last throughout their natural life span'.

The framework that we propose in this review is grounded in classical motivational theory (which is part of the 'ethological' theory). Such theories propose that behaviour is governed by a series of motivational systems that compete with each other for their ultimate expression. A motivational system can be considered to be a brain-state that is controlled by both internal (endogenous) and external (exogenous) factors [5, 37, 38]. In the case of feeding motivation, the tendency to eat can be influenced by endogenous factors such as a specific nutrient deficit and/or exogenous factors such as the sight or smell of food. If feeding motivation becomes the dominant motivation, an individual will express feeding behaviour. This is expressed in two phases termed appetitive and consummatory [1]. In the appetitive phase the individual will seek food, and in the consummatory phase the food that has been acquired is consumed. Both positive and negative feedback loops operate to regulate the expression of behaviour to both avoid the animal

dithering between activities [39, 40] and ensure that behaviours are terminated once they have achieved their goal [41]. Once an appropriate type and quantity of food has been consumed to adequately reduce the deficit between the desired and actual nutrient intake [5], an individual will express a characteristic, post-prandial, sequence of behaviour followed by a period of quiescence (the 'satiety cascade') [42, 43].

We propose that it is during the appetitive, consummatory and post-prandial phases of feeding that the pre-verbal infant, neonate and pet has the ability to communicate with its caregiver to influence the types and quantity of food offered. Our framework predicts that the type and quantity of food offered by caregivers will be influenced by (1) the anticipatory behaviour expressed during the appetitive phase of feeding, (2) behavioural signals/cues expressed during the consummatory phase of feeding and (3) the structure of the satiety cascade.

In the following sections, we will review the evidence that exists in support of these predictions and discuss the ways in which pets may influence the type and quantity of food offered to them.

Methodologies to Study Non-verbal Communication During Feeding

The question, 'why does an animal do that?' can be interpreted in different ways. Niko Tinbergen [44] recognized that there were four different levels of explanation in studies of animal behaviour: (1) causation, (2) ontogeny, (3) phylogeny and (4) adaptation. Causation and ontogeny can be classed as *proximate* mechanisms and question 'what are the stimuli that start and stop the expression of the behaviour?' and 'how does the behaviour change over time?' respectively. Phylogeny and adaptation can be classed as *ultimate* mechanisms and question 'how does this behaviour relate to behaviours expressed by other species?' and 'how did this behaviour evolve?'

Almost all of the behavioural sciences involve the measurement of behaviour, either through direct observations, coded from videotapes, or rated along scales. A number of techniques are available, and these are selected to adequately test the hypothesis in question [45]. All behaviour studies require a list of behaviours to be defined, each with a series of unambiguous descriptions to allow observers to identify each behavioural element. Behaviour can be coded continuously to yield information concerning the rate of occurrence and proportion of time spent expressing the different behavioural elements. Time sampling can be used to catalogue behaviour at a repeating time interval throughout the testing period to yield information concerning the proportion of the total number of scans in which an individual is expressing a given behavioural element.

Once the behaviour of an individual or group of animals has been measured, it becomes possible to examine sequences of behaviours and to reveal patterns. For example, it may be significant that behaviour *A* often is seen to follow behaviour *B*. The use of pattern detection algorithms such as THEME analysis (Noldus Information Technology bv, The Netherlands) can be used to reveal the pattern of behaviour over time and describe its complexity and organization ('t-patterns' see [46]). It is also possible to examine whether the behaviour of one individual affects that of another or whether synchrony exists between individuals (see [47] for an example).

To investigate the causation of behaviour, it is possible to manipulate the motivational state and/or the ecological and social context of a test subject or population and measure the effect on behaviour. This can be achieved through changes to the endogenous and exogenous factors that combine to determine motivational strength.

There are many concepts investigated and different methodologies employed in the psychological study of human infants. These arise because of a primary focus on cognitive ability [48] in conjunction with a lack of linguistic competence in the infant. Language is a core medium of cognitive functioning and is an essential tool for researchers to probe cognitive activity. Yet, language cannot be the vehicle for cognition in infancy, and researchers must rely on non-linguistic indices of behaviour to make inferences about cognitive abilities [49]. One of the central tenets of infant studies is that the mental state of infants can only be inferred from direct observation of their behaviour. This emphasis arises from Piaget's careful, longitudinal studies of infant behaviour [50, 51]. One of his major contributions concerns the development of object permanence. However, several challenges have arisen to Piaget's notion that objects do not exist for infants unless they can perceive them. Researchers have attempted to circumvent this by measuring infant's visual response to object occlusions in order to investigate object permanence [52, 53]. Looking tasks appear to assess more accurately the information that infants gather about the physical properties of objects. However, in all of these experiments, a human observer estimates gaze direction, which is limited in that it does not allow accurate determination of where infants look and does not take into account short glances. An eye-tracking system (ETS) is a powerful tool to investigate perceptual and cognitive functions because eye movements provide a multifaceted measure of performance that permits stronger inferences to be drawn [54]. Advancements in automatic corneal reflection eye trackers have enabled researchers to use eye movements as a measure of infant cognitive and perceptual abilities. The automated corneal–reflection system is used to track infant eye movements and direction of gaze to either stationary or moving visual targets with implications for a diverse set of research areas [55].

When studying communication within a pet–human dyad, it is possible to directly ask the human questions. However, because the essence of communication is

interaction, observing dyadic behaviour can yield significant insights into the nature of the social interaction between pet and owner. Such ethological research of communication and social interactions encompasses the methodologies and theoretical background of observational and experimental evolutionary behavioural biology and cognitive ethology. The latter is mainly derived from primate work [34] and biological personality theory (including the coping style concept [56]). Some of the experimental methodologies used to study cognitive processes in the dog have been reviewed elsewhere [4, 30] and illustrate how effectively the methodologies used in human cognitive science can be transferred to studies of animals. In particular, expectancy violation [57, 58], mental state attribution [59], choice of target when begging [60, 61] and use of demonstrators in pointing and gaze following have been found to be of value [62]. The majority of studies of social cognition that exist in the literature examine whether and how pets read the signals given by humans [57–59, 61–63]. However, few studies exist that examine whether and how pets influence human behaviour.

