

Chapter 2

Hunger Associated with Restricted Feeding Systems

Bert J. Tolkamp and Rick B. D'Eath

Abstract Hunger and satiety are normally alternating animal states that determine feeding patterns in animals with free access to food. However, chronic hunger can result if access to food is restricted deliberately over long periods. Such systems of quantitative food restriction are widely applied during rearing and/or the dry period in some animals, such as broiler breeders and sows, to avoid the negative health and welfare consequences of ad libitum feeding in animals destined for breeding. Quantitative restriction is associated with signs of hunger such as increased feeding motivation, activity, and stereotypic behaviour. An alternative approach to restrict energy intake is to provide food of a reduced quality. The benefits of these alternative diets for animal welfares are controversial: some researchers conclude that they result in more normal feeding behaviour, promote satiety, and thus improve animal welfare; others argue that 'metabolic hunger' remains irrespective of how the restriction of energy intake is achieved. These disagreements between researchers are a result of differences in (1) assumptions about what determines feeding behaviour and controls food intake, (2) the assessment of the value of the different methodologies that have been used to measure animal hunger, and (3) the weighting placed on 'naturalness' of behaviour as a determinant of welfare. Some problems associated with commonly-used behavioural and physiological measures of hunger are discussed. The development of welfare-friendly feeding systems for broiler breeders and sows would benefit greatly from a better understanding of the controls of food intake and from better methodologies to measure animal hunger.

2.1 Introduction

In many farming systems (fast-growing pigs or beef bulls, and lactating dairy cows), high intakes of food (i.e. energy and nutrients) are beneficial because these allow the achievement of high performance levels. However, in other farm animals (such as dry cows, sows or ewes, and broiler breeders during rearing and

B.J. Tolkamp (✉) • R.B. D'Eath

Animal and Veterinary Sciences Group SRUC, The Roslin Institute Building, Easter Bush, Midlothian EH25 9RG, UK

e-mail: Bert.Tolkamp@sruc.ac.uk; Rick.DEath@sruc.ac.uk

lay), as well as in many pets, zoo animals, and even humans, high-energy intakes associated with the ad libitum intake of high-quality diets can have very detrimental effects on health and welfare (Schwitzer and Kaumanns 2001; Gough 2005; Stubbs and Tolkamp 2006; D'Eath et al. 2009). High-energy intake in such animals is associated with extensive lipid deposition and (associated) lowered fertility, ascites, lameness, heart problems, diabetes, metabolic diseases, etc. (Hocking and Whitehead 1990; Aviagen 2001; Mench 2002). The only way to avoid these health and welfare problems is to apply feeding systems that deliberately prevent the sustained daily consumption of large amounts of energy. Animals in several of these systems are assumed to be chronically hungry, which is a considerable welfare concern (D'Eath et al. 2009). In addition, restricted access to food (sometimes complete withdrawal of food for up to 1 or 2 weeks) is still practised in some countries to induce moulting in laying hens (Bell 2003). The practice is considered particularly detrimental for animal welfare (Webster 2003) and is therefore not applied at all in some countries, such as the UK ('In no circumstances may birds be induced to moult by withholding feed and water'; Defra 2002: 11). Alternative methods, frequently relying on the supply of low-quality poultry food (such as alfalfa; McReynolds et al. 2009) or with specific nutrient imbalances (such as excessive zinc; Park et al. 2004), may achieve the same goals and help combat disease (such as *Salmonella* infections), as well as addressing the welfare concern caused by hunger associated with food withdrawal (Aygün and Yetisir 2009; Howard et al. 2012). For that reason, the emphasis here will be on hunger associated with feeding systems of sows and poultry breeders. Questions are discussed relating to normal feeding behaviour, the nature of hunger, possible ways of measuring it, the type of feeding systems that are thought to be associated with hunger, and possible ways of alleviating the welfare problems associated with quantitative food restriction.

2.2 What Is Hunger?

Feeding is amongst the most natural of all animal behaviours as it has a profound effect on the survival of the individual and its reproductive success, i.e. its evolutionary fitness. Normal feeding behaviour of an animal with continuous access to food shows a typical temporal structure of feeding bouts (frequently called meals) separated by nonfeeding intervals (Tolkamp et al. 2011). It is generally assumed that animals end a meal when they are satiated (Metz 1975; Le Magnen 1985; Forbes 1995; Zorrilla et al. 2005). As a result, the probability is very low of animals starting a meal shortly after finishing one. With the passing of time, however, satiety wears off and the gradually increasing feeding motivation or hunger will systematically increase the probability of animals starting a meal. Similarly, an animal starting a meal is assumed to be hungry, whilst the increasing amount of food consumed during the meal will gradually decrease hunger and increase satiation, thereby increasing the probability of animals ending the meal (Tolkamp

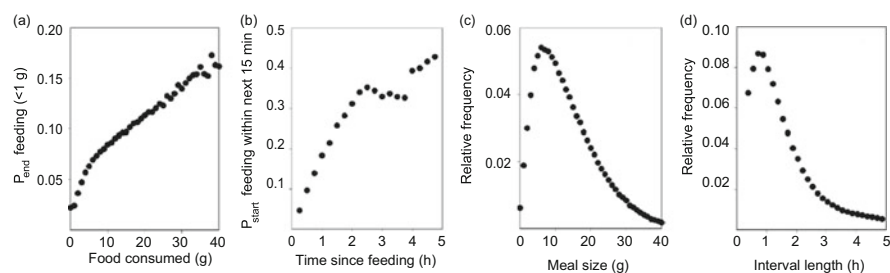


Fig. 2.1 (a) Probability of broilers ending a meal before consuming another gram of food (P_{end}) in relation to the amount of food already consumed; (b) the probability of broilers starting a meal (P_{start}) in relation to the time since the last meal; (c) the frequency distribution of meal size; (d) the frequency distribution of the length of between-meal intervals. Re-drawn after data presented by Howie et al. (2009a) and Tolkamp et al. (2011)

et al. 2011). Figure 2.1 illustrates these principles and their consequences for the distribution of meal size and between-meal interval length for broiler chickens. Similar relationships can be found for other species, including pigs, cows, ducks, turkeys, rats, and dolphin calves (Tolkamp et al. 2011). This illustrates the fact that ‘hunger’ can be considered as a natural motivational state that leads to feeding behaviour, and hunger has, therefore, been seen as one of the ‘most basic, primitive, and unremitting of all motivating forces’ (Webster 1995). Patterns of normal feeding behaviour as characterized in Fig. 2.1 occur in semi-wild (dolphin calves; Tolkamp et al. 2011) as well as domesticated animals and seem to be virtually unaffected by genetic selection for productive traits in intensively selected farm animals, such as broiler chickens (Howie et al. 2009b; Tolkamp et al. 2011, 2012). These findings contradict the view that animals from genetic lines that have been intensively selected for productive traits are in a constant state of hunger, even when fed ad libitum (Burkhart et al. 1983; Bokkers et al. 2004).

