

Ethics of feeding: the omnivore dilemma

IHE Kasanen^{*†}, DB Sørensen[‡], B Forkman[‡] and P Sandøe[‡]

[†] National Laboratory Animal Centre, University of Kuopio, PO Box 1627, FI-70211 Kuopio, Finland

[‡] Faculty of Life Sciences, University of Copenhagen, Denmark

* Contact for correspondence and requests for reprints: iiris.kasanen@uku.fi

Abstract

The way in which animals are fed is an important aspect of their welfare. Not only does food provide the energy and nutrients vital for survival, but feeding is also associated with a number of other factors contributing to the well-being of animals. The feeding method can determine the animals' abilities to fulfil basic behavioural needs, such as foraging. The aim of this paper is to review and discuss the dilemma of choosing between *ad libitum* feeding (AL) and dietary restriction (DR). AL can produce obese individuals with severe health problems, though it does appear to be compatible with welfare-friendly management systems. On the other hand, DR is often associated with improved physical health and longevity but can leave animals suffering from hunger, frustration or aggression. The species discussed are the laboratory rat, pigs and poultry all of which are omnivores sharing many characteristics in their eating habits. The welfare implications of different feeding methods depend upon the definition of welfare used. Based on a definition of welfare in terms of functioning, DR could be considered the best way to feed animals, because it results in improved physical health and longevity. If welfare is defined in terms of natural living, it is also a requirement for the animal to be able to engage in natural foraging behaviours. From the feelings-based approach, DR can be viewed as preferable only in circumstances when animals are anticipated to live so long that they would otherwise suffer from the negative long-term consequences of AL. It is argued that incentives are needed to make farmers spend resources to ensure that farm animals are allowed to have their foraging-related needs fulfilled. Feeding of laboratory animals creates special dilemmas when it is important either to under- or over-nourish the animals for experimental purposes, in such instances there is a need for Refinement.

Keywords: *ad libitum*, animal welfare, dietary restriction, ethics, rat, sow

Introduction

Feeding of animals in our care creates a dilemma. On one hand, animals should not be allowed to suffer from hunger or from frustration due to the lack of possibilities to perform feeding-related behaviours. On the other hand, unrestricted access to food may impact negatively on the animals' health. This dilemma may be viewed partly as a technical issue in the provision of feeding systems which cater in the best possible way for both the short- and long-term needs of the animals. However, technical solutions are rarely perfect in every respect and therefore there will also be an ethical element to this dilemma.

The aim of this paper is to discuss the ethical problems which arise when deliberating how best to feed animals in our care. Firstly, there are differing and conflicting ideas of what constitutes a good animal life; and depending on whether we emphasise feeling, function or natural living in our definition of animal welfare, different views will emerge regarding the optimal way to feed a captive animal. Secondly, animals are kept with specific human

purposes in mind and sometimes these purposes favour feeding animals in ways which are less than optimal from the point of view of animal welfare.

In some species, the ethical problems relating to feeding seem to be easier to resolve than in others. Herbivorous species, such as cattle and horses, do not pose a major problem — at least in principle. Here, both nutritional and behavioural needs can be met by providing an opportunity to graze or consume large quantities of fibre-rich food. In practice, of course, these ideas may not be implemented. For example, many horses live mainly on concentrated feed and therefore may suffer from frustration because they cannot perform feeding-related behaviours (Parker *et al* 2008).

Some carnivorous species, eg dogs, are adapted to eating occasional large meals, which should be a feeding regime easily put into practice. Other species, eg cats, feed primarily on small prey, resulting in a preference for several small meals spread throughout the day (Leyhausen 1979; Bradshaw 2006). However, feeding can be associated with welfare issues also in carnivores. One problem is over-

feeding; the prevalence of obesity is high in pet dogs and cats, resulting in serious health problems (Colliard *et al* 2009). The behavioural needs of carnivores have been investigated less extensively than those of production and laboratory animals. For example, it could be argued that carnivores have a high motivation to perform species-specific foraging and hunting behaviours (eg tracking and hunting prey) and are not satisfied with 'free' meals.

In omnivorous species, such as rats, pigs and poultry, which are the focus of this paper, the problems are not only difficult to resolve in practice, but also in theory. These are species which, in their natural environment, will spend large amounts of time foraging (Dawkins 1989; Balcombe 2006a). However, the actual food eaten is relatively energy-dense and consumed within a short period of time. In laboratories or on farms, the nutritional requirements of these animals are rather easily met, but the need to forage is more difficult to satisfy. If there is free access to highly-palatable food, these animals will quickly become obese and might suffer from obesity-associated diseases. If some form of dietary restriction (DR) is implemented, the behavioural needs are usually neglected.

There is a vast scientific literature on DR and its effects on animals. This literature is clearly relevant to the present ethical discussion. However, DR is not all or nothing but instead, occurs in degrees. The method of DR may have ethical implications. Therefore, in the following section of the paper we will aim to define more clearly different feeding regimes ranging from *ad libitum* (AL) to severe degrees of feed restriction. In addition, most of the literature does not focus specifically on the consequences for animal welfare. Therefore, in the following section of the paper, we will review the literature in the light of different definitions of animal welfare and in the light of a discussion on how to balance animal welfare against various human-orientated concerns.

Definitions of feeding regimes

Feeding regimes may range from AL to total deprivation where no food is available. Of course, in daily animal husbandry, the standard will range from AL to a certain degree of restricted feeding depending upon the species in question and the purpose.