Animal–Animal Communication During Feeding

'A key question in parent–offspring conflict is if provisioning is controlled primarily by parents or by their offspring, and how this interaction is mediated behaviourally' [64].

In altricial species, the caregiver invests a large effort in assisting the neonate to grow and survive. The ontogeny of parental investment is a function of the simultaneous resolution of conflicts or interests between members of the family [65]. Within this developing relationship, different forms of communication arise that have been selected through evolution to increase the fitness of both the caregiver and neonate [3]. Parent–offspring communication is often studied from the perspective of the caregiver, but it is clear that the neonate also has a significant impact on the relationship. In this section of the review, we consider the evidence that exists in the literature to illuminate the ways in which the neonates of wild animals negotiate with their caregivers to influence 'when', 'what' and 'how much' food is offered to them. We also consider examples where such behaviours exist between mature members of the same species.

When a parent returns to the nest with food, altricial birds beg for food using both noisy calls and behavioural signals such as gaping [66–73]. This begging behaviour can be viewed as being evolutionarily maladaptive because conspicuous calls and behavioural displays may betray the location of the nest to listening and watching predators, in addition to being energy intensive to produce. So why have such behaviours evolved? It has been hypothesized that begging calls are 'honest' signals of need and the intensity of the call reveals the hunger level of the nestling to the parent [74–76]. This allows the parents to feed selectively those individuals who can benefit the most. It has been demonstrated that the caloric costs of begging are far outweighed by the benefits [77]. When the between-sibling variation in hunger levels is large, the brood may benefit from signalling their willingness to contest the next food item delivered to the nest. Sibling barn owls, *Tyto alba*, have been found to negotiate to influence the level of begging behaviour which, in turn, affects the brood food allocation [78].

Social insects are also known to invest energy in the maternal care of their offspring. For example, insect larvae and nymphs are able to interact with their mothers to potentially influence their level of investment [79, 80]. In accordance with our current understanding of food solicitation in altricial birds, insect begging behaviours are thought to have evolved either as honest signals of need, or as competitive signals with the goal of manipulating the parent into giving more [80]. Insect begging can also be studied physiologically as some species emit both pheromones and hormones as signals to solicit parental care. Studies in birds have shown that late-hatched offspring beg more than early hatched offspring at a given level of general food deprivation, and similar observations have also been made in some insect species. The larvae of the burying beetle, *Nicrophorus orbicollis*, also express begging behaviour and it has been reported that food deprived larvae spend more time begging than replete larvae. Furthermore, junior larvae spend more time begging than their senior counterparts at a common level of food deprivation (although there are no detectible interactions between food deprivation and hatching status) [81].

In mammalian (non-human) species, it is also clear that the behaviour of the neonate can profoundly influence when, what and how much food is offered to them. For example, rat pups suckle milk from their dam for a period of approximately 3 weeks post-partum. They are able to find and attach to the nipples within hours of birth [82] and suckling provides the sole source of nutrition for the first 2 weeks of life [83]. During the first few days of lactation, the mother provides the structure for suckling and controls its occurrence [84, 85]. However, during late lactation, the pups begin to initiate and control episodes of suckling [86].

The survival of the vampire bat, *Desmodus rotundus*, is reliant on a feeding strategy that often involves one animal soliciting food from another. The energy budget of vampire bats is finely balanced and can result in starvation if an animal is food deprived for as little as 48–72 h [87]. In an individual night, it is possible that approximately 8% of adults will be unsuccessful in feeding [88]. Therefore, unsuccessful bats solicit regurgitated blood from one of their roost-mates. Hungry bats first groom their roost-mate by licking under the wings and then directly on the donors lips [88]. This behaviour has been found to be an adaptive strategy that is essential to the survival of vampire bats and has been characterized as reciprocal altruism

[89]. Such food sharing has only been observed in a few other mammalian species such as wild dogs, hyenas, chimpanzees and human beings [88].

In the wolf, weaning occurs over a period of about 10 weeks. From about 5 weeks of age, the gastro-intestinal system has matured sufficiently to accommodate solid food, although the strength of the pup's bite is not sufficient to chew large pieces of meat. It is from this age that the pups begin to solicit food from other pack members [90]. When a pack member approaches the den, hungry pups are seen to rush over to the adult wolf and 'poke their muzzles around the adult's mouth' in an action termed 'licking-up' [90]. This behaviour seems irresistible, and studies have shown that approximately 75% of adults regurgitate as soon as they are met by a pup/pups [91]. 'Licking up' is also seen in adult wolves where it may serve as a signal of appeasement during social conflict.

Those animals that obtain regurgitated food from their caregiver are following a beneficial strategy that helps them to safely learn about new food items. All neonatal animals have to learn to discriminate food from non-food items and build a 'cognitive menu' concerning which food cues (e.g. tastes) are associated with defined positive and negative nutritional outcomes [1]. Regurgitated food can be considered to be safe because the knowledge the giver has amassed during its own development has caused it to avoid foods that lead to illness and select foods that lead to the acquisition of beneficial nutrients. In this manner, animals can rapidly pass knowledge from generation to generation without the costs associated with trial-and-error learning [92].

The provision of food can also be viewed as being an advert of social attention that establishes and maintains the social bond. This may become an important component of social behaviour, and the precise nature of food provision may be affected by individual personality and attachment style.

Despite the volume of literature that documents begging as an honest signal of need, it can be argued that this may not always be the case [93]. It is possible that begging may also, in some circumstances, reflect sibling competition for food items. Such 'scramble competition' can be shaped by adaptive learning to maximize energetic rewards [93, 94]. Begging may only be honest when the potential for conflict is low and food availability is not limiting [95, 96]. Whether begging is classified as an honest signal of need or as scramble competition has consequent implications for how the parent–offspring communication is interpreted.