For this reason, it may appear odd that ‘freedom from hunger and thirst’ features high in the ‘Five Freedoms’ that form part of most codes of recommendation for animal welfare (FAWC 1992; AWAC 1994). It is obvious that the term ‘hunger’ can have very different connotations in different contexts (for a brief discussion of thirst, see Kyriazakis and Tolkamp 2011). On the one hand, feeding might never occur unless an animal experiences hunger as a (short-term) motivational state that will result in a search for, and consumption of, food. On the other hand, hunger can also be defined (as in this chapter) as a ‘negative subjective state of an animal that is chronically undernourished’ (D’Eath et al. 2009). In this definition, the longer term is emphasized because (1) it differentiates clearly from the (appetitive) hunger associated with control of short-term feeding behaviour, and (2) chronic restriction has a larger effect on feeding motivation than acute deprivation (Savory et al. 1993; Ferguson and Paule 1995, 1997; Bokkers et al. 2004). The term ‘undernourished’ can refer to energy as well as nutrient supply; restricted feeding regimes are, however, almost invariably aimed at restricting energy intake and the term will be interpreted here in that sense. The definition emphasizes animals’ subjective

states because these are a critical component of animal welfare (Dawkins 1990; Duncan 1993; Fraser and Duncan 1998; Fraser et al. 1997), even though these may not always be easily measured.

2.2.1 Measurement of Hunger in Relation to Quantitative Food Restriction

There are three broad types of indicators of hunger (including the stress associated with it) that have been used to evaluate hunger in relation to quantitative restriction of access to food: (1) (changes in) observed behaviour, (2) physiological indicators, and (3) specific behavioural tests. These have been reviewed extensively by D'Eath et al. (2009) and are briefly summarized and updated here.

Behavioural Indicators of Stress Associated with Hunger The feeding motivation of animals subjected to quantitative food restriction is usually very high. Any food made available is consumed immediately and various behaviours occur after feeding ends that are thought to be a result of unsatisfied feeding motivation (D'Eath et al. 2009). Quantitative restriction generally results in an increase in behaviours relating to foraging (Epling and Pierce 1988; Dewasmes et al. 1989; Koubi et al. 1991; Weed et al. 1997) and in overall activity (indicated by reduced resting; Savory and Lariviere 2000; Hocking 2004). These are generally redirected oral behaviours, such as spot-pecking by boiler breeders (Sandilands et al. 2005, 2006; Nielsen et al. 2011), and chain or bar chewing and rooting in substrate by sows (Appleby and Lawrence 1987). The drinker can also be targeted and excessive drinking or water spillage occurs frequently in feed-restricted animals (Rushen 1984; Sandilands et al. 2005). These redirected oral behaviours can become stereotypic (i.e. repetitive and unvarying whilst not serving an immediately obvious function; Mason and Latham 2004). Stereotypic behaviour generally increases with the level of food restriction in chickens (Savory et al. 1996) and pigs (Brouns et al. 1994; Bergeron et al. 2000). Such stereotypes represent the expression of foraging behaviour, modified by the physical constraints of the environment (Lawrence and Terlouw 1993). In summary, the behavioural effects of quantitative restriction are largely agreed upon by different researchers and there is almost universal agreement that these behavioural effects indicate that quantitative restriction results in hunger (D'Eath et al. 2009).

2.2.2 Physiological Indicators of Stress Associated with Hunger

Some indicators of feeding and stress physiology have been used extensively by researchers that investigated hunger in broiler breeders and sows and the most relevant are briefly reviewed here.

Plasma Cortisol or Corticosterone Concentration Measures of stress physiology such as glucocorticoids [Plasma Cortisol or Corticosterone Concentration (PCC)] and other measures of hypothalamic–pituitary–adrenal axis (HPA) functioning are widely used in animal welfare [reviewed in Mormède et al. (2007)]. PCC is probably the most widely used indicator of stress associated with chronic hunger in broilers and sows (D’Eath et al. 2009). Although PCC may seem an ideal indicator of stress at first sight, there are a number of interpretational problems (D’Eath et al. 2009; see also discussion below). There is, in addition, an issue related to the use of PCC as an indicator of hunger that was raised by D’Eath et al. (2009) but has been analysed only superficially before (Kyriazakis and Tolkamp 2011). In some studies (Hocking et al. 1996; Kubíková et al. 2001; de Jong et al. 2003), PCC is recorded in birds of a given age subjected to different nutritional treatments (frequently ranging from severe restriction to ad libitum). Such studies generally show that PCC at a given age is higher in birds with more restricted access to food than birds with more liberal (or ad libitum) access to food. This has been interpreted as evidence for higher stress levels associated with restricted feeding regimes, at least at severe restriction levels (de Jong et al. 2003). The differential feeding regimes in these studies had, however, also strong effects on the daily amount of energy and nutrients available to the birds for body weight gain and, therefore, on the weight that was attained at the age when PCC was measured (with higher weights always associated with more liberal feed supply). The consequences are that there seems to be a strong relationship between bird body weight and PCC in these studies (see Fig. 2.2). That raises the question whether the variation in PCC in these studies was caused by variation in levels of stress associated with feeding level or (partly at least) by variation in body weight per se. Doubt about the validity of PCC as an indicator of hunger is reinforced by data obtained in studies in which PCC has been recorded repeatedly (i.e. at different ages) in birds subjected to the same feeding regime. Such studies suggest that body

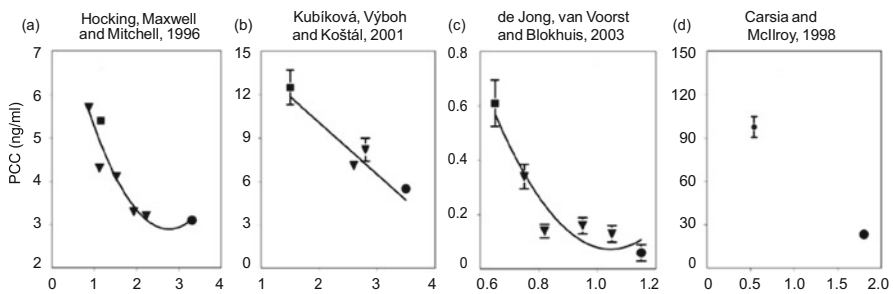


Fig. 2.2 Plasma corticosterone concentration (PCC) against group mean body weight during rearing in broiler breeders aged 7 weeks (c), 12 weeks (a), or 13 weeks (b), and turkeys aged 5 weeks (d). Feeding treatments were high-quality food, fed either ad libitum (*large filled circle*) or in restricted amounts, i.e. close to commercial recommendations (*square*), other levels of restriction (*triangles*), or low-protein food fed ad libitum (*small filled circle*). Drawn lines are the best fitting linear plus quadratic [as suggested by Hocking et al. (1996)] or linear regression lines of group mean PCC on group mean body weight