In the literature, AL feeding is most often understood to consist of continuous access to unlimited amounts of palatable food. AL food intake does not equal the hypothetical maximal food intake of a maximally-palatable diet, since it is greatly dependent on many factors, such as the environment, the social setting, the diet itself, the age and the activity level of the animal (Keenan *et al* 1998).

DR is defined as any method of feeding that limits the amount of calories consumed by the animal compared to the AL food intake of that species. In general, there are two types of restricted feeding: quantitative and qualitative. In quantitative DR, the quantity of food consumed by the animal is restricted, ie the animal does not receive enough feed to maintain its body mass compared to an AL-fed

control. Quantitative DR can be implemented by simply restricting the amount of food given to the animal, by restricting the amount of time food is available or by making access to food more difficult. Quantitative DR is commonly used in some species, such as mini pigs and dogs, in which the prevalence of obesity is high and problems associated with obesity are common. (Lund *et al* 2006). Quantitative DR is also sometimes used in experimental animals, when the animal model *per se* requires restricted feeding or when the experimental setup requires the animals to be hungry (eg behavioural tests where the animals are being rewarded with food).

In qualitative DR, the food is available AL, but the quality of the food is altered resulting in a lowered energy intake. For example, the energy density can be lowered by increasing the fibre content of the diet. A high fibre diet can also be used to alleviate the effects of quantitative restriction (Robert *et al* 1997). However, in the species discussed in this paper, DR is most often accomplished by a quantitative restriction of the standard diet.

A third restriction in relation to food and feeding, is when the animal is fed enough to meet its physiological demands (quantity and quality is sufficient) and hence follows a normal growth curve, but it lacks the opportunities to perform species-specific feeding-related behaviours. Hence, the animal will not have satisfied its need for foraging behaviour. Such a restriction of 'behavioural opportunities' can result from a feeding method where food is obtained very easily or ingested very rapidly with little effort needed on the behalf of the animal (eg pigs fed high concentrate food without additional roughage).

Current feeding practices

In laboratory rodents, the feeding methods are designed to comply with the internationally-standardised feeding routines and to minimise the amount of time required to feed the animals. There are large numbers of animals to be fed and the time spent per animal is a major factor determining the efficacy of an animal facility. The most common method of feeding laboratory rodents is AL, ie to have food pellets available in the wire-grid food hopper at all times. When DR is used (most commonly in research associated with obesity and ageing), it is typically implemented by single-housing the animals and providing them with one pre-calculated meal during the day-time. The food used in DR regimes is most often the standard laboratory rodent food, but simply in reduced quantities. We will designate this way of restricting food intake as 'the traditional method of DR'. The severity of the restriction varies greatly from study-to-study. The amount of food offered has ranged from 20 to 85% of the food intake of the AL counterparts, though most often a moderate dietary restriction, ie 60 to 80% of the AL food intake, is used. (Pugh *et al* 1999) Here, the degree of DR is reported, where possible, as the percentage of the food or caloric intake of the animals compared to their AL-fed counterparts. It must be noted, however, that the AL food intake has varied greatly from study-to-study, and thus the percentages of DR cannot be directly compared with each other (Keenan *et al* 1998).

Broilers are typically fed AL (De Jong & Jones 2006), except when conventional broiler lines are used for organic production. On the other hand, the parent animals, ie broiler breeders, are subjected to severe DR, being provided with as little as 25–33% of their AL food intake. This is done to prevent the health problems associated with their massive growth potential and to promote reproductive performance (Brillard 2001; Mench 2002)

In general, most fattening pigs are fed close to AL feeding levels — although the actual food might not be available at all times, being provided once or a few times daily (Nielsen *et al* 2006). Intermittent feeding is especially common when liquid feeding systems are used (Rasmussen *et al* 2006). In contrast, boars and gilts/sows are fed restrictedly, initially during their rearing period (75–100% of AL), and then more severely when they are fully grown (at about 60% of AL) (Nielsen *et al* 2006).

Feeding, animal welfare and ethics

There are two somewhat different ethical dilemmas related to feeding. The first is the issue of overfeeding. For some animals, satisfying their hunger will lead to the long-term negative consequences of obesity and obesity-related diseases. The most extreme example is perhaps the broiler breeder (Hocking *et al* 2002). Here, the long-term interests and the health of the animal conflict with its short-term interests.

The second dilemma is the issue of behavioural needs. The behavioural needs associated with foraging may or may not be satisfied, independently of the level of physiological hunger. It has been claimed that providing the animal with the opportunity to perform foraging behaviour may even alleviate some of the negative consequences of hunger (Robert *et al* 1997; De Leeuw & Ekel 2004). There is no animal welfare problem associated with satisfying this need, but there are often practical problems and financial implications and thus ultimately a potential conflict between the interests of the farmers and the animals.

There is extensive literature covering the effects of AL vs DR on behaviour, physiological parameters, mortality and morbidity, especially in rodents. However, there is a paucity of studies primarily assessing the welfare implications of different feeding methods. Thus, the majority of publications deal with caloric intake, health and life expectancy, and in many cases, the welfare associated with the feeding method is either neglected or difficult to interpret. Some of the results reviewed here are taken from DR regimes where severe levels of dietary restriction have been used. Although we are not proposing such extreme ways of feeding as being a welfare-friendly alternative for animal husbandry, they can serve as examples while discussing the dilemma of feeding methods.