Application of Animal–Animal Knowledge to Studies of the Pet

There is some evidence to suggest that puppies will increase their begging activity in the pre-weaning period in an attempt to obtain more milk from the dam [97]. It is suggested that during the weaning process, puppies balance the relative costs and benefits of obtaining either milk or solid food. The behaviour of the dam towards her litter is known to change during weaning in a manner that is consistent with theories of parent–offspring conflict. Between 2 and 7 weeks of age, she decreases her caregiving behaviour, decreases both the frequency and duration of nursing bouts, and increases the level of aggression towards the puppies. In response, the puppies, increase the level of care-seeking and contact-seeking behaviour [98], which could be considered an honest signal of need. However, this assertion would require further testing.

Cats are known to show several modes of maternal care [99]. Some individuals rear their litters in a solitary manner. Others adopt a more communal, cooperative, strategy where litters are pooled and care is given by more than one mother and also non-breeding 'helpers'. In such cases, the non-breeding adults are sometimes observed to provide food for the breeding adults. Whether this food provisioning is sensitive to the needs of the lactating mothers and litters is unclear.

It is known that kittens develop a characteristic 'milk treading' behaviour whilst they are suckling where their forepaws are placed on either side of the nipple and moved in a series of treading steps [100]. It is believed that this behaviour stimulates milk flow when it is not let down as quickly as the kitten requires. It remains unclear whether this behavioural strategy is used honestly or may reflect a form of scramble competition.

Domestic dogs are known to share many behavioural traits with their lupine ancestors. Malm [101] found that the 'licking up' behaviour exhibited by wolves is also present in the domestic dog. A survey of 263 Swedish dog breeders revealed that more than 60% had observed regurgitation among their dogs (and in some cases the breeders had observed dogs other than the dam regurgitating). The study reported a strong link between begging and regurgitation at approximately 4 weeks of age, and it was concluded that regurgitation is an important element of the weaning process in dogs.

Infant–Human Communication During Feeding

Even from the first days of life, the food choice and intake of human infants is controlled by innate food preferences and aversions, and self-regulation [102]. During the ontogeny of feeding behaviour, the infant makes the transition from an exclusively milk diet to a modified adult diet at weaning. This is a period of rapid development and dietary change, and it is during these early years that eating plays a central role in determining future food choices and weight status [103]. As is the case with other animals, the provision of food also plays a central role in social bonding and is most marked when the infant is consuming solely milk (be this bottle- or breast-fed).

The attitude of the infant's caregiver affects both meal size and the frequency of feeding [104]. However, as is the case with other altricial animals, the infant is also in control. Neville et al. [105] demonstrated that milk is often still available following the termination of a breast-fed meal. This finding was confirmed by Dewey and Lonnerdal [106], who studied the feeding behaviour of infants between 6 and 21 weeks of age. Such observations are suggestive of the infant being able to learn to control meal size. However, the factors that control meal size remain largely unstudied and the extent to which their effects may be modified by learning and experience is unknown [104].

The degree to which meal size correlates with either the pre- or post-prandial interval determines whether an individual has a reactive or anticipatory pattern of intake control [104, 107]. When meal size is correlated with the pre-prandial interval, it is reactive to the level of hunger; whereas when meal size correlates with the post-prandial interval, it is anticipatory of future hunger. Wright [108] found that at 4 weeks of age, breast-fed infants took their largest meal in the morning following a longer overnight interval, but by 24 weeks of age, infants took their largest meal in the evening prior to the overnight fast. The latter post-prandial correlation is typical of adult eating patterns.

Bottle- and breast-fed infants have been found to have different patterns of intake across the day. It has been argued that the difference arises because of the breast-fed infant being able to regulate their intake in a manner unlikely to be possible in bottle-fed infants because of the restrictions in the amount of milk offered at each meal. In breast-fed infants, milk is viewed as being offered in excess and, therefore, it is the infant that is in control of 'how much' is consumed [109].

Gender differences have also been found in the ability of human males and females to judge levels of hunger in infants with females being more adept at recognizing hunger variation than males [108]. Parallels exist within the animal–animal feeding context as it has been found that males are less sensitive to begging than females [70, 110].

At weaning, the infant has to make the transition from milk to solid food and learn to accept an adult diet. One-year-old children are variable in their patterns of food choice and intake from meal to meal. This is consistent with models of learned food preferences and aversions, and neophobia. Measurements taken from a single meal will not reliably summarize children's feeding behaviour and food refusal is a common feature of eating behaviour at this age [111]. Such food refusal may also represent an (unconscious) attempt by the infant to test the caregiver and introduce a conflict that makes the caregiver more dependent upon the infant. 'Difficult' infants probably get more attention and monopolize their caregiver and thereby promote a stronger social bond. Indeed, weaning itself can be viewed as being under control of the infant, with mothers believing that the introduction of solids is 'baby-led and initiated by some physical characteristic or behavioural action of the infant' [112].

Application of Infant–Human Knowledge to Studies of the Pet

Malm and Jensen [97] studied the within- and between-litter variation in milk and solid food intake in puppies. They found evidence that the puppies that obtained most milk were also most active towards the dam. They also reiterated the similarities that exist between humans and other animals in the psychological importance of suckling and the maintenance of social bonding.

As was stated earlier, the use of 'milk treading' by kittens to increase the volume of milk produced firmly confirms that they are, at least in part, in control of meal size [100]. This is in accordance with the studies of human infants [104–106].

Patterns of food intake have been relatively well studied in the cat [113–117], and some evidence exists for the dog [118]. These studies suggest that when pets are given unrestricted access to a nutritionally complete diet, they will self-regulate their level of food intake. Kane et al. [116] found that cats eat approximately 16 meals/day and consume a mean of 4.8 g DM/meal. This level of intake was equivalent to the cat's maintenance requirement and was independent of the format of the food offered (dry commercial, wet commercial or casein-based purified). If cats have the ability to self-regulate their feed intake at or around maintenance requirements, it must be questioned what causes this regulation to fail in the home environment.