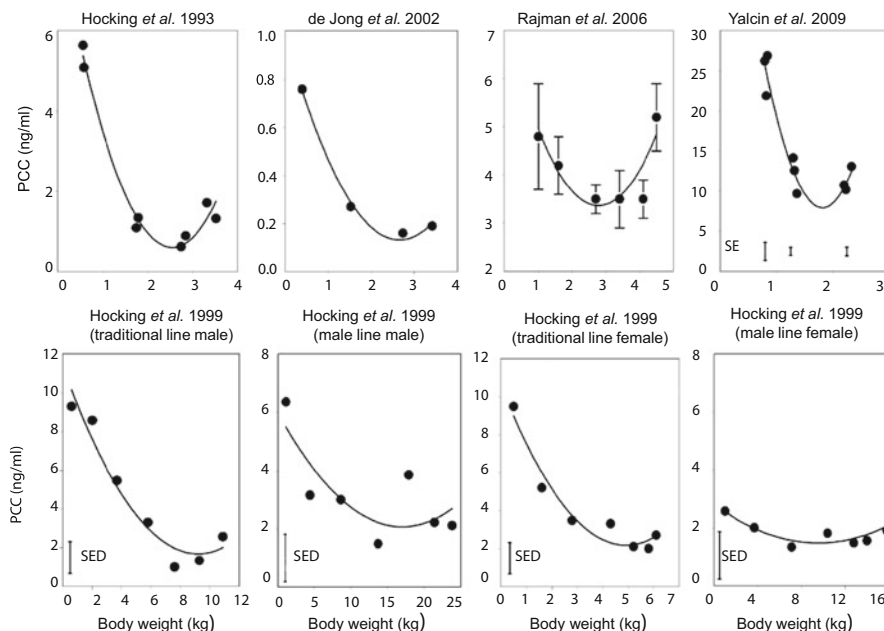


Fig. 2.3 Relationship between body weight and plasma corticosterone concentration (PCC) in broiler breeders (*top panels*) and turkeys (*bottom panels*) with continuous ad libitum access to high-quality food. *Drawn lines* are the best fitting linear plus quadratic regression lines of group mean PCC on group mean body weight [as suggested by Hocking et al. (1996)]

weight in itself has a considerable effect on PCC in ad libitum-fed as well as restricted animals (Kyriazakis and Tolkamp 2011). Figure 2.3 shows examples of the observed relationship between PCC and body weight in five studies in which all birds were fed ad libitum. Most graphs show that, in ad libitum-fed birds, PCC initially declined fast with increasing age and body weight, but in some studies subsequently stabilized (or even slightly increased again) at higher body weights. This decline in PCC is unlikely to be associated with a decrease in hunger with age or body weight because in these studies all birds were fed ad libitum throughout.

Other Physiological Indicators of Hunger-Related Stress Ratios of white blood cells [the frequently analysed heterophil-to-lymphocyte ratio (HLR)] are a common method of animal welfare assessment, including stress related to hunger, especially in broiler breeders. Some of the criticism applied to PCC also applies to this indicator and it is therefore hardly surprising that the results are confusing (D'Eath et al. 2009). Different studies find that HLR increases, stays the same, or decreases in response to different levels of quantitative restriction (D'Eath et al. 2009). A similar confused picture emerged for both poultry and pigs when other immune markers were evaluated, and we concluded that these are not reliable indicators of hunger (D'Eath et al. 2009).

The concentrations of several plasma nutrients, metabolites, and hormones (such as glucose, nonesterified fatty acids, beta-hydroxybutyrate, insulin, etc.) or their ratios have been measured as alternative indicators of chronic hunger in feed-restricted animals (de Jong et al. 2003, 2005; Nielsen et al. 2011). As discussed by D'Eath et al. (2009), the concentrations of such substances usually vary throughout the day (also in response to variation in meal patterns) and are intimately linked with energy supply and/or energy status of the animal, which make them less suitable as indicators of hunger as it is experienced by the animal. More recent attempts to quantify hunger is the measurement of gene expression for peptides such as neuropeptide Y or Agouti-related protein (AGRP), the latter sometimes being referred to as the 'hunger peptide'. Although there is strong evidence that expression of such genes is related to levels of feed restriction (Boswell et al. 1999; Dunn et al. 2012), the evidence that this is related to animals' subjective state is at present not entirely convincing. There are, therefore, in our view, at present no clear physiological indicators of hunger as a result of quantitative feed restriction. This is a serious limitation for those interested in quantifying the seriousness of hunger states associated with various forms of energy intake restrictions as currently practised in animal farming.

2.2.3 Specific Behavioural Tests of Feeding Motivation to Evaluate Hunger

In the absence of unequivocal clear physiological indicators, tests of feeding motivation seem a valuable tool in the assessment of hunger because feeding motivation is expected to reflect directly the animal's own subjective state of hunger (Dawkins 1990). There are a number of types of test that have been used to measure feeding motivation as an indicator of hunger, and below is an updated summary of the detailed review by D'Eath et al. (2009).

2.2.3.1 Feeding Rate and Compensatory Feed Intake

Although increasing levels of food deprivation usually increase short-term feeding rate, there are considerable problems associated with the interpretation of such tests (D'Eath et al. 2009). There is the question of when to test (relative to normal feeding time in the restricted treatments) and the problem that animals subjected to feed restriction are accustomed to feeding very fast, especially when there is competition with conspecifics (Nielsen 1999). Decisions that are made to overcome these problems may make treatment comparisons rather arbitrary (Sandilands et al. 2005), especially when different food qualities are tested (D'Eath et al. 2009).

2.2.3.2 Operant Responding

Operant conditioning for a food reward is an effective way of measuring feeding motivation, as the ratio of cost (lever pressing) to reward (food) can be altered by the experimenter. The method has been validated for quantitative restriction, and increasing restriction generally results in increasing feeding motivation (D'Eath et al. 2009). The method is, however, problematic when comparing treatments with access to different food qualities (see below).