Results will be relative to a definition of animal welfare

Finding the best way to feed an animal or a group of animals is, of course, a partly technical issue, but values also come into play. Thus, different views about the nature of animal welfare will result in different answers to the question: ‘how does the feeding regime affect animal welfare?’ Here, we

will refer to three main approaches: function, natural living and feelings (Fraser 1997; Sandøe & Christiansen 2008). According to the first approach, an animal has a high level of welfare if, from a functional point of view, it is able to cope. To maintain welfare, it should be ensured that the animal does not become seriously ill. Signs of good welfare coincide with signs of good physical health according to this functional approach. According to the second, natural living, approach, the crux is that the animal is able to perform a wide range of species-specific forms of behaviour. Viewed from this perspective, it is a problem for an animal’s welfare if it lives an ‘impoverished’ life where some forms of behaviour are downplayed or reduced. Finally, from the feelings approach, what matters is that an animal must avoid pain and other negative feelings and be able to obtain pleasure and other positive feelings. Often, these three approaches will converge to similar conclusions about what is good for an animal since, in many cases, health, natural living and feeling good go hand-in-hand. However, this is not always the case, especially when one considers the situation with respect to feeding.

In the function approach, it may be considered of positive value to maintain animals on some form of DR since this is associated with optimal health — one consistent finding emerging from the many studies comparing AL and DR is that if one maintains the individual on a diet with a lower calorie intake than that which the animal is motivated to eat, one can increase the animal’s lifespan (Masoro 2006).

Adherents of the natural living approach may agree on the value of some form of DR because it is not natural for animals always to have food available in abundance. However, viewed from this approach, it would be important to add some form of enrichment to allow the animals to engage in foraging behaviour.

According to the feelings-based approach to animal welfare, the feelings of the animals are of importance. However, in traditional animal research, the focus has been on negative mental states, such as aggression and anxiety, and hence no experiments reporting direct effect on feeding regimes on positive feelings such as happiness or optimism have been completed. In the feelings-based approach, DR is a problem by definition. DR regimes expose the animals to hunger — and hunger is clearly a negative feeling. The only way to justify hunger from a feelings-based approach is that it is compensated by positive feelings or the avoidance of other negative feelings. It is a common human experience that staying hungry for a short time may very well be compensated by enhanced pleasure when the meal is finally served. There is no reason why a similar experience should not occur in animals. In pigs, it has been demonstrated that anticipating a food reward is more reinforcing than actually obtaining the food (de Jonge *et al* 2008). Several papers have confirmed that in humans and in animals, this expression of anticipatory behaviour is associated with release of dopamine in the reward centres in the brain (Spruijt *et al* 2001; de la Fuente-Fernandez *et al* 2002; O’Doherty *et al*

2002; Berridge 2007). In weaning pigs, a period of anticipating food enrichments significantly increases positive behaviours such as play (Dudink *et al* 2006).

However, more prolonged feelings of hunger which will normally accompany DR seem to be more difficult to justify from a feelings approach, this being reinforced by the fact that hunger may be associated with other negative signs, such as aggression and depression (Vitousek *et al* 2004). The only cases where it will be possible to justify this situation with reference to animal welfare is when DR is the only way to prevent the animals in question from experiencing negative feelings even more unpleasant than hunger and the other negative states associated with DR.

Problems of AL

The most prominent problems of AL feeding are the detrimental effects it can have on health. In laboratory rats, DR (45–90% of AL) reduces the incidence of degenerative kidney disease (Hubert *et al* 2000; Duffy *et al* 2004b), endocrine disturbances (Keenan & Soper 1995; Keenan *et al* 1996) and other common causes of morbidity (Hubert *et al* 2000; Duffy *et al* 2004b). The incidence of neoplastic disease is also significantly lower in DR (50–90% of AL) rats (Keenan & Soper 1995; Duffy *et al* 2004a).

In animals bred for meat production, an increased growth rate compared to their ancestral species often results in increased disease incidence when the animals are fed AL. In modern broilers, this increase in growth rate has resulted in birds suffering from ascites (Julian *et al* 1987; Deeb *et al* 2002) and sudden death syndrome (Bessei 2006), two diseases less often seen in the restricted fed breeding stock (Mench 2002). A secondary effect of excessive growth rate is the induction of leg problems (eg tibial dyschondroplasia) (de Jong & Jones 2006) often associated with pain (Danbury *et al* 2000). Techniques to mechanically reduce the bodyweight or forcing the birds to walk have resulted in decreased leg problems (Thorp & Duff 1988; Rutten *et al* 2002).

The negative effects associated with AL feeding in sows have been rarely discussed; mostly because sows kept for meat production are hardly ever fed AL. In laboratory animals, on the other hand, obese mini pigs are used as models for obesity-related human diseases such as diabetes (Raun *et al* 2007). No welfare assessment studies have been conducted on obese laboratory mini pigs, but one would not be surprised to encounter welfare problems due to leg problems and impairment of natural behaviours, eg due to difficulties in walking in these grossly obese individuals.

If one takes the feelings-based approach, pain due to leg problems, kidney diseases and other health problems constitute a welfare problem. Moreover, animals suffering from leg problems and neoplastic disease may very well experience an inability to perform species-specific behaviours and thus — also from a perspective of natural living — these conditions result in lowered welfare. Obviously, from the perspective of biological functioning, suffering from diseases which may reduce biological fitness resulting in fewer offspring or even lead to the death of the animal is not

good animal welfare. Hence, all three ethical approaches are in agreement that feeding AL may constitute a welfare problem in the cases mentioned above.