Using the same methodologies that are used in infant cognition studies, it has been possible to describe the ways in which pets can interact with the owner around feeding. Gácsi et al. [61] found that dogs will selectively beg from humans on the basis of whether their eyes or face is visible. Miklósi et al. [62] found that both cats and dogs could use pointing cues given by humans to locate hidden food, but only dogs were adept at signalling the location of hidden food to a naïve owner as cats appeared to lack some of the components of the required attention-getting behaviour.

Pet–Human Communication During Feeding

As is probably true for all dyadic social relationships, owner and pet may negotiate their positions via iterative interactions. Food provisioning and feeding may be a key example of this ongoing owner–pet negotiation because it is important for the animal to be fed, and for the owner to provide food. Feeding interactions do not necessarily cause the social bond [119]. However, receiving or providing food is deeply rooted in the psychology of social

animals (including man), especially where it is linked with social bonding.

Relationships between cats and owners are considered to be complex, with contributions being made from both parties [120, 121]. Owners often report a perfect fit with their cats [122], and this may be mainly the result of the flexibility and variability of cat social behaviour [123], which enables them to adapt [124]. For example, cat behaviour and the time spent interacting with the owner is known to be influenced by the activity, mood, gender and age of the owner [121, 125]. In human and non-human animals, personality (synonymous with 'individual behavioural phenotype' or 'coping style' [56]) is a major determinant of decision-making, such as how individuals respond to environmental challenges and how they interact socially [126–130]. Recent, as yet unpublished data support this proposition within the feeding context in human–cat and human–dog dyads (Kurt Kotrschal, personal communication, 2008).

In modern households, cats usually receive their food from their owner but do not reciprocate by catching mice. However, they may trade social attention. Some owners regard their cats and dogs as social companions and supporters and evidently are rewarded by the social attentiveness of their pet. The social significance of this companionship is less clear for the cat, although well-socialized cats actively seek human contact [124, 131]. It is unlikely that well-socialized cats interact with humans solely to ensure that they are fed, and it is probable that they are capable of developing social bonds with 'their' humans [119, 132].

Cats are often described to be finicky eaters that have the potential to make owners nervous and tense whilst feeding their pet. Cats can suddenly refuse a food that it has previously eaten without problems. In such circumstances, owners are likely to offer a different variety of food in an attempt to encourage eating. It is conceivable that cats learn that feed refusal is a strategy that they can employ to influence 'what' they are fed. In addition, such a strategy would allow them to manipulate their owners and could be used as a powerful tool in a dyadic 'war for attention'. Using finicky eating habits, cats could efficiently condition their owners to act their way and, thereby, almost entirely dominate this context of the relationship. This dyadic conflict model predicts that finicky feeding and other socially demanding habits arise in pets whose owners actually readily engage in such negotiations, which, in turn, would depend on owner personality. However, this remains to be tested.

Pre-feeding, begging behaviour can be a powerful means to influence 'when' and 'how much' food is offered. Whether such behaviour is an honest signal of feeding motivation in cats and dogs is unclear. It is intuitive to suggest that a hungry cat or dog will increase its expression of begging behaviour. However, in addition to the endogenous elevation in feeding motivation, expectation (conditioned by being fed regularly at a certain time of the day) and social components may have roles in the timing and intensity of begging. In both dogs and cats, begging behaviour can involve rubbing and following the owner, vocalization, sniffing or licking an empty bowl. It is possible that pets can beg for food in excess of their current nutritional needs and that this may be a function of the degree of autonomy that the pet has developed. For example, if an owner acts in a way to maximize the dependency of their pet upon them, this is likely to also intensify the animal's begging behaviour. This is yet another idea which remains to be tested.

During eating, the macrostructure and microstructure of feeding behaviour can be interpreted by the owner to make judgements about how much their pet enjoys the food that has been offered. Not all of this 'behavioural coding' by the owner is necessarily happening at the conscious level and, in fact, owners seem to differ widely in correctly interpreting the behaviour of their cats around feeding (Gracey, Bauer, Wedl and Kotrschal, unpublished). The behaviours shown by cats when expecting food may be categorized as high-arousal social contact behaviours. Other behavioural elements may be integrated by individual cats through classical conditioning reinforced by positive owner–cat interactions [133]. The resulting judgements of cat behaviour would be of value to the human owner to judge the success of the food choices that they have made on their pet's behalf.

In the post-prandial period, the behaviour of the pet may convey information about how satisfying the meal was. The satiety cascade is sensitive to the discrepancy between the desired and actual nutrient intake, and a nutritionally replete pet is likely only to express characteristic behaviours when the level of feeding motivation is falling and low. It remains to be tested whether the degree of satiation and/or satisfaction with the food offered affects how likely a cat would be to engage in relaxed play and other behaviours that are rewarding for the owner.

There are phylogenetic differences between the social behaviour of dogs and cats. It is generally accepted that the domestic dog has evolved from the wolf, *Canis lupus*, and the domestic cat has evolved from the African wildcat, *Felis silvestris lybica*. The wolf is a social group-living species that has highly developed social cognitive skills [4], whereas the African wildcat is a solitary species that seldom lives in groups. Domestic pets have undergone two selective processes [4]. The first is domestication that involves biological and cultural changes [4, 134], particularly an unspecific selection for tameness, which may also be contingent with a genomic disintegration, leading to a variety of phenotypes [135]. The second is genetic selection, where pets have been bred for desirable traits such as appearance or roles in society [4, 136]. It would be intuitive to suggest that dogs may be more adept at influencing the food offered to them by their owners than cats because of their evolutionary history. However, it is also possible that both cats and dogs can learn new food

solicitation strategies in the domestic environment and that such abilities will have been co-selected during breeding programmes. However, the latter explanation would include the former because dogs, being descendents of highly social ancestors, may show greater learning dispositions in this respect than cats.

Conclusions/Summary

The objective of this paper is to review information that may provide a better understanding how owners are influenced by the feeding behaviour of their pets. The thesis of our review is that pets are able to influence both the type and quantity of food offered to them by their owners and that their degree of success will be determined by their owner's personality and attitudes.