2.2.3.3 Choice Testing and Conditioned Place Preference or Aversion Testing

Recently, attempts have been made to quantify hunger associated with restricted feeding practices with the aid of choice and Conditioned Place Preference (CPP) or Conditioned Place Aversion (CPA) testing. Buckley et al. (2011) used a Y-maze paradigm in which food-restricted broilers could choose between differently coloured arms of a Y-maze to obtain a small or large food reward. The original hypothesis (i.e. the more severe the food restriction and resulting hunger, the sooner the birds would learn the task) was proven false, however, as the most severely restricted birds were least likely to complete the test successfully. The authors concluded that severe food restriction may limit the birds' ability to learn and that, as a result, the test could not quantify the seriousness of the hunger associated with different restriction levels. Other methods such as CPP and CPA can be useful tools in animal welfare assessment because they allow measurement of the reinforcing properties of a stimulus in extinction. Dixon et al. (2011) used CPP/CPA techniques in a series of experiments with broiler breeders to determine the best methodology for establishing CPP/CPA. The experiments showed, however, a number of methodological issues (especially strong preferences for environments birds were not housed in immediately before the test) that restricted the suitability of these tests for the quantitative welfare assessment of chronically food-restricted birds (Dixon et al. 2013).

2.2.4 Possible Ways of Alleviating Hunger Associated with Quantitative Food Restriction

In ruminant production systems, avoidance of excessive gain in condition (or moderate weight loss in over-fat animals) is generally achieved by giving animals ad libitum access to lower quality foods (usually a forage) by which the voluntary energy intake is reduced. A typical example is the provision of dry cows with no or limited amounts of concentrate and ad libitum access to forage such as grazing, silage, or straw. Such systems allow animals to express their normal

patterns of feeding behaviour and are not associated with (stress caused by) hunger (Tolkamp et al. 2002).

In response to the concerns over the negative animal welfare consequences of hunger associated with quantitative food restriction, dietary manipulation has also been proposed as an alternative to quantitative restriction for monogastrics like broiler breeders and dry sows (Meunier-Salaün et al. 2001; Mench 2002; Hocking 2004; Ru and Bao 2004; D'Eath et al. 2009). If food is reduced in quality, but offered ad libitum, this is called qualitative restriction (Sandilands et al. 2006). Such diets can restrict intake because ad libitum-fed animals consume less energy from low-quality foods (Brouns et al. 1995; Savory et al. 1996; West and York 1998; Whittemore et al. 2002; Tolkamp et al. 2005; Johnston et al. 2006). Diets where food quality is reduced but food is not offered ad libitum (Zuidhof et al. 1995; Danielsen and Vestergaard 2001; de Jong et al. 2005) can be called 'rationed alternative diets'. Here, we refer to qualitative restriction and rationed alternative diets as 'alternative diets'. Such alternative diets usually involve using foods of lowered quality through the addition of bulky ingredients containing dietary fibre, such as sugar beet pulp (Whittaker et al. 2000; Danielsen and Vestergaard 2001), wheat bran and cobs (Robert et al. 1997), or oat hulls (Sandilands et al. 2005), although other preparations known to suppress appetite have also been used in poultry (phenylpropanolamine, Oyawoye and Krueger 1990; monensin sodium, Savory et al. 1996; calcium propionate, Savory and Lariviere 2000), sometimes in combination with fibrous ingredients (Sandilands et al. 2005, 2006).

Whether such alternative diets reduce hunger and so enhance animal welfare in comparison with quantitative restriction is controversial, and the reasons behind this controversy are briefly discussed below. Most research involves broiler breeders (the parent stock of meat chickens) that are severely restricted during rearing (25–50 % of ad libitum intake, Savory et al. 1993; Renema et al. 2007) or non-lactating sows, which are restricted during pregnancy (50–60 % of ad libitum intake, Lawrence et al. 1989). Although the problem also clearly applies to companion animals (Butterwick and Hawthorne 1998; Umeda et al. 2006), we focus on these groups for the evidence that is briefly reviewed below.

2.3 Alternative Diets

2.3.1 *Effects on Behaviour*

The provision of alternative diets, in comparison with quantitative restriction of food intake, generally leads to a number of behavioural changes and there is broad agreement between studies about the type of changes that can be observed (D'Eath et al. 2009). Feeding and foraging behaviour appear more 'natural', i.e. the animal is in control of its feeding behaviour, meals are ended whilst food is still available,

and more normal meal patterns can be observed over the day (Savory et al. 1996; Meunier-Salaün et al. 2001; Hocking 2004). However, 'naturalness of behaviour' is considered more important for the assessment of animal welfare by some (Kiley-Worthington 1989; FAWC 1998: 'Freedom to express normal behaviour') than by others (Dawkins 1990; Broom and Johnson 1993; Duncan 1993). In addition, redirected oral behaviour and stereotypies generally decrease considerably (D'Eath et al. 2009). It is generally assumed that (1) quantitative food restriction plays a central role in the development of post-feeding oral stereotypies (Dantzer 1986; Appleby and Lawrence 1987; Lawrence and Terlouw 1993; Mason and Latham 2004), (2) these appear to reflect frustrated motivation (Mason et al. 2007), and (3) are a sign of reduced welfare as they develop under suboptimal environmental conditions (Dantzer 1986; Mason and Latham 2004). A reduction in redirected oral behaviours and stereotypies can then be interpreted as signalling improved animal welfare (Bergeron et al. 2000; Danielsen and Vestergaard 2001; Zonderland et al. 2004; Sandilands et al. 2005). At the same time, however, the duration of feeding activity is usually much longer under qualitative compared with quantitative restriction, and the total duration of oral behaviours is frequently similar under quantitative and qualitative restriction regimes (D'Eath et al. 2009). If oral behaviours are substitutable and functionally equivalent outlets for unsatisfied feeding motivation, a decrease of redirected oral behaviours and stereotypies under qualitative restriction is then not necessarily a sign of improved welfare (Savory and Maros 1993; Dailey and McGlone 1997; McGlone and Fullwood 2001). A reduction in stereotypic oral behaviour in animals subjected to qualitative compared with quantitative restriction is, therefore, considered a clear indication of reduced hunger by some—but certainly not by all—investigators (D'Eath et al. 2009; Kyriazakis and Tolkamp 2011).