On the other hand, DR (60–80% of AL) may lead to a down-regulation of reproductive functions in rodents, especially in females (Martin *et al* 2007; Rehm *et al* 2008). Nonetheless, even though DR (60% of AL) is known to impair reproductive function at an early phase, it has been shown to prolong reproductive life by delaying the age-associated decline in reproductive function (Nelson *et al* 1995; Chen *et al* 2005; Selesniemi *et al* 2008; Sharov *et al* 2008).

Benefits of AL

Laboratory rats fed AL and used for short-term experiments and fattening pigs seem to be free of serious health problems within their limited life expectancy. In the absence of AL-induced morbidity and related pain, there are no benefits from DR which — from the point of view of the feelings approach — can justify prolonged hunger. Tipping the scale further in AL's favour, DR can cause significantly increased levels of aggression in rodents, where severe aggression and even cannibalism can be induced by DR regimes, in which the rats are fed only once a day (Adams *et al* 1994; Pugh *et al* 1999; Pahlavani & Vargas 2001). Also, in pigs, DR has been shown to increase the level of aggression (Petherick & Blackshaw 1987; Meunier-Salaun *et al* 2001), which may be associated with negative feelings from the perspective of the aggressor and which will certainly evoke negative feelings in those individuals subject to aggression from pen- or cage-mates.

Attempts to avoid aggression by resorting to single housing are not a favourable solution since rats and pigs are highly sociable animals and are known to suffer if they are not group-housed (Serra *et al* 2005; Krohn *et al* 2006; Perello *et al* 2006; Brenes *et al* 2008). Thus, one could argue that the best solution is simply to proceed with AL, allowing the rats to be fat and friendly rather than lean and mean. A similar line of thought seems to apply to fattening pigs.

Working for food

In many situations, AL will not be sufficient to fulfil the feeding-related needs of animals. Under natural circumstances, behaviours relating to foraging account for a huge proportion of the time budgets of omnivorous animals such as rats, pigs and poultry. In red junglefowl (*Gallus gallus* spp) (the ancestral species of the domestic fowl), the hens were found to ground peck in 60% of all one-minute observations and to be scratching the ground in more than 30% of these times (Dawkins 1989). Corresponding figures for rooting and foraging in sows under natural conditions vary between 22 and 28% of the total day-time (Stolba & Woodgush 1989; Buckner *et al* 1998). In wild rats (*Rattus norvegicus*), a large part of their active time is spent exploring their surroundings. Presumably a large portion of this activity is dedicated to foraging behaviour. The actual eating takes much less time and occurs mainly during the night. (Barnett 1951, 1963; Calhoun 1962). In the wild or under semi-natural conditions, animals will explore their

surroundings, search for information on changes and seek new options, even though their preferred food resources have not yet been fully exploited (Forkman 1996; Inglis *et al* 1997, 2001; Sherwin 2007). It should also be noted that exploratory behaviour can be rewarding for the animals even when no food is found (Van Der Harst *et al* 2003).

From a natural living perspective, it is imperative to allow the animal to perform these kinds of species-specific foraging behaviours if one wishes to ensure good welfare. Moreover, often the activity relating to such behaviours will promote physical health and thus improve welfare from the functional point of view. From the feelings-based approach, it could be argued that animals seek pleasure and that choosing to perform certain species-specific behaviours such as swimming in mink (*Neovison vison*) and playing in young dogs (*Canis lupus familiaris*) actually makes the animals feel good (Mason *et al* 2001; Balcombe 2006b).

Animals provided only with readily accessible food, ie food that is very rapidly consumed, may develop abnormal behaviours that can be viewed as signs of frustration (Redbo & Nordblad 1997). Therefore, one way to ensure optimal welfare from both the natural living and the feelings approach may be to enrich the lives of these animals by devising systems that force the animals to work for their food.

Here, two different approaches seem to be possible. One approach is to force the animals to work in order to obtain their basic diet.

An example of this approach is the diet board designed for laboratory rats (Kemppinen *et al* 2008; Kasanen *et al* 2009a,b). The diet board is a simple wooden board with food pellets embedded into it. It is more difficult to gain access to the food and hence the animals consume less food than AL-fed controls. The diet board produces a mild-to-moderate degree of DR; the animals maintain a bodyweight that is 85% of the AL-fed controls (Kasanen *et al* 2009a). The diet board is present in the cage at all times, allowing the animals to maintain a similar diurnal rhythm of eating and resting as the AL-fed controls (Kemppinen *et al* 2008). Group housing can be combined easily with diet board feeding since the diet board is large enough to allow several animals to eat simultaneously from different parts of the board. This feeding method is compliant with the natural living approach to animal welfare: the animals have to work to obtain their food. The diet board might also have housing refinement value for the animals since it divides the cage into compartments, thus increasing the complexity of the cage environment which is now legally mandated (ETS No 123, 2007/526/EC [EC 2007]). Furthermore, the diet board offers the animals a degree of control over their environment. Even when total energy intake remains low, the possibility of trying to find food can decrease the stressfulness of DR (Appleby & Lawrence 1987). In essence, this is a combination of DR and enrichment which is by all standards superior to DR without enrichment.

The second approach would be to make the animals work for only a part of their diet. The basic nutritional needs would be satisfied by AL feeding whereas foraging behav-

iours would be encouraged by providing the animals with the opportunity work for highly palatable treats.

Balancing animal and human interests

In real life, discussions about the ethics of animal feeding cannot be simply limited to how best to improve or ensure animal welfare. In reality, the debate is about how best to balance the issue of animal welfare against a number of other concerns relating to human interests.