It has been demonstrated that strong parallels exist in both animal–animal and infant–human dyads that offer insights into the social control of food intake in the pet–human dyad. In particular, it seems that begging behaviour and finicky eating habits may be powerful tools that pets could use to control 'when', 'what' and 'how much' they are fed. This has been described as a push–pull relationship where the personality of both the neonate and caregiver may exert an influence.

As the aetiology of obesity in pet cats and dogs has its roots in the heart of the pet–owner relationship, it should become a priority to better understand the factors that control the types and quantity of food offered to domestic pets. It is too simple to view the provision of pet food as being a one-way process because it is clear that the pet is also, at least in part, in control. In addition, it is also too simple to assume that the palatability of food will be the only factor determining food acceptance.

It has been highlighted that owners may be influenced by (1) finicky eating, (2) begging, (3) the macrostructure of eating behaviour, (4) the microstructure of eating behaviour and (5) the sequence of behaviour expressed during the post-prandial satiety-cascade. The relative contribution of each factor towards the final nature of food provision may vary according to both pet and owner personality and the species of pet in question.

As many of our propositions concerning the pet–human dyad are speculative, we conclude that much more research is needed in this area. Priority should be given to accelerate our understanding of pet–human communication in relation to feeding in order to better address the problem of pet obesity.

References

1. Day JEL, Kyriazakis I, Rogers PJ. Food choice and intake: towards a unifying framework of learning and feeding motivation. Nutrition Research Reviews 1998;11(1):25–43.

2. Slater PJB, Halliday T. Behaviour and Evolution. Cambridge University Press, Cambridge, UK; 1994.

3. Godfray HCJ. Signalling of need by offspring to their parents. Nature 1991;352(6333):328–30.

4. Cooper JJ, Ashton C, Bishop S, West R, Mills DS, Young RJ. Clever hounds: social cognition in the domestic dog (Canis familiaris). Applied Animal Behaviour Science 2003;81(3):229–44.

5. Day JEL, Kyriazakis I, Rogers PJ. Feeding motivation in animals and humans: a comparative review of its measurement and uses. Nutrition Abstracts and Reviews A 1997;67(2):69–79.

6. Freeman LM, Abood SK, Fascetti AJ, Fleeman LM, Michel KE, Laflamme DP, et al. Disease prevalence among dogs and cats in the United States and Australia and proportions of dogs and cats that receive therapeutic diets or dietary supplements. Journal of the American Veterinary Medical Association 2006;229(4):531–4.

7. McGreevy PD, Thomson PC, Pride C, Fawcett A, Grassi T, Jones B. Prevalence of obesity in dogs examined by Australian veterinary practices and the risk factors involved. Veterinary Record 2005;156(22):695–702.

8. Robertson ID. The association of exercise, diet and other factors with owner-perceived obesity in privately owned dogs from metropolitan Perth, WA. Preventive Veterinary Medicine 2003;58(1–2):75–83.

9. Laflamme DP. Nutrition for aging cats and dogs and the importance of body condition. Veterinary Clinics of North America: Small Animal Practice 2005;35(3):713–42.

10. Hurst P. All things considered: feeding dogs and cats – different needs for different stages. Veterinary Technician 2004;25(8):538–47.

11. Butterwick RF, Hawthorne AJ. Advances in dietary management of obesity in dogs and cats. Journal of Nutrition 1998;128(12 Suppl.):2771S–5S.

12. Legrand-Defretin V. Energy requirements of cats and dogs: what goes wrong? International Journal of Obesity 1994;18(Suppl. 1):S8–13.

13. Jackson C, Gray C. The dog's too fat – and so is the client: how to handle delicate consultations. In Practice 2005;27(4):219–21.

14. LaVigne DW. Thoughts on solutions to pet obesity. Journal of the American Veterinary Medical Association 2008;232(10):1460.

15. Hawn R. Taking on canine and feline obesity. Veterinary Technician 2005;26(1):51–2.

16. Stuart B. Offering solutions to pet obesity. Journal of the American Veterinary Medical Association 2008;232(7):993.

17. Alexander RD. The evolution of social behaviour. Annual Reviews in Ecology and Systematics 1974;5(1):325–83.

18. Hamilton WD. The genetical evolution of social behaviour. I. Journal of Theoretical Biology 1964;7(1):1–16.

19. Hamilton WD. The genetical evolution of social behaviour. II. Journal of Theoretical Biology 1964;7(1):17–52.

20. Dunbar RIM. The social brain hypothesis. Evolutionary Anthropology 1998;6(5):178–90.

21. Byrne RW, Whiten A. Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys. Clarendon Press, Oxford, UK; 1988.

22. Wilson ER. Biophilia. Harvard University Press, Cambridge, MA; 1986.

23. Podberscek A, Paul ES, Serpell J. Companion Animals and Us: Exploring the Relationships between People and Pets. Cambridge University Press, Cambridge, UK; 2005.

24. Goodson JL. The vertebrate social behavior network: evolutionary themes and variations. Hormones and Behavior 2005;48(1 Special Issue):11–22.

25. Panksepp J. Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, Oxford, UK; 1998.

26. Wascher CAF, Scheiber IBR, Kotrschal K. Heart rate modulation in bystanding geese watching social and non-social events. Proceedings of the Royal Society B: Biological Sciences 2008;275(1643):1653–59.

27. McEwen BS, Wingfield JC. The concept of allostasis in biology and biomedicine. Hormones and Behavior 2003;43(1):2–15.

28. DeVries AC, Glasper ER, Detillion CE. Social modulation of stress responses. Physiology and Behavior 2003;79(3):399–407.

29. Hare B, Tomasello M. Human-like social skills in dogs? Trends in Cognitive Sciences 2005;9(9):439–44.

30. Miklósi A, Topál J, Csányi V. Comparative social cognition: what can dogs teach us? Animal Behaviour 2004;67(6):995–1004.