2.3.2 Effects on Physiological Indicators

At present, there are no physiological indicators that can be used with confidence to assess the effects of various degrees of quantitative restriction of food intake as discussed above. It is even more problematic to use indicators such as PCC to assess the effects on (the stress caused by) hunger associated with alternative diets in comparison with quantitative food restriction. As discussed by D'Eath et al. (2009), these problems include (1) the considerable diurnal variation in PCC in relation to variation in feeding patterns associated with different feeding regimes; (2) PCC also rises in response to pleasurable or exciting stimuli, reflecting emotional arousal; (3) PCC is not usually a good measure of a chronic stress (such as might result from chronic food restriction), since the HPA axis adapts and PCC levels tend to return to baseline; and (4) the important metabolic role of corticosterone makes it particularly difficult to interpret PCC as a welfare measure to determine levels of hunger in different feeding treatments. Birds subjected to qualitative food restriction that results in similar reductions in growth rate (compared with ad libitum

feeding) as quantitative food restriction generally have comparable PCC (Sandilands et al. 2005). But in view of the arguments mentioned earlier, it is not clear at all whether this means that there is no difference in stress between qualitative and quantitative food restriction or that (in our view more likely) PCC is not suitable to measure stress caused by chronic hunger associated with different feeding systems. Similar critical comments can be made for the other proposed physiological indicators (D'Eath et al. 2009; Kyriazakis and Tolkamp 2011).

2.3.3 Effects as Measured via Specific Tests

Although operant testing has been successfully applied to quantify hunger associated with different levels of quantitative restriction and to compare effects of different fibre types (Souza da Silva et al. 2012), the application and interpretation is much more problematic when alternative diets are considered in comparison with quantitative restriction. Because animals in these regimes are accustomed to different foods, it is not immediately clear which food should be offered during the test (the same problem applies for the tests of feeding rate and compensatory feeding). For instance, when the reward consists of the usual (treatment) food (Robert et al. 1997; Savory and Lariviere 2000), it is difficult to decide what constitutes 'equivalent responding' (equal weights of food, equal energy per reward, equal access time?) when comparing across treatments (D'Eath et al. 2009). When all treatments are tested with the same food (Lawrence et al. 1989; Ramonet et al. 2000), the reward food is often of high quality. The food reward then represents a greater contrast with their usual food for animals fed alternative diets than for animals subjected to quantitative restriction, which in itself may result in larger responses in such animals (Ramonet et al. 2000; Savory and Lariviere 2000). As discussed by D'Eath et al. (2009), these differences in reward type can explain much of the variation in the findings of different studies using sows and their interpretation. Similar problems apply to the question of the timing of the tests. With alternative diets, operant responding for food after a meal is typically low and stays low for longer before beginning to rise and is high again before the next meal (Robert et al. 1997; Day et al. 1996). In contrast, under quantitative restriction, operant responding for food is similarly high at different tested time points (Lawrence et al. 1989; Ramonet et al. 2000; Savory and Lariviere 2000). This is usually interpreted as indicating that alternative diets result in satiety for at least part of the day (Robert et al. 1997; Savory and Lariviere 2000), although others have interpreted this result more in terms of a constraint, where, for example, gut distension inhibits further feeding, despite a continuing demand for energy (metabolic hunger; Day et al. 1996).

2.3.4 Perspectives

At present, the use of qualitative food restriction as an alternative to quantitative restriction to alleviate hunger in (mainly) broiler breeders and sows is controversial. The contrast in policy and practice between these commercially important monogastric species is also confused. EU recommendations ensure that sows are given qualitative restriction or more usually rationed alternative diets in which they have access to fibre in addition to concentrate. This is done on the basis that it will alleviate hunger. In contrast, simple quantitative restriction of broiler breeders is still routine practice throughout the world.

To decide whether or not qualitative restriction can alleviate the welfare problem of hunger in such animals, two important questions need to be addressed. The first relates to the characterization or quantification of levels of animal hunger. Good decisions about the suitability of different feeding systems in relation to animal welfare can be taken only if the consequences of these different systems for the animals' experience in terms of hunger can be measured. For this purpose, modified behavioural tests (such as choice, operant responding, and CPP/CPA) and Qualitative Behavioural Assessment (Wemelsfelder et al. 2001, 2009) and perhaps also (changes in) the expression of specific genes may prove effective. The second question relates to the structure of the animals' foraging programmes, notably their apparent goals. If animals are pure intake rate maximizers subject to constraints, there is perhaps little hope that alternative feeding strategies can be developed that achieve both welfare goals (i.e. avoiding the negative welfare consequences associated with ad libitum feeding of high-quality food and the hunger associated with restrictive feeding practices). However, if animals are optimizers (i.e. trying to achieve the best possible combination of costs and benefits with their behaviour; Illius et al. 2002; Tolkamp et al. 2002; Forbes 2007), efforts can be made to identify what it is exactly that animals respond to and perhaps more appropriate diets can subsequently be developed. Until these issues have been resolved, the search for feeding systems that alleviate hunger and avoid the negative consequences of excessive energy intake at the same time may prove to be elusive.

2.4 Conclusions

Some researchers have concluded that welfare of animals such as dry sows and broiler breeders is improved by alternative diets because foraging behaviour is more normal and characteristics of the food enhance satiety (Zuidhof et al. 1995; Robert et al. 1997; Zonderland et al. 2004; Souza da Silva et al. 2012). This view is reflected in policy: in the EU, there has been a requirement that sows receive 'a sufficient quantity of bulky or high-fibre food as well as high-energy food' since 2001 (EC Council 2001), and this is implemented in the member states through legislation (Netherlands: de Leeuw et al. 2004) or codes of practice (UK: Defra

2003). Other researchers, however, emphasize the conflicting evidence and interpretations of the welfare benefits of alternative diets (Day et al. 1996; Meunier-Salaün et al. 2001; Mench 2002; Hocking 2004; Ru and Bao 2004; de Jong et al. 2005; D'Eath et al. 2009). A third group has argued that there is no convincing evidence of any welfare benefits of such alternative diets because (1) the hunger indicators of total oral behaviours and activity remain similar between quantitative restriction and alternative diets, and (2) that if nutrient requirements and energy needs remain unsatisfied, 'metabolic hunger' will occur (Lawrence et al. 1989; Owen 1992; Savory et al. 1996; Dailey and McGlone 1997; Savory and Lariviere 2000; McGlone and Fullwood 2001). Hence the development of welfare-friendly feeding systems for broiler breeders and sows would benefit greatly from a better understanding of the controls of food intake and from better methodologies to measure animal hunger.