With respect to farm animals, the latter concerns relate mainly to production efficiency. The main objectives underlying animal feeding are to reduce costs and increase production. Fortunately, but not invariably, efficiency and physical health often move in the same direction.

There are huge problems in motivating farmers to spend resources to ensure that they meet not only the nutritional needs but also the behavioural needs of animals in relation to foraging. Improvements can be achieved via voluntary production schemes (welfare labels) where the farmer gains economic benefits from providing the animals with possibilities to express their behavioural needs. The current European legislation also recognises the behavioural needs of animals, for example by mandating that pigs should have the possibility to root (2001/93/EU 1993 [EC 2001]).

One particular problem with some farm animal species is that the animals have been bred especially for their ability to grow rapidly and have a pronounced appetite. This especially affects the parental generation, for example broiler breeders, which typically have to be kept on a severely-restricted diet to ensure longevity and reproductive performance. It does seem that feed management alone cannot resolve these problems; there needs to be a change in the breeding goals (Brillard 2001; Decuyper *et al* 2006; Sandilands *et al* 2006)

In experimental animals, a genuine dilemma arises when adverse feeding regimes are an integral part of the study. This may be the case when animals are experiencing severe DR, eg to induce malnutrition, to model eating disorders or, conversely, when animals are fed AL in studies where they are modelling the metabolic syndrome or diabetes. In animal experimentation, this kind of negative impact on the animal is part of the experiment, but nevertheless it is widely accepted that researchers using experimental animals are obliged to reduce suffering by 'Refinement' of experimental procedures and housing, by 'Reduction' of the number of animals used or, if possible, by 'Replacement' of live animals with the use of suitable alternatives (Russell & Burch 1959).

Feeding laboratory animals AL with the purpose of inducing, eg obesity, increases the likelihood of welfare problems in these animals. 'Refinement' in such a scenario could include allowing pigs to exercise, monitoring leg problems and treatment with pain killers if necessary and helping the animals performing maintenance behaviours, eg by providing access to 'back-scratching devices'.

Dietary restriction, on the other hand, may leave the animals with excess time otherwise used for feeding and a lack of ability to perform feeding-related behaviour, such as

foraging. One possibility of 'Refinement' could be adding complexity to the animals' environment, requiring them to search and work for access to food. Providing food that the animals really enjoy may increase the pleasure of finally being fed, thus adding to positive welfare (Balcombe 2006b). Moreover, it could be postulated that announcing feeding, allowing for a period of positive anticipation, may increase animal welfare (de Jonge *et al* 2008).

For laboratory rodents, the method of feeding also has a 'Reduction' dimension. DR could lead to a reduction in the numbers of laboratory rodents used in experiments in two ways: by increased longevity and decreased variation. The lifespan of laboratory rats has decreased considerably over recent decades (Keenan *et al* 1996). This results in more animals being needed for safety evaluations to compensate for the increased mortality. This is especially true for long-term safety evaluation studies which, in rats, can last up to two years. Improving survival of the animals by DR could translate into millions fewer animals being used annually (Hubert *et al* 2000). AL feeding in rodents is associated with extensive variations in bodyweight, survival and tumour incidence (Keenan *et al* 1996), complicating the interpretation of research results. The traditional methods of DR have been shown to reduce inter-individual variation in several parameters (Duffy *et al* 2001; Leakey *et al* 2003a,b; Carney *et al* 2004). Decreased variation would mean that fewer animals could be used in experiments while still achieving the same statistical power.

Conclusion and animal welfare implications

DR can enhance the physical health, fitness and coping capabilities of an animal but it has been associated with behavioural changes and pathology indicative of decreased welfare. AL, on the other hand, has well-known detrimental effects on health, ie obesity and increased morbidity and mortality, but might be easier to incorporate into otherwise more welfare-friendly ways of animal housing. However, the current practices of AL or DR rarely address the issue of behavioural needs.

From the function approach to animal welfare, DR could be considered as the best way to feed animals, because it results in improved physical health and longevity. From the natural living approach, DR could be acceptable, if not preferable in theory; clearly AL availability of food cannot be considered as natural. However, in reality, the DR regimes are also often far from natural. In the natural living approach, the possibility to satisfy the behavioural needs associated with feeding and foraging are emphasised. From the feelings-based approach (which is the foundation for most animal welfare legislation), it is highly important to feed animals a sufficient amount of calories to avoid permanent hunger and the other negative feelings associated with DR. The only cases where DR can be viewed as improving animal welfare are situations when animals are anticipated to live so long that they may end up suffering from the negative long-term effects of AL or when the animals in question have such a strong motivation to eat that AL may damage their well-being even in the short term.

The authors conclude that irrespective of the level of caloric intake, it should be a priority to provide the animals with opportunities to display species-specific foraging behaviours.

Acknowledgements

The preparation of this paper was supported financially by the Finnish Ministry of Education, the Academy of Finland, the ECLAM and ESLAV Foundation, UFAW, the Research and Science Foundation of Farnos, the Finnish Foundation of Veterinary Sciences and the Oskar Öflund Foundation.

