The temporal structure of feeding behavior

Bert J. Tolkamp,1 David J. Allcroft,2 Juan P. Barrio,3 Tobias A. G. Bley,6 Jennifer A. Howie,1 Troels B. Jacobsen,7 Colin A. Morgan,4 Diederik P. N. Schweitzer,1 Samantha Wilkinson,1 Martin P. Yeates,1 and Ilias Kyriazakis5

1Animal Health Group, SAC, Edinburgh, United Kingdom; 2BioSS, Edinburgh, United Kingdom; 3Departamento de Ciencias Biomédicas, and Instituto de Biomedicina, Universidad de León, León, Spain; 4Sustainable Livestock Systems, Scottish Agricultural College, Odense, Denmark, Edinburgh, United Kingdom; 5School of Agriculture, Food and Rural Development, Newcastle University, Newcastle upon Tyne, United Kingdom; 6Farm Animal Ethology and Poultry Production, University of Hohenheim, Stuttgart, Germany; and 7Institute of Biology, University of Southern Denmark, Odense, Denmark

Submitted 4 October 2010; accepted in final form 19 April 2011

Tolkamp BJ, Allcroft DJ, Barrio JP, Bley TAG, Howie JA, Jacobsen TB, Morgan CA, Schweitzer DPN, Wilkinson S, Yeates MP, Kyriazakis I. The temporal structure of feeding behavior. Am J Physiol Regul Integr Comp Physiol 301: R378–R393, 2011. First published April 27, 2011; doi:10.1152/ajpregu.00661.2010.—Meals have long been considered relevant units of feeding behavior. Large data sets of feeding behavior of cattle, pigs, chickens, ducks, turkeys, dolphins, and rats were analyzed with the aims of 1) describing the temporal structure of feeding behavior and 2) developing appropriate methods for estimating meal criteria. Longer (between-meal) intervals were never distributed as the negative exponential assumed by traditional methods, such as log-survivorship analysis, but as a skewed Gaussian, which can be (almost) normalized by log-transformation of interval lengths. Log-transformation can also normalize frequency distributions of within-meal intervals. Meal criteria, i.e., the longest interval considered to occur within meals, can be estimated after fitting models consisting of Gaussian functions alone or of one Weibull and one or more Gaussian functions to the distribution of log-transformed interval lengths. Nonuniform data sets may require disaggregation before this can be achieved. Observations from all species were in conflict with assumptions of random behavior that underlie traditional methods for criteria estimation. Instead, the observed structure of feeding behavior is consistent with 1) a decrease in satiety associated with an increase in the probability of animals starting a meal with time since the last meal and 2) an increase in satiation associated with an increase in the probability of animals ending a meal with the amount of food already consumed. The novel methodology proposed here will avoid biased conclusions from analyses of feeding behavior associated with previous methods and, as demonstrated, can be applied across a range of species to address questions relevant to the control of food intake.

Understanding the control of daily food intake is highly relevant for those interested in weight gain and energy balance in humans (24); rodents, which are frequently used as model animals (79); pets (9); captive wild animals (33); or farm animals (21). Knowledge of the control mechanisms could assist nutritionists, behavioral neurobiologists, and veterinary surgeons in their attempts to design strategies to combat the current obesity “epidemics” in humans (62, 63), and animals kept in zoos (57). Such analyses can also assist in 1) testing hypotheses on the control of food intake and diet selection (70, 76), 2) developing automated systems for the early detection of health and welfare problems (26), 3) designing feeding systems that improve efficiency and animal welfare (16), and 4) identifying relevant feeding behavior traits for inclusion in breeding programs for farm animals (29, 31).

It has been argued that an understanding of the control of food intake requires understanding of what causes the initiation and cessation of eating (21, 38). The biologically most appropriate unit of eating behavior is a meal (69), and average daily food intake is determined, at least in a formal sense, by meal frequency and meal size (10, 38). Geary (24) has set out some of the reasons for the paradoxical situation that, despite this direct relationship, meal pattern analysis does not form a more important part of current research into animal food intake control. The lack of unanimity as to the appropriate definition of meals was identified as one of the main contributing factors.

