



Review

Review: Quantifying animal feeding behaviour with a focus on pigs



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HIGHLIGHTS

- Feeding behaviour can be influenced by multiple factors.
- Several sensors exist to measure feeding behaviour in group-housed pigs.
- Units of feeding behaviour can be feeding visits, meals or raw registrations.
- Numerous methods for meal determination exist, with interesting recent advances.

ARTICLE INFO

Article history:

Received 9 April 2014

Accepted 29 September 2014

Available online 20 October 2014

Keywords:

Feeding behaviour

Visit

Meal

Sensor

Methodology

Pig

ABSTRACT

The study of animal feeding behaviour is of interest to understand feeding, to investigate the effect of treatments and conditions or to predict illness. This paper reviews the different steps to undertake when studying animal feeding behaviour, with illustrations for group-housed pigs. First, one must be aware of the mechanisms that control feeding and the various influences that can change feeding behaviour. Satiety is shown to largely influence free feeding (*ad libitum* and without an operant condition) in animals, but 'free' feeding seems a very fragile process, given the many factors that can influence feeding behaviour. Second, a measurement method must be chosen that is compatible with the goal of the research. Several measurement methods exist, which lead to different experimental set-ups and measurement data. Sensors are available for lab conditions, for research on group-housed pigs and also for on-farm use. Most of these methods result in a record of feeding visits. However, these feeding visits are often found to be clustered into meals. Thus, the third step is to choose which unit of feeding behaviour to use for analysis. Depending on the situation, either meals, feeding visits, other raw data, or a combination thereof can be suitable. Meals are more appropriate for analysing short-term feeding behaviour, but this may not be true for disease detection. Further research is therefore needed. To cluster visits into meals, an appropriate analysis method has to be selected. The last part of this paper provides a review and discussion of the existing methods for meal determination. A variety of methods exist, with the most recent methods based on the influence of satiety on feeding. More thorough validation of the recent methods, including validation from a behavioural point of view and uniformity in the applied methods is therefore necessary.

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1. Introduction

Feeding behaviour of animals has been studied extensively for more than 50 years. The reported studies aimed to understand feeding behaviour [84], investigate the effects of treatments [65], diets [42] or housing conditions [26], or predict illness [13]. Different measuring methods have been used depending on the species and study, resulting in different data available for analysis. Observations of feeding behaviour were typically clustered into meals and therefore the gathered raw data were transformed to 'meal' data to perform further analysis. However, no unique criterion for defining a meal could be identified. Therefore, the state of the art on measuring feeding behaviour is critically reviewed for laboratory and farm animals with a focus on pigs. Emphasis is on the criteria to convert raw data into meals. Special attention is given to measurements of group-housed pigs and the recent advances in applying these systems on-farm.

First, a general introduction on feeding behaviour is given with a focus on the mechanisms of free feeding. Second, we give an overview of the methods that have been proposed for measuring feeding in pigs. The results of these measurements are 'feeding visits', defined based on the start and stop time of the visits to the feed trough and sometimes including the amount of feed taken. In the third section the different definitions of visits and meals (clustered visits) are discussed together with the advantages and disadvantages of these units of feeding. The last section presents a detailed discussion of the different methods that have been used to register meals.

2. Feeding behaviour

2.1. Understanding feeding motivation

Several researchers have investigated the patterns of spontaneous feeding to obtain insight into the mechanisms of feeding. Free feeding behaviour has been investigated in rats [51], zebra finches [71], monkeys [60], pigs [6], cows [79] and many other species. The aim of these studies was often to propose a model for human physiology [59] or to establish the regulatory signals present in feeding [14]. Davies [14] reported that meal frequency was controlled by short-term regulatory signals in rats, while meal size was more regulated by long-term influences.

One of the main questions has been "Is feeding controlled by hunger, satiety or both?" This has been investigated by means of prandial correlations, the correlations between feeding and the intervals before or after feeding. Linking hunger and satiety with pre- or postprandial correlations has gotten mixed up in literature, however. Decastro [19] stated that "... the *ad lib* feeding rat regulated its intake on the basis of how much it had just eaten (satiety) rather than how long it had been since last feeding (hunger)". Decastro [19] thus relates satiety with the correlation between meal size and the subsequent between-feeding interval (postprandial correlation) and hunger with the correlation between meal size and the previous between-feeding interval (pre-

prandial correlation). Savory [68] and Tolkamp et al. [76] used the opposite hypothesis, however. To avoid confusion, we will use the hypothesis of Decastro throughout this study. Recently, the control of food intake has also been investigated by examining the probability of an animal starting and ending a meal versus the time since the last meal and the amount of feed consumed [76].

When satiety controls feeding, a high correlation between meal size and postprandial interval (interval following the meal) can be expected. This has been reported in rats [14,19,51], monkeys [60], birds [22,71,76] and cows [79]. In other words, an animal will start feeding again when its satiety feeling is below a certain critical point. The time at which this occurs is correlated with the size of the previous meal. Clearance of the stomach and gastrointestinal tract and metabolic utilisation of the food were large determinants to this effect. However, (secondary) influences of quantity and quality of food and diurnal rhythms have also been reported [14,50]. Decastro [19] showed that for rats, stomach energy content at the end of a meal had the strongest correlation with the following inter-meal interval, while meal size (or even meal duration) were very often used as (weak) measures for this energy content. Diurnal patterns in feeding could also be explained by satiety. For example, Kraly et al. [48] concluded that nocturnal feeding in rats was controlled by decreased satiety at nighttime versus daytime.

When hunger is the main control factor, animals are expected to regulate their meal size based on the time since the last feeding. A significant correlation between meal size and the pre-prandial interval (interval preceding the meal) was only found in specific situations, such as for very large inter-meal intervals in rats [51], for some zebra finches as a result of accidental encounters with the feed [71], and for broilers [7]. Several authors have suggested that meal offset is rather determined by feedback signals of stomach distension and caloric content of the meal [19,50].

The observations reported for pigs were quite different from those for the animals described above (often individually-housed laboratory animals). Bigelow and Houpt [6] found no correlation between meal size and pre- or postprandial intervals in immature female pigs. Musial et al. [59] also found no correlation between meal size and postprandial interval, but a moderate correlation between meal size and pre-prandial interval in mini-pigs housed in pairs. Young and Lawrence [84] found that 60% of the group-housed growing-finishing pigs in their study showed no prandial correlation, 26% showed postprandial correlation, 10% showed pre-prandial correlation and the remaining 4% showed both types of regulation. Montgomery et al. [56] found no important correlations in their pigs. These discrepancies are hypothesised to be due to the pigs' intrinsic need for routing and foraging [18], synchronised feeding [40] and the social constraints which force group-housed pigs to adapt their feeding behaviour [77,84].

In summary, most animal studies agree that free feeding is mostly regulated by satiety (postprandial correlation) and that hunger mechanisms (pre-prandial correlation) only play a role in specific situations. An animal will start to feed when its satiety level is below a certain point, but in free feeding no build-up of hunger will occur. Meal size is

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