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References

- Appleby MC, Lawrence AB (1987) Food restriction as a cause of stereotypic behavior in tethered gilts. *Anim Prod* 45(1):103–110
- Aviagen (2001) Parent stock management manual: ross 308. Aviagen, Midlothian
- AWAC [Animal Welfare Advisory Committee] (1994) Annual report. Ministry of Agriculture and Fisheries, Wellington
- Aygun A, Yetisir R (2009) Researches on the response of different hybrid layers with respect to egg production performances of forced molting programs with and without feed withdrawal. *J Anim Vet Adv* 8(12):2680–2686
- Bell DD (2003) Historical and current molting practices in the US table egg industry. *Poult Sci* 82:965–970
- Bergeron R, Bolduc J, Ramonet Y, Meunier-Salaün MC, Robert S (2000) Feeding motivation and stereotypies in pregnant sows fed increasing levels of fibre and/or food. *Appl Anim Behav Sci* 70(1):27–40
- Bokkers EAM, Koene P, Rodenburg TB, Zimmerman PH, Spruijt BM (2004) Working for food under conditions of varying motivation in broilers. *Anim Behav* 68:105–113
- Boswell T, Dunn IC, Corr SA (1999) Hypothalamic neuropeptide Y mRNA is increased after feed restriction in growing broilers. *Poult Sci* 78(8):1203–1207
- Broom DM, Johnson KG (1993) Stress and animal welfare. Chapman and Hall, London
- Brouns F, Edwards SA, English PR (1994) Effect of dietary fiber and feeding system on activity and oral behavior of group-housed gilts. *Appl Anim Behav Sci* 39(3–4):215–223
- Brouns F, Edwards SA, English PR (1995) Influence of fibrous feed ingredients on voluntary food intake of dry sows. *Anim Feed Sci Technol* 54(1–4):301–313
- Buckley LA, McMillan LM, Sandilands V, Tolcamp BJ, Hocking PM, D'Eath RB (2011) Too hungry to learn? Hungry broiler breeders fail to learn a Y-maze food quantity discrimination task. *Anim Welf* 20(4):469–481
- Burkhart CA, Cherry JA, Vankrey HP, Siegel PB (1983) Genetic selection for growth-rate alters hypothalamic satiety mechanisms in chickens. *Behav Genet* 13(3):295–300
- Butterwick RF, Hawthorne AJ (1998) Advances in dietary management of obesity in dogs and cats. *J Nutr* 128(12; Suppl):2771S–2775S

- Carsia RJ, McIlroy PV (1998) Dietary protein restriction stress in the domestic Turkey (*Meleagris gallopavo*) induces hypofunction and remodeling of adrenal steroidogenic tissue. *Gen Comp Endocrinol* 109(1):140–153
- D'Eath RB, Tolkamp BJ, Kyriazakis I, Lawrence AB (2009) 'Freedom from hunger' and preventing obesity: the animal welfare implications of reducing food quantity or quality. *Anim Behav* 77(2):275–288
- Dailey JW, McGlone JJ (1997) Oral/nasal/ facial and other behaviors of sows kept individually outdoors on pasture, soil or indoors in gestation crates. *Appl Anim Behav Sci* 52(1–2):25–43
- Danielsen V, Vestergaard EM (2001) Dietary fibre for pregnant sows: effect on performance and behaviour. *Anim Feed Sci Technol* 90(1–2; Special Issue):71–80
- Dantzer R (1986) Behavioral, physiological and functional aspects of stereotyped behavior: a review and a re-interpretation. *J Anim Sci* 62(6):1776–1786
- Dawkins MS (1990) From an animal's point of view: motivation, fitness and animal welfare. *Behav Brain Sci* 13(1):1–61
- Day JEL, Kyriazakis I, Lawrence AB (1996) The use of a second-order schedule to assess the effect of food bulk on the feeding motivation of growing pigs. *Anim Sci* 63(3):447–455
- de Jong IC, van Voorst S, Ehlhardt DA, Blokhuis HJ (2002) Effects of restricted feeding on physiological stress parameters in growing broiler breeders. *Br Poult Sci* 43(2):157–168
- de Jong IC, van Voorst AS, Blokhuis HJ (2003) Parameters for quantification of hunger in broiler breeders. *Physiol Behav* 78(4–5):773–783
- de Jong IC, Enting H, van Voorst A, Blokhuis HJ (2005) Do low-density diets improve broiler breeder welfare during rearing and laying? *Poult Sci* 84(2):194–203
- de Leeuw JA, Jongbloed AW, Verstegen MWA (2004) Dietary fiber stabilizes blood glucose and insulin levels and reduces physical activity in sows (*Sus scrofa*). *J Nutr* 134(6):1481–1486
- Defra [Department for Environment, Food and Rural Affairs] (2002) Code of recommendations for the welfare of livestock: laying hens. Defra Publications, London
- Defra (2003) Code of recommendations for the welfare of livestock: pigs. Defra Publications, London
- Dewasmes G, Duchamp C, Minaire Y (1989) Sleep changes in fasting rats. *Physiol Behav* 46(2):179–184
- Dixon LM, Sandilands V, Bateson M, Brocklehurst S, Tolkamp BJ, D'Eath RB (2011) Using conditioned place aversion techniques as a novel tool for measuring affective states: broiler breeders find unpredictable wind aversive. *Br Poult Abstr* 7(1):40–41
- Dixon LM, Sandilands V, Bateson M, Brocklehurst S, Tolkamp BJ, D'Eath RB (2013) Conditioned place preference or aversion as animal welfare assessment tools: limitations in their application. *Appl Anim Behav Sci* 148(1–2):164–176
- Duncan IJH (1993) Welfare is to do with what animals feel. *J Agric Environ Ethics* 6(Special Suppl 2):8–14
- Dunn IC, Wilson PW, Smulders TV, D'Eath RB, Boswell T (2012) Hypothalamic agouti-related peptide mRNA levels as a potential integrated measure of hunger state in birds. *Br Poult Abstr* 8(1):20–21
- EC Council (2001) Council Directive 2001/88/EC of 23rd October 2001 amending Directive 91/630/EEC laying down minimum standards for the protection of pigs. *Off J Eur Communities* 316:1–4
- Epling WF, Pierce WD (1988) Activity-based anorexia: a biobehavioral perspective. *Int J Eat Disord* 7(4):475–485
- FAWC [Farm Animal Welfare Council] (1992) FAWC updates on the five freedoms. *Vet Rec* 131:357
- FAWC [Farm Animal Welfare Council] (1998) Report on the welfare of broiler breeders. FAWC, London
- Ferguson SA, Paule MG (1995) Lack of effect of prefeeding on food-reinforced temporal response differentiation and progressive ratio responding. *Behav Process* 34(2):153–160