References

- Adams DB, Cowan CW, Marshall ME and Stark J** 1994 Competitive and territorial fighting: Two types of offense in the rats. *Physiology & Behavior* 55: 247-254
- Appleby MC and Lawrence AB** 1987 Food restriction as a cause of stereotypic behaviour in tethered gilts. *Animal Production* 45: 103-110
- Balcombe JP** 2006a Laboratory environments and rodents' behavioural needs: a review. *Laboratory Animals* 40: 217-235
- Balcombe JP** 2006b *Pleasurable Kingdom, First Edition*. Macmillan: New York, USA
- Barnett SA** 1951 Feeding, social behaviour and interspecific competition in wild rats. *Behaviour* 3: 229-243
- Barnett SA** 1963 *The Rat: A Study in Behaviour, First Edition*. Aldine Publishing Company: Chicago, USA
- Berridge KC** 2007 The debate over dopamine's role in reward: the case for incentive salience. *Psychopharmacology* 191(3): 391-431
- Bessei W** 2006 Welfare of broilers: a review. *Worlds Poultry Science Journal* 62(3): 455-466
- Bradshaw JW** 2006 The evolutionary basis for the feeding behavior of domestic dogs (*Canis familiaris*) and cats (*Felis catus*). *The Journal of Nutrition* 136(7): 1927S-1931S
- Brenes JC, Rodríguez O and Fornaguera J** 2008 Differential effect of environment enrichment and social isolation on depressive-like behavior, spontaneous activity and serotonin and norepinephrine concentration in prefrontal cortex and ventral striatum. *Pharmacology Biochemistry and Behavior* 89(1): 85-93
- Brillard JP** 2001 Future strategies for broiler breeders: an international perspective. *Worlds Poultry Science Journal* 57(3): 243-250
- Buckner LJ, Edwards SA and Bruce JM** 1998 Behaviour and shelter use by outdoor sows. *Applied Animal Behaviour Science* 57(1-2): 69-80
- Calhoun JB** 1962 *The Ecology and Sociology of the Norway Rat, First Edition*. Public Health Services: Bethesda, Maryland, USA
- Carney EW, Zaboltny CL, Marty MS, Crissman JW, Anderson P, Woolhiser M and Holsapple M** 2004 The Effects of feed restriction during in utero and postnatal development in rats. *Toxicological Sciences* 82(1): 237-249
- Chen H, Luo L, Liu J, Brown T and Zirkin BR** 2005 Aging and caloric restriction: effects on Leydig cell steroidogenesis. *Experimental Gerontology* 40(6): 498-505
- Colliard L, Paragon BM, Lemuet B, Benet JJ and Blanchard G** 2009 Prevalence and risk factors of obesity in an urban population of healthy cats. *Journal of Feline Medicine and Surgery* 11(2): 135-140
- Danbury TC, Weeks CA, Chambers JP, Waterman-Pearson AE and Kestin SC** 2000 Self-selection of the analgesic drug carprofen by lame broiler chickens. *Veterinary Record* 146(11): 307-311
- Dawkins MS** 1989 Time budgets in red junglefowl as a baseline for the assessment of welfare in domestic-fowl. *Applied Animal Behaviour Science* 24(1): 77-80