31. Frank H, Frank MG. On the effects of domestication on canine social development and behavior. Applied Animal Ethology 1982;8(6):507–25.

32. Wilson CC, Turner DC. Companion Animals in Human Health. Sage Publications, London, UK; 1998.

33. Friedmann E, Katcher AH, Meislich D. When pet owners are hospitalized: Significance of companion animals during hospitalization. In: Katcher AH, Beck AM, editors. New perspectives on our lives with companion animals. University of Pennsylvania Press, Philadelphia; 1983. p. 346–50.

34. Aureli F, Waal FBM. Natural Conflict Resolution. University of California Press, Berkeley, CA; 2000.

35. de Waal FBM. The first kiss. In: Aureli F, de Waal FBM, editors. Natural Conflict Resolution Berkeley. University of California Press, Berkeley, CA; 2000. p. 15–33.

36. Anderson RA, Anderson RJ. Nutrition and Behaviour in Dogs and Cats: Proceedings of the First Nordic Symposium on Small Animal Veterinary Medicine, Oslo, 15–18 September 1982. Pergamon Press, Oxford, UK; 1984.

37. Bolles RC. Theory of Motivation. Harper and Row, New York, NY; 1967.

38. Toates FM. Motivational Systems. Cambridge University Press, Cambridge, UK; 1986.

39. Houston A, Sumida B. A positive feedback model for switching between two activities. Animal Behaviour 1985;33(1):315–25.

40. Wiepkema PR. Positive feedbacks at work during feeding. Behaviour 1971;39(2):266–73.

41. McFarland D. Feedback Mechanisms in Animal Behaviour. Academic Press, London, UK; 1971.

42. Bellisle F. Functional foods and the satiety cascade. Nutrition Bulletin 2008;33(1):8–14.

43. Hinton EC, Parkinson JA, Holland AJ, Arana FS, Roberts AC, Owen AM. Neural contributions to the motivational control of appetite in humans. European Journal of Neuroscience 2004;20(5):1411–18.

44. Tinbergen N. On aims and methods of ethology. Zeitschrift für Tierpsychologie 1963;20:410–33.

45. Martin P, Bateson P. Measuring Behaviour: An Introductory Guide. Cambridge University Press, Cambridge, UK; 1993.

46. Anolli L. The Hidden Structure of Interaction: From Neurons to Culture Patterns. IOS Press, Amsterdam, The Netherlands; 2005.

47. Docking CM, Van de Weerd HA, Day JEL, Edwards SA. The influence of age on the use of potential enrichment objects and synchronisation of behaviour of pigs. Applied Animal Behaviour Science 2008;110(3–4):244–57.

48. Horowitz FD. Exploring Developmental Theories: Towards a Structural/Behavioral Model of Development. Lawrence Erlbaum Associates, Publishers, Hillsdale, NJ; 1987.

49. Haith MM, Benson JB. Infant cognition. In: Damon W, Kuhn D, Siegler R, editors. Handbook of Child Psychology: Vol. 2, Cognition, Perception and Language, 5th ed. Wiley, New York, NY; 1998. p. 199–254.

50. Piaget J. The Origins of Intelligence in Children. International Universities Press, Madison, CT; 1952.

51. Piaget J. Le langage et la pensée du point de vue génétique. Acta Psychologica 1954;10(C):51–60.

52. Baillargeon R. Young infants' reasoning about the physical and spatial properties of a hidden object. Cognitive Development 1987;2(3):179–200.

53. Baillargeon R, Spelke ES, Wasserman S. Object permanence in five-month-old infants. Cognition 1985;20(3):191–208.

54. Hayhoe MM. Advances in relating eye movements and cognition. Infancy 2004;6(2):267–74.

55. Aslin RN, McMurray B. Automated corneal-reflection eye tracking in infancy: Methodological developments and applications to cognition. Infancy 2004;6(2):155–63.

56. Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, et al. Coping styles in animals: current status in behavior and stress-physiology. Neuroscience and Biobehavioral Reviews 1999;23(7):925–35.

57. Elgier AM, Jakovcevic A, Mustaca AE, Bentosela M. Learning and owner–stranger effects on interspecific communication in domestic dogs (Canis familiaris). Behavioural Processes 2009;81:44–9.

58. Bentosela M, Barrera G, Jakovcevic A, Elgier AM, Mustaca AE. Effect of reinforcement, reinforcer omission and extinction on a communicative response in domestic dogs (Canis familiaris). Behavioural Processes 2008;78(3):464–9.

59. Virányi Z, Topál JO, Gácsi MA, Miklósi A, Csányi V. Dogs respond appropriately to cues of humans' attentional focus. Behavioural Processes 2004;66(2):161–72.

60. Gaunet F. How do guide dogs of blind owners and pet dogs of sighted owners (*Canis familiaris*) ask their owners for food? Animal Cognition 2008;11(3):475–83.

61. Gácsi M, Miklód Á, Varga O, Topál J, Csányi V. Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. Animal Cognition 2004;7(3):144–53.

62. Miklósi Á, Pongrácz P, Lakatos G, Topál J, Csányi V. A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. Journal of Comparative Psychology 2005;119(2):179–86.

63. Pongrácz P, Miklósi Á, Kubinyi E, Gurobi K, Topál J, Csányi V. Social learning in dogs: The effect of a human demonstrator on the performance of dogs in a detour task. Animal Behaviour 2001;62(6):1109–117.

64. Quillfeldt P, Masello JF. Context-dependent honest begging in Cory's shearwaters (*Calonectris diomedea*): influence of food availability. Acta Ethologica 2004;7(2):73–80.

65. Royle NJ, Hartley IR, Parker GA. Parental investment and family dynamics: Interactions between theory and empirical tests. Population Ecology 2004;46(3):231–41.

66. Iacovides S, Evans RM. Begging as graded signals of need for food in young ring-billed gulls. Animal Behaviour 1998;56(1):79–85.