- Ferguson SA, Paule MG (1997) Progressive ratio performance varies with body weight in rats. *Behav Process* 40(2):177–182
- Forbes JM (1995) Voluntary food intake and diet selection in farm animals. CABI, Wallingford
- Forbes JM (2007) A personal view of how animals control their intake and choice of food: minimal total discomfort. *Nutr Res Rev* 20(2):132–146
- Fraser D, Duncan IJ (1998) ‘Pleasures’, ‘pains’ and animal welfare: toward a natural history of affect. *Anim Welf* 7(4):383–396
- Fraser D, Weary DM, Pajor EA, Milligan BN (1997) A scientific conception of animal welfare that reflects ethical concerns. *Anim Welf* 6(3):187–205
- Gough A (2005) Obesity in small animals and longevity in dogs. *Vet Times* 35:10–11
- Hocking PM (2004) Measuring and auditing the welfare of broiler breeders. In: Weeks CA, Butterworth A (eds) *Measuring and auditing broiler welfare*. CABI, Wallingford, pp 19–35
- Hocking PM, Whitehead CC (1990) Relationship between body fatness, ovarian structure and reproduction in mature females from lines of genetically lean or fat broilers given different food allowances. *Br Poult Sci* 31(2):319–330
- Hocking PM, Maxwell MH, Mitchell MA (1993) Welfare assessment of broiler breeder and layer females subjected to food restriction and limited access to water during rearing. *Br Poult Sci* 34:443–458
- Hocking PM, Maxwell MH, Mitchell MA (1996) Relationships between the degree of food restriction and welfare indices in broiler breeder females. *Br Poult Sci* 37(2):263–278
- Hocking PM, Maxwell MH, Mitchell MA (1999) Welfare of food restricted male and female turkeys. *Br Poult Sci* 40(1):19–29
- Howard ZR, O’Byrne CA, Crandall PG, Ricke SC (2012) Salmonella Enteritidis in shell eggs: current issues and prospects for control. *Food Res Int* 45(2; Special Issue):755–764
- Howie JA, Tolkamp BJ, Avendaño S, Kyriazakis I (2009a) A novel flexible method to split feeding behaviour into bouts. *Appl Anim Behav Sci* 116(2–4):101–109
- Howie JA, Tolkamp BJ, Avendaño S, Kyriazakis I (2009b) The structure of feeding behavior in commercial broiler lines selected for different growth rates. *Poult Sci* 88(6):1143–1150
- Illius AW, Tolkamp BJ, Yearsley J (2002) The evolution of the control of food intake. *Proc Nutr Soc* 61(4):465–472
- Johnston SL, Grune T, Bell LM, Murray SJ, Souter DM, Erwin SS, Yearsley JM, Gordon IJ, Illius AW, Kyriazakis I, Speakman JR (2006) Having it all: historical energy intakes do not generate the anticipated trade-offs in fecundity. *Proc R Soc Lond B Biol Sci* 273(1592):1369–1374
- Kiley-Worthington M (1989) Ecological, ethological, and ethically sound environments for animals: toward symbiosis. *J Agric Environ Ethics* 2(4):323–347
- Koubi HE, Robin JP, Dewasmes G, Lemaho Y, Frutoso J, Minaire Y (1991) Fasting-induced rise in locomotor activity in rats coincides with increased protein utilization. *Physiol Behav* 50(2):337–343
- Kubířková L, Výboh P, Košťál L (2001) Behavioural, endocrine and metabolic effects of food restriction in broiler breeder hens. *Acta Vet Brno* 70(3):247–257
- Kyriazakis I, Tolkamp BJ (2011) Hunger and thirst. In: Appleby MC, Mench JA, Olsson IAS, Hughes BO (eds) *Animal welfare*. CABI, Wallingford, pp 44–63
- Lawrence AB, Terlouw EMC (1993) A review of the behavioural factors involved in the development and continued performance of stereotypic behaviors in pigs. *J Anim Sci* 71(10):2815–2825
- Lawrence AB, Appleby MC, Illius AW, Macleod HA (1989) Measuring hunger in the pig using operant conditioning: the effect of dietary bulk. *Anim Prod* 48(1):213–220
- Le Magnen J (1985) *Hunger*. Cambridge University Press, Cambridge
- Mason G, Latham N (2004) Can’t stop, won’t stop: is stereotypy a reliable animal welfare indicator? *Anim Welf* 13(Suppl):S57–S69
- Mason G, Clubb R, Latham N, Vickery S (2007) Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Appl Anim Behav Sci* 102(3–4):163–188

- McGlone JJ, Fullwood SD (2001) Behavior, reproduction, and immunity of crated pregnant gilts: effects of high dietary fiber and rearing environment. *J Anim Sci* 79(6):1466–1474
- McReynolds JL, Genovese KJ, He H, Swaggerty CL, Byrd JA, Ricke SC, Nisbet DJ, Kogut MH (2009) Alfalfa as a nutritive modulator in maintaining the innate immune response during the molting process. *J Appl Poult Res* 18(3):410–417
- Mench JA (2002) Broiler breeders: feed restriction and welfare. *Worlds Poult Sci J* 58(1):23–29
- Metz JHM (1975) Time patterns of feeding and rumination in domestic cattle. *Communications of the Agricultural University*, No. 75-12. Wageningen, The Netherlands
- Meunier-Salaün MC, Edwards SA, Robert S (2001) Effect of dietary fibre on the behaviour and health of the restricted fed sow. *Anim Feed Sci Technol* 90(1–2; Special Issue):53–69
- Mormède P, Andanson S, Auferin B, Beerda B, Guemene D, Malnikvist J, Manteca X, Manteuffel G, Prunet P, Van Reenen CG, Richard S, Veissier I (2007) Exploration of the hypothalamic-pituitary-adrenal function as a tool to evaluate animal welfare. *Physiol Behav* 92(3):317–339
- Nielsen BL (1999) On the interpretation of feeding behaviour measures and the use of feeding rate as an indicator of social constraint. *Appl Anim Behav Sci* 63(1):79–91
- Nielsen BL, Thodberg K, Malmkvist J, Steinfeldt S (2011) Proportion of insoluble fibre in the diet affects behaviour and hunger in broiler breeders growing at similar rates. *Animal* 5(8):1247–1258
- Owen JB (1992) Genetic aspects of appetite and feed choice in animals. *J Agric Sci* 119(2):151–155
- Oyawoye EO, Krueger WF (1990) Potential of chemical regulation of food intake and body weight of broiler breeder chicks. *Br Poult Sci* 31(4):735–742
- Park S, Birkhold SG, Kubena LF, Nisbet DJ, Ricke SC (2004) Effects of high zinc diets using zinc propionate on molt induction, organs, and postmolt egg production and quality in laying hens. *Poult Sci* 83(1):24–33
- Rajman M, Juráni M, Lamošová D, Máčajová M, Sedlačková M, Košťál L, Ježová D, Výboh P (2006) The effects of feed restriction on plasma biochemistry in growing meat type chickens (*Gallus gallus*). *Comp Biochem Physiol A Mol Integr Physiol* 145(3):363–371
- Ramonet Y, Bolduc J, Bergeron R, Robert S, Meunier-Salaün MC (2000) Feeding motivation in pregnant sows: effects of fibrous diets in an operant conditioning procedure. *Appl Anim Behav Sci* 66(1–2):21–29
- Renema RA, Rustad ME, Robinson FE (2007) Implications of changes to commercial broiler and broiler breeder body weight targets over the past 30 years. *Worlds Poult Sci J* 63(3):457–472
- Robert S, Rushen J, Farmer C (1997) Both energy content and bulk of food affect stereotypic behaviour, heart rate and feeding motivation of female pigs. *Appl Anim Behav Sci* 54(2–3):161–171
- Ru YJ, Bao YM (2004) Feeding dry sows ad libitum with high fibre diets. *Asian Aust J Anim Sci* 17(2):283–300
- Rushen J (1984) Stereotyped behaviour, adjunctive drinking and the feeding periods of tethered sows. *Anim Behav* 32(4):1059–1067
- Sandilands V, Tolkamp BJ, Kyriazakis I (2005) Behaviour of food restricted broilers during rearing and lay—effects of an alternative feeding method. *Physiol Behav* 85(2):115–123
- Sandilands V, Tolkamp BJ, Savory CJ, Kyriazakis I (2006) Behaviour and welfare of broiler breeders fed qualitatively restrictive diets during rearing: are there viable alternatives to quantitative restriction? *Appl Anim Behav Sci* 96(1–2):53–67
- Savory CJ, Larivière JM (2000) Effects of qualitative and quantitative food restriction treatments on feeding motivational state and general activity level of growing broiler breeders. *Appl Anim Behav Sci* 69(2):135–147
- Savory CJ, Maros K (1993) Influence of degree of food restriction, age and time of day on behavior of broiler breeder chickens. *Behav Process* 29(3):179–190