Feeding behavior is recorded in terms of “feeding events,” which may result from interpretation of visual observation (33) and analysis of video footage (2) or may consist of records of bites (71), pecks (40),licks (54),removals of a food pellet (79),uninterrupted jaw movements (45),weights of food containers at regular intervals (15), or (and increasingly so) as durations of visits to electronic feeders (28, 67, 74). If such feeding events occur randomly in time, feeding behavior will be entirely unstructured and then the lengths of intervals between feeding events will have a negative exponential distribution (44). Animals of most species, however, structure their feeding behavior by concentrating their feeding activity in bouts (21, 38).

A feeding bout can be defined as a cluster of feeding events that are separated by relatively short nonfeeding intervals, while each bout is separated from the previous and the subsequent bout by relatively long intervals (Fig. 1). If an appropriate method is available for estimating meal criteria, i.e., the maximum between-feeding interval lengths that are acceptable as within-meal intervals, identified bouts can be called meals.

One of the main problems in evaluating analyses of feeding behavior is the enormous variation in meal criteria that are applied within species (e.g., 29, 60, 66, 74). At least, part of the contradictory conclusions of meal pattern analyses must be attributed to this enormous variation in estimated meal criteria (24). At its worst, meal criteria have been chosen entirely arbitrarily or simply copied from another publication without regard for the actual structure of the observed behavior. However, even when meal criteria estimates are based on some analysis of the observed structure of feeding behavior, there is a strong suspicion that inappropriate methods have been used, resulting in meal criteria that are too short and have little biological meaning (e.g., 66, 67, 77). The use of such inappro-
appropriate criteria can easily lead to conclusions that are completely opposite from those drawn after analysis of the same data but based on a biologically more correct meal criterion estimate (79).

We have developed a new method to analyze the temporal pattern of feeding and to define meals. First, we discuss the methodology that was developed on the basis of feeding behavior of dairy cows (65–67, 70, 76, 77). Clifton (12) suggested that our method might not be suitable for nonruminants. Here, we test this suggestion by analyzing large data sets of individual feeding behavior that were obtained with animals from six nonruminating species: neonate dolphin calves, growing pigs, female broilers, Pekin ducks, male turkeys, and Wistar rats. We demonstrate that valuable information about the structure of feeding behavior can be extracted only if 1) appropriate methods are used to group feeding behavior into bouts and 2) inappropriate pooling of nonuniform data is avoided. The developed methodology should enable us to reach conclusions about the controls of food intake in a variety of species.

DAIRY COW MODEL DEVELOPMENT

Data Collection and Analysis

Data were collected with computerized feeders, as described in detail before (64). In brief, lactating dairy cows wearing transponders were group-housed in a cubicle yard. Each cow had access to at least six electronic feeders supplying ad libitum a mixed ration consisting of silage and concentrates (68, 70; Table 1). Feeders were locked by a gate that opened upon recognition of a cow transponder, stayed open as long as the animal interrupted at least one of two infrared sensor beams and closed again when the animal withdrew from the feeder and interruption of the beams ended. Feeders were linked to a computer that recorded the start- and end-time of each visit (to the nearest second) and the amount of food consumed (to the nearest 0.1 kg). From these visit records, between-feeding intervals were calculated for each cow, and these data formed the basis of our main analysis. Water was supplied ad libitum in two water troughs.

Log-survivorship [or log-frequency, which is based on the same principles (58)] analysis constitutes the most frequently used methodology to estimate meal criteria. Relative log-survivorship plots for the between-feeding interval lengths observed were calculated by first log-transforming (using natural logarithms, $\log_e$) the number of intervals divided by $\log_e(n)$ for each between-feeding interval length $t$ and then dividing the obtained number by $\log_e(n)$. A probability density function (pdf) consisting of two negative exponentials (37) was fitted to the cumulative frequency distributions of between-feeding interval lengths and drawn in a graph (after $\log_e$-transformation):

Table 1. Characteristics of the experiments in which the data of the seven species were collected