- de Jong IC and Jones B** 2006 Feed restriction and welfare in domestic birds. In: Bels V (ed) *Feeding in Domestic Vertebrates. From Structure to Behaviour, First Edition* pp 120-135. CABI: Cambridge, UK
- de Jonge FH, Tilly S, Baars AM and Spruijt BM** 2008 On the rewarding nature of appetitive feeding behaviour in pigs (*Sus scrofa*): Do domesticated pigs contrafreeload? *Applied Animal Behaviour Science* 114(3-4): 359-372
- de la Fuente-Fernandez R, Phillips AG, Zamburlini M, Sossi V, Calne DB, Ruth TJ and Stoessl AJ** 2002 Dopamine release in human ventral striatum and expectation of reward. *Behavioural Brain Research* 136(2): 359-363
- De Leeuw JA and Ekkel ED** 2004 Effects of feeding level and the presence of a foraging substrate on the behaviour and stress physiological response of individually housed gilts. *Applied Animal Behaviour Science* 86(1-2): 15-25
- Decuyper E, Hocking PM, Tona K, Onagbesan O, Bruggeman V, Jones EKM, Cassy S, Rideau N, Metayer S, Jegu Y, Putterflam J, Tesseraud S, Collin A, Duclos M, Trevidy JJ and Williams J** 2006 Broiler breeder paradox: a project report. *Worlds Poultry Science Journal* 62(3): 443-453
- Deeb N, Shlosberg A and Cahaner A** 2002 Genotype-by-environment interaction with broiler genotypes differing in growth rate 4. Association between responses to heat stress and to cold-induced ascites. *Poultry Science* 81(10): 1454-1462
- Dudink S, Simonse H, Marks I, de Jonge FH and Spruijt BM** 2006 Announcing the arrival of enrichment increases play behaviour and reduces weaning-stress-induced behaviours of piglets directly after weaning. *Applied Animal Behaviour Science* 101(1-2): 86-101
- Duffy PH, Seng JE, Lewis SM, Mayhugh MA, Aidoo A, Hattan DG, Casciano DA and Feuers RJ** 2001 The effects of different levels of dietary restriction on aging and survival in the Sprague-Dawley rat: implications for chronic studies. *Aging (Milan, Italy)* 13(4): 263-272
- Duffy PH, Lewis SM, Mayhugh MA, Trotter RW, Latendresse JR, Thorn BT and Feuers RJ** 2004a The effects of different levels of dietary restriction on neoplastic pathology in the male Sprague-Dawley rat. *Aging Clinical and Experimental Research* 16(6): 448-456
- Duffy PH, Lewis SM, Mayhugh MA, Trotter RW, Thorn BT, Feuers RJ and Turturro A** 2004b The effects of different levels of dietary restriction on non-neoplastic diseases in male Sprague-Dawley rats. *Aging Clinical and Experimental Research* 16(1): 68-78
- EC** 2001 2001/93/EU 1993, Commission Directive 2001/93/EC of 9 November 2001 amending Directive 91/630/EEC laying down minimum standards for the protection of pigs. Brussels, Belgium
- EC** 2007 ETS No 123 Appendix A of the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (ETS No. 123) Guidelines for accommodation and care of animals. Strasbourg, France. <http://conventions.coe.int/Treaty/EN/Treaties/Html/123-A.htm>
- Forkman B** 1996 The foraging behaviour of Mongolian gerbils: A behavioural need or a need to know? *Behaviour* 133: 129-143
- Fraser D** 1997 Science in a value-laden world: keeping our thinking straight. *Applied Animal Behaviour Science* 54(1): 29-32
- Hocking PM, Bernard R and Robertson GW** 2002 Effects of low dietary protein and different allocations of food during rearing and restricted feeding after peak rate of lay on egg production, fertility and hatchability in female broiler breeders. *British Poultry Science* 43(1): 94-103
- Hubert M, Laroque P, Gillet J and Keenan KP** 2000 The effects of diet, *ad libitum* feeding, and moderate and severe dietary restriction on body weight, survival, clinical pathology parameters, and cause of death in control Sprague-Dawley Rats. *Toxicological Sciences* 58(1): 195-207
- Inglis IR, Forkman B and Lazarus J** 1997 Free food or earned food? A review and fuzzy model of contrafreeloading. *Animal Behaviour* 53(6): 1171-1191
- Inglis IR, Langton S, Forkman B and Lazarus J** 2001 An information primacy model of exploratory and foraging behaviour. *Animal Behaviour* 62: 543-557
- Julian, RJ, Friars GW, French H and Quinton M** 1987 The relationship of right ventricular hypertrophy, right ventricular failure, and ascites to weight-gain in broiler and roaster chickens. *Avian Diseases* 31(1): 130-135
- Kasanen IH, Inhila KJ, Nevalainen JI, Vaisanen SB, Mertanen AM, Mering SM and Nevalainen TO** 2009a A novel dietary restriction method for group-housed rats: weight gain and clinical chemistry characterization. *Laboratory Animals* 43(2): 138-148
- Kasanen IH, Inhila KJ, Vainio OM, Kiviniemi VV, Hau J, Scheinin M, Mering SM and Nevalainen TO** 2009b The diet board: welfare impacts of a novel method of dietary restriction in laboratory rats. *Laboratory Animals* 43: 215-223
- Keenan KP and Soper KA** 1995 The effects of *ad libitum* overfeeding and moderate dietary restriction on Sprague-Dawley rat survival, spontaneous carcinogenesis, chronic disease, and the toxicologic response to pharmaceuticals. In: Hart RW, Neumann DA and Robertson RT (eds) *Dietary Restriction: Implications for the Design and Interpretation of Toxicity and Carcinogenicity Studies, First Edition* pp 99-126. ILSI Press: Washington DC, USA
- Keenan KP, Laroque P, Ballam GC, Soper KA, Dixit R, Mattson BA, Adams SP and Coleman JB** 1996 The effects of diet, *ad libitum* overfeeding, and moderate dietary restriction on the rodent bioassay: the uncontrolled variable in safety assessment. *Toxicologic Pathology* 24(6): 757-768
- Keenan KP, Laroque P and Dixit R** 1998 Need for dietary control by caloric restriction in rodent toxicology and carcinogenicity studies. *Journal of Toxicology and Environmental Health. Part B, Critical Reviews* 1(2): 135-148
- Kemppinen N, Meller A, Mauranen K, Kohila T and Nevalainen T** 2008 Work for food, a solution to restricting food intake in group housed rats? *Scandinavian Journal of Laboratory Animal Science* 35(2): 81-90
- Krohn TC, Sørensen DB, Ottesen JL and Hansen AK** 2006 The effects of individual housing on mice and rats: a review. *Animal Welfare* 15: 343-352
- Leakey JEA, Seng JE and Allaben WT** 2003a Body weight considerations in the B6C3F1 mouse and the use of dietary control to standardize background tumor incidence in chronic bioassays. *Toxicology and Applied Pharmacology* 193: 237-265
- Leakey JEA, Seng JE, Latendresse JR, Hussain N, Allen LJ and Allaben WT** 2003b Dietary controlled carcinogenicity study of chloral hydrate in male B6C3F1 mice. *Toxicology and Applied Pharmacology* 193: 266-280
- Leyhausen P** 1979 *Cat Behaviour. The Predatory and Social Behavior of Domestic and Wild Cats, First Edition*. Garland Press: New York, USA
- Lund RM, Armstrong PJ, Kirk CA and Klausner JS** 2006 Prevalence and risk factors for obesity in adult dogs from private US veterinary practices. *International Journal of Applied Research in Veterinary Medicine* 4: 177-186