67. Leonard ML, Horn AG. Age-related changes in signalling of need by nestling tree swallows (*Tachycineta bicolor*). Ethology 2006;112(10):1020–6.

68. Porkert J, Špinka M. Begging in common redstart nestlings: scramble competition or signalling of need? Ethology 2006;112(4):398–410.

69. Goodship NM, Buchanan KL. Nestling testosterone controls begging behaviour in the pied flycatcher, *Ficedula hypoleuca*. Hormones and Behavior 2007;52(4):454–60.

70. Quillfeldt P, Masello JF, Hamer KC. Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, *Puffinus puffinus*. Animal Behaviour 2004;68(3):613–20.

71. Smiseth PT, Amundsen T. Senior and junior nestlings in asynchronous bluethroat broods differ in their effectiveness of begging. Evolutionary Ecology Research 2002;4(8):1177–89.

72. Mathevon N, Charrier I. Parent–offspring conflict and the coordination of siblings in gulls. Proceedings of the Royal Society B: Biological Sciences 2004;271(Suppl. 4):S148–51.

73. Rodríguez-Gironés MA. Sibling competition stabilizes signalling resolution models of parent–offspring conflict. Proceedings of the Royal Society B: Biological Sciences 1999;266(1436):2399–402.

74. Smith HG, Montgomerie R. Nestling American robins compete with siblings by begging. Behavioral Ecology and Sociobiology 1991;29(4):307–12.

75. Kilner R, Johnstone RA. Begging the question: are offspring solicitation behaviours signals of need? Trends in Ecology and Evolution 1997;12(1):11–15.

76. Leonard ML, Horn AG. Need and nestmates affect begging in tree swallows. Behavioral Ecology and Sociobiology 1998;42(6):431–6.

77. Bachman GC, Chappell MA. The energetic cost of begging behaviour in nestling house wrens. Animal Behaviour 1998;55(6):1607–18.

78. Roulin A. Effects of hatching asynchrony on sibling negotiation, begging, jostling for position and within-brood food allocation in the barn owl, *Tyto alba*. Evolutionary Ecology Research 2004;6(7):1083–98.

79. Rauter CM, Moore AJ. Do honest signalling models of offspring solicitation apply to insects? Proceedings of the Royal Society B: Biological Sciences 1999;266(1429):1691–6.

80. Mas F, Kölliker M. Maternal care and offspring begging in social insects: chemical signalling, hormonal regulation and evolution. Animal Behaviour 2008;76(4):1121–31.

81. Smiseth PT, Moore AJ. Does resource availability affect offspring begging and parental provisioning in a partially begging species? Animal Behaviour 2002;63(3):577–85.

82. Hall WG, Williams CL. Suckling isn't feeding, or is it? A search for developmental continuities. Advances in the Study of Behavior 1983;13:220–54.

83. Blass EM, Hall WG, Teicher MH. The ontogeny of suckling and ingestive behaviors. Progress in Psychobiology and Physiological Psychology 1979;8:243–99.

84. Rosenblatt JS. The basis of synchrony in the behavioral interaction between the mother and her offspring in the laboratory rat. Determinants of Infant Behaviour 1965;3:3–45.

85. Galef Jr BJ. The ecology of weaning: parasitism and the achievement of independence by altricial mammals. In: Gubernick DJ, Klopfer PH, editors. Parental Care. Plenum Press, New York, NY; 1981. p. 211–41.

86. Thiels E, Cramer CP, Alberts JR. Behavioural interactions rather than milk availability determine decline in milk intake in weanling rats. Physiology and Behaviour 1988;42(6):507–15.

87. McNab BK. Energetics and the distribution of vampires. Journal of Mammalogy 1973;54(1):131–44.

88. Wilkinson GS. Food sharing in vampire bats. Scientific American 1990;262(2):64–70.

89. DeNault LK, McFarlane DA. Reciprocal altruism between male vampire bats, *Desmodus rotundus*. Animal Behaviour 1995;49(3):855–6.

90. Packard JM. Wolf behavior: reproductive, social and intelligent. In: Mech LD, Boitani L, editors. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, IL; 2003. p. 35–66.

91. Mech LD, Wolf PC, Packard JM. Regurgitative food transfer among wild wolves. Canadian Journal of Zoology 1999;77(8):1192–5.

92. Galef Jr BG, Whiskin EE. Interaction of social and individual learning in food preferences of Norway rats. Animal Behaviour 2001;62(1):41–6.

93. Budden AE, Wright J. Learning during competitive positioning in the nest: do nestlings use ideal free 'foraging' tactics? Behavioral Ecology and Sociobiology 2005;58(3):227–36.

94. Kedar H, Rodriguez-Girones MA, Yedvab S, Winkler DW, Lotem A. Experimental evidence for offspring learning in

parent–offspring communication. Proceedings of the Royal Society B: Biological Sciences 2000;267(1454):1723–7.

95. Royle NJ, Hartley IR, Parker GA. Begging for control: when are offspring solicitation behaviours honest? Trends in Ecology and Evolution 2002;17(9):434–40.

96. Parker GA, Royle NJ, Hartley IR. Begging scrambles with unequal chicks: interactions between need and competitive ability. Ecology Letters 2002;5(2):206–15.

97. Malm K, Jensen P. Weaning in dogs: within- and between-litter variation in milk and solid food intake. Applied Animal Behaviour Science 1996;49(3):223–35.

98. Malm K, Jensen P. Weaning and parent–offspring conflict in the domestic dog. Ethology 1997;103(8):653–64.

99. Feldman HN. Maternal care and differences in the use of nests in the domestic cat. Animal Behaviour 1993;45(1): 13–23.

100. Robinson I. Behavioural development of the cat. In: The WALTHAM Book of Dog and Cat Behaviour. Pergamon Press, Oxford, UK; 1992. p. 53–64.

101. Malm K. Regurgitation in relation to weaning in the domestic dog: a questionnaire study. Applied Animal Behaviour Science 1995;43(2):111–22.

102. Westenhoefer J. Establishing good dietary habits – capturing the minds of children. Public Health Nutrition 2001;4(1A):125–9.