- Savory CJ, Carlisle A, Maxwell MH, Mitchell MA, Robertson GW (1993) Stress, arousal and opioid peptide-like immunoreactivity in restricted-fed and ad-lib-fed broiler breeder fowls. *Comp Biochem Physiol A Physiol* 106(3):587–594
- Savory CJ, Hocking PM, Mann JS, Maxwell MH (1996) Is broiler breeder welfare improved by using qualitative rather than quantitative food restriction to limit growth rate? *Anim Welf* 5(2):105–127
- Schwitzer C, Kaumanns W (2001) Body weights of ruffed lemurs (*Varecia variegata*) in European zoos with reference to the problem of obesity. *Zoo Biol* 20(4):261–269
- Souza da Silva C, van den Borne JJGC, Gerrits WJJ, Kemp B, Bolhuis JE (2012) Effects of dietary fibers with different physicochemical properties on feeding motivation in adult female pigs. *Physiol Behav* 107(2):218–230
- Stubbs RJ, Tolkamp BJ (2006) Control of energy balance in relation to energy intake and energy expenditure in animals and humans: an ecological perspective. *Br J Nutr* 95(4):657–675
- Tolkamp BJ, Friggens NC, Emmans GC, Kyriazakis I, Oldham JD (2002) Meal patterns of dairy cows consuming diets with a high or a low ratio of concentrate to grass silage. *Anim Sci* 74(2):369–382
- Tolkamp BJ, Sandilands V, Kyriazakis I (2005) Effects of qualitative food restriction during rearing on the performance of broiler breeders during rearing and lay. *Poult Sci* 84(8):1286–1293
- Tolkamp BJ, Allcroft DJ, Barrio JP, Bley TAG, Howie JA, Jacobsen TB, Morgan CA, Schweitzer DPN, Wilkinson S, Yeates MP, Kyriazakis I (2011) The temporal structure of feeding behavior. *Am J Physiol Regul Integr Comp Physiol* 301(2):R378–R393
- Tolkamp BJ, Howie JA, Bley TAG, Kyriazakis I (2012) Prandial correlations and the structure of feeding behaviour. *Appl Anim Behav Sci* 137(1–2):53–65
- Umeda TY, Bauer JE, Otsuji K (2006) Weight loss effect of dietary diacylglycerol in obese dogs. *J Anim Physiol Anim Nutr* 90(5–6):208–215
- Webster AJF (1995) *Animal welfare—a cool eye towards Eden*. Blackwell Science, Oxford
- Webster AJF (2003) Physiology and behavior of the hen during induced molt. *Poult Sci* 82(6):992–1002
- Weed JL, Lane MA, Roth GS, Speer DL, Ingram DK (1997) Activity measures in Rhesus monkeys on long-term calorie restriction. *Physiol Behav* 62(1):97–103
- Wemelsfelder F, Hunter TEA, Mendl MT, Lawrence AB (2001) Assessing the ‘whole animal’: a free choice profiling approach. *Anim Behav* 62(2):209–220
- Wemelsfelder F, Knierim U, Schulze Westerath H, Lentfer T, Staack M, Sandilands V (2009) Qualitative behaviour assessment. In: Forkman B, Keeling L (eds) *Assessment of animal welfare measures for layers and broilers*. Welfare Quality Reports, No. 9 (Sixth Framework Programme). Cardiff University, Cardiff, pp 113–119
- West DB, York B (1998) Dietary fat, genetic predisposition, and obesity: lessons from animal models. *Am J Clin Nutr* 67(3; Suppl):505S–512S
- Whittaker X, Edwards SA, Spoolder HAM, Corning S, Lawrence AB (2000) The performance of group-housed sows offered a high fibre diet ad libitum. *Anim Sci* 70(1):85–93
- Whittemore EC, Kyriazakis I, Tolkamp BJ, Emmans GC (2002) The short-term feeding behavior of growing pigs fed foods differing in bulk content. *Physiol Behav* 76(1):131–141
- Yalçın S, Bruggeman V, Buyse J, Decuyper E, Cabuk M, Siegel PB (2009) Acclimation to heat during incubation: 4. Blood hormones and metabolites in broilers exposed to daily high temperatures. *Poult Sci* 88(9):2006–2013
- Zonderland JJ, De Leeuw JA, Nolten C, Spoolder HAM (2004) Assessing long-term behavioural effects of feeding motivation in group-housed pregnant sows; what, when and how to observe. *Appl Anim Behav Sci* 87(1–2):15–30
- Zorrilla EP, Inoue K, Fekete EM, Tabarin A, Valdez GR, Koob GF (2005) Measuring meals: structure of prandial food and water intake of rats. *Am J Physiol Regul Integr Comp Physiol* 288(6):R1450–R1467
- Zuidhof MJ, Robinson FE, Feddes JJR, Hardin RT, Wilson JL, McKay RI, Newcombe M (1995) The effects of nutrient dilution on the well-being and performance of female broiler breeders. *Poult Sci* 74(3):441–456

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