- Martin, B, Pearson M, Kebejian L, Golden E, Keselman A, Bender M, Carlson O, Egan J, Ladenheim B, Cadet JL, Becker KG, Wood W, Duffy K, Vinayakumar P, Maudsley S and Mattson MP** 2007 Sex-dependent metabolic, neuroendocrine, and cognitive responses to dietary energy restriction and excess. *Endocrinology* 148: 4318-4333
- Mason GJ, Cooper J and Clarebrough C** 2001 Frustrations of fur-farmed mink. *Nature* 410: 35-36
- Masoro EJ** 2006 Dietary restriction-induced life extension: a broadly based biological phenomenon. *Biogerontology* 7: 153-155
- Mench JA** 2002 Broiler breeders: feed restriction and welfare. *Worlds Poultry Science Journal* 58: 23-29
- Meunier-Salaun MC, Edwards SA and Robert S** 2001 Effect of dietary fibre on the behaviour and health of the restricted fed sow. *Animal Feed Science and Technology* 90: 53-69.
- Nelson JF, Karelus K, Bergman MD and Felicio LS** 1995 Neuroendocrine involvement in aging: evidence from studies of reproductive aging and caloric restriction. *Neurobiology of Aging* 16: 837-856
- Nielsen BL, Thodberg K, Dybkjaer L and Vestergaard EM** 2006 Feeding behaviour of pigs. In: Bels V (ed) *Feeding in Domestic Vertebrates. From Structure to Behaviour, First Edition* pp 156-178. CAB: Cambridge, UK.
- O'Doherty JP, Deichmann R, Critchley HD and Dolan RJ** 2002 Neural responses during anticipation of a primary taste reward. *Neuron* 33: 815-826
- Pahlavani MA and Vargas DA** 2001 Aging but not dietary restriction alters the activation-induced apoptosis in rat T cells. *FEBS Letters* 491: 114-118
- Perello M, Chacon F, Cardinali DP, Esquifino AI and Spinedi E** 2006 Effect of social isolation on 24-h pattern of stress hormones and leptin in rats. *Life Sciences* 78: 1857-1862
- Petherick JC and Blackshaw JK** 1987 A review of the factors influencing the aggressive and agonistic behavior of the domestic pig. *Australian Journal of Experimental Agriculture* 27: 605-611
- Pugh TD, Klopp RG and Weindruch R** 1999 Controlling caloric consumption: protocols for rodents and rhesus monkeys. *Neurobiology of Aging* 20: 157-165
- Rasmussen DK, Weber R and Wechsler B** 2006 Effects of animal/feeding-place ratio on the behaviour and performance of fattening pigs fed via sensor-controlled liquid feeding. *Applied Animal Behaviour Science* 98: 45-53
- Raun K, von Voss P and Knudsen LB** 2007 Liraglutide, a once-daily human glucagon-like peptide-1 analogue, minimizes food intake in severely obese minipigs. *Obesity* 15: 1710-1716
- Redbo S and Nordblad A** 1997 Stereotypies in heifers are affected by feeding regime. *Applied Animal Behavioural Science* 53: 193-204
- Rehm S, White TE, Zahalka EA, Stanislaus DJ, Boyce RW and Wier PJ** 2008 Effects of food restriction on testis and accessory sex glands in maturing rats. *Toxicologic Pathology* 36: 687-694
- Robert S, Rushen J and Farmer C** 1997 Both energy content and bulk of food affect stereotypic behaviour, heart rate and feeding motivation of female pigs. *Applied Animal Behaviour Science* 54: 161-171
- Russell WMS and Burch RL** 1959 *The Principles of Humane Experimental Technique, First Edition*. Methuen: London, UK
- Rutten M, Leterrier C, Constantin P, Reiter K and Bessei W** 2002 Bone development and activity in chickens in response to reduced weight-load on legs. *Animal Research* 51: 327-336
- Sandilands V, Tolkamp BJ, Savory CJ and Kyriazakis I** 2006 Behaviour and welfare of broiler breeders fed qualitatively restricted diets during rearing: are there viable alternatives to quantitative restriction? *Applied Animal Behaviour Science* 96: 53-67
- Sandøe P and Christiansen S** 2008 *Ethics of Animal Use*. Blackwell Publishing: Oxford, UK
- Selesniemi K, Lee HJ and Tilly JL** 2008 Moderate caloric restriction initiated in rodents during adulthood sustains function of the female reproductive axis into advanced chronological age. *Aging Cell* 5: 622-629
- Serra M, Pisu MG, Floris I and Biggio G** 2005 Social isolation-induced changes in the hypothalamic-pituitary-adrenal axis in the rat. *Stress* 8: 259-264
- Sharov AA, Falco G, Piao Y, Poosala S, Becker KG, Zonderman AB, Longo DL, Schlessinger D and Ko MS** 2008 Effects of aging and calorie restriction on the global gene expression profiles of mouse testis and ovary. *BMC Biology* 6: 24
- Sherwin CM** 2007 The motivation of group-housed laboratory mice to leave an enriched laboratory cage. *Animal Behaviour* 73: 29-35
- Spruijt BM, van den Bos R and Pijlman FTA** 2001 A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. *Applied Animal Behaviour Science* 72: 145-171
- Stolba A and Woodgush DGM** 1989 The behavior of pigs in a semi-natural environment. *Animal Production* 48: 419-425
- Thorp BH and Duff SRI** 1988 Effect of exercise on the vascular pattern in the bone extremities of broiler fowl. *Research in Veterinary Science* 45: 72-77
- Van Der Harst JE, Fermont PCJ, Bilstra AE and Spruijt BM** 2003 Access to enriched housing is rewarding to rats as reflected by their anticipatory behaviour. *Animal Behaviour* 66: 493-504
- Vitousek KM, Manke FP, Gray JA and Vitousek MN** 2004 Caloric restriction for longevity: II, The systematic neglect of behavioural and psychological outcomes in animal research. *European Eating Disorders Review* 12: 38-360