103. Savage JS, Fisher JO, Birch LL. Parental influence on eating behavior: conception to adolescence. The Journal of Law, Medicine and Ethics 2007;35(1):22–34.

104. Birch LL. The control of food intake by young children: the role of learning. In: Capaldi ED, Powley TL, editors. Taste, Experience, and Feeding. American Psychological Association, Washington, DC; 1990. p. 116–35.

105. Neville MC, Keller R, Seacat J, Lutes V, Neifert M, Casey C, et al. Studies in human lactation: milk volumes in lactating women during the onset of lactation and full lactation. American Journal of Clinical Nutrition 1988;48(6):1375–86.

106. Dewey KG, Lonnerdal B. Infant self-regulation of breast milk intake. Acta Paediatrica Scandanavia 1986;75(6):893–8.

107. Le Magnen J. Hunger. Cambridge University Press, Cambridge, UK; 1985.

108. Wright P. Learning experiences in feeding behaviour during infancy. Journal of Psychosomatic Research 1988;32(6):613–19.

109. Crow RA, Fawcett JN, Wright P. Maternal behavior during breast- and bottle-feeding. Journal of Behavioral Medicine 1980;3(3):259–77.

110. Kölliker M, Richner H, Werner I, Heeb P. Begging signals and biparental care: nestling choice between parental feeding locations. Animal Behaviour 1998;55(1):215–22.

111. Young B, Drewett R. Eating behaviour and its variability in 1-year-old children. Appetite 2000;35(2):171–7.

112. Anderson AS, Guthrie CA, Alder EM, Forsyth S, Howie PW, Williams FLR. Rattling the plate – reasons and rationales for early weaning. Health Education Research 2001;16(4): 471–9.

113. Peachey SE, Jean Harper E. Aging does not influence feeding behavior in cats. Journal of Nutrition 2002; 132(6 Suppl. 1):1735S–9S.

114. Collier G, Johnson DF, Morgan C. Meal patterns of cats encountering variable food procurement cost. Journal of the Experimental Analysis of Behavior 1997;67(3):303–10.

115. Kane E, Leung PMB, Rogers QR, Morris JG. Diurnal feeding and drinking patterns of adult cats as affected by changes in the level of fat in the diet. Appetite 1987;9(2):89–98.

116. Kane E, Rogers QR, Morris JG. Feeding behavior of the cat fed laboratory and commercial diets. Nutrition Research 1981;1(5):499–507.

117. Kanarek RB. Availability and caloric density of the diet as determinants of meal patterns in cats. Physiology and Behavior 1975;15(5):611–18.

118. Rashotte ME, Smith JC, Austin T. Twenty-four-hour free-feeding patterns of dogs eating dry food. Neuroscience and Biobehavioral Reviews 1984;8(2):205–10.

119. Bowlby J. Attachment and Loss, Vol. 1, Attachment. Hogarth, London, UK; 1969.

120. Turner DC. The ethology of the human–cat relationship. Schweizer Archiv fur Tierheilkunde 1991;133(2):63–70.

121. Mertens C. Human–cat interactions in the home setting. Anthrozoos 1991;4(4):214–31.

122. Karsh EB, Turner DC. The Human–Cat Relationship. The Domestic Cat: the Biology of its Behaviour. Cambridge University Press, Cambridge, UK; 1988. p. 159–77.

123. Mertens C, Turner DC. Experimental analysis of human–cat interactions during first encounters. Anthrozoos 1988;2(2):83–97.

124. Leyhausen P. The tame and the wild – another just-so story. In: Turner DC, Bateson P, editors. The Domestic Cat: The Biology of its Behaviour. Cambridge University Press, Cambridge, UK; 1988. p. 57–66.

125. Rieger G, Turner DC. How depressive moods affect the behavior of singly living persons toward their cats. Anthrozoos 1999;12(4):224–33.

126. Buss D. Human nature and individual differences: the evolution of human personality. In: Pervine LA, John OP, editors. Handbook of Personality: Theory and Research, 2nd ed. Guildford Press, New York, NY; 1999. p. 31–56.

127. Groothuis TGG, Carere C. Avian personalities: characterization and epigenesis. Neuroscience and Biobehavioral Reviews 2005;29(1 Special Issue):137–50.

128. Gosling SD, John OP. Personality dimensions in nonhuman animals: A cross-species review. Current Directions in Psychological Science 1999;8(3):69–75.

129. Kralj-Fišer S, Scheiber IBR, Blejec A, Moestl E, Kotrschal K. Individualities in a flock of free-roaming greylag geese: Behavioral and physiological consistency over time and across situations. Hormones and Behavior 2007;51(2): 239–48.

130. Sih A, Bell AM, Johnson JC, Ziemba RE. Behavioral syndromes: an integrative overview. Quarterly Review of Biology 2004;79(3):241–77.

131. Turner DC. The human–cat relationship. In: Turner DC, Bateson P, editors. The Domestic Cat: The Biology of its Behaviour, 2nd ed. Cambridge University Press, Cambridge, UK; 2000. p. 194–206.

132. Curley JP, Keverne EB. Genes, brains and mammalian social bonds. Trends in Ecology and Evolution 2005;20(10):561–7.

133. Serpell J, jagoe J. Early experience and the development of behaviour. In: Serpell J, editor. The Domestic Dog: Its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge; 1995. p. 79–102.

134. Clutton-Brock J. Origins of the dog: domestication and early history. In: Serpell J, editor. The Domestic Dog: Its Evolution, Behaviour, and Interactions with People. Cambridge University Press, Cambridge, UK; 1995. p. 7–20.

135. Belyaev DK. Genetic aspects of animal domestication. In: Belyaev DK, editor. Problems of Animal and Plant Domestication. Nauka, Moscow, Russian Federation; 1972. p. 39–45.

136. Coppinger R, Schneider R. Evolution of working dogs. In: Serpell J, editor. The Domestic Dog: Its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge, UK; 1995. p. 21–47.