<table>
<thead>
<tr>
<th></th>
<th>Cow</th>
<th>Pig</th>
<th>Dolphin</th>
<th>Broiler</th>
<th>Duck</th>
<th>Turkey</th>
<th>Rat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Animals, $n$</td>
<td>16–38</td>
<td>62</td>
<td>11</td>
<td>3,470</td>
<td>480</td>
<td>3,341</td>
<td>6</td>
</tr>
<tr>
<td>Animal sex</td>
<td>♂</td>
<td>♂ + ♀</td>
<td>♂ + ♀</td>
<td>♂</td>
<td>♂ + ♀</td>
<td>♂</td>
<td>♂</td>
</tr>
<tr>
<td>Animal age, wk</td>
<td>104–468</td>
<td>9–24</td>
<td>0–2</td>
<td>0.5–2.3</td>
<td>2–4</td>
<td>3–6</td>
<td>18–21</td>
</tr>
<tr>
<td>Animal weight, kg</td>
<td>500–745</td>
<td>24–114</td>
<td>0–2</td>
<td>0.5–2.3</td>
<td>1.1–3.0</td>
<td>21.7–26.3</td>
<td>0.67</td>
</tr>
<tr>
<td>Animals/pen, max</td>
<td>50</td>
<td>10</td>
<td>0.2</td>
<td>130</td>
<td>160</td>
<td>250</td>
<td>1</td>
</tr>
<tr>
<td>Pen size, m²</td>
<td>316</td>
<td>10.2</td>
<td>8.1</td>
<td>16.2</td>
<td>16</td>
<td>14.4</td>
<td>1</td>
</tr>
<tr>
<td>Feeders per pen</td>
<td>28</td>
<td>1</td>
<td>8</td>
<td>28</td>
<td>16</td>
<td>16</td>
<td>1</td>
</tr>
<tr>
<td>Animals/feeder, max</td>
<td>2</td>
<td>10</td>
<td>10.2</td>
<td>10</td>
<td>16</td>
<td>14.4</td>
<td>1</td>
</tr>
<tr>
<td>Light: dark, h</td>
<td>daylight</td>
<td>daylight</td>
<td>daylight</td>
<td>20:4</td>
<td>17:7</td>
<td>14:10</td>
<td>12:12</td>
</tr>
<tr>
<td>Weeks/animal, max</td>
<td>40</td>
<td>15</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Feeding episodes, $n$</td>
<td>209,025</td>
<td>7,678</td>
<td>6,800</td>
<td>2,162,973</td>
<td>209,309</td>
<td>851,513</td>
<td>62,707</td>
</tr>
</tbody>
</table>

$n$, number; max, maximum.
pdf = N₁ exp(-λ₁t) + (N - N₁) exp(-λ₂t),  \( (1) \)

with \( t \) equal to interval length, \( N₁ \) equal to the number of intervals resulting from the fast process, \( N \) equal to the total number of intervals, and \( λ₁ \) and \( λ₂ \) equal to the rate parameters associated with the fast and slow processes. The fast and slow processes are generally thought (e.g., 37, 58, 61) to result in within- and between-meal intervals, respectively, and then the meal criterion \( T_c \) can be estimated from the model parameters as

\[
T_c = \left[ 1/(λ₁ - λ₂) \right] \log_e \left[ \left( N₁λ₂ \right) / \left( Nλ₁ \right) \right] \quad (2)
\]

Additional mixed models were fitted to the frequency distributions of loge-transformed between-feeding interval lengths. Such models could contain one or more Gaussian functions:

\[
\text{pdf} = \left[ 1/(σ \sqrt{2π}) \right] \exp \left[ - \left[ \log_e(t) - μ \right]² / (2σ²) \right] \quad (3)
\]

with \( \log_e(t) = \log_e \)-transformed between-feeding interval length (measured in seconds) and \( μ \) and \( σ \) equal to the mean and standard deviation of the Gaussian function. They could also contain a Weibull function

\[
\text{pdf} = \left[ ct^{(c-1)/α} \right] \exp \left[ - (\log_e(t)/α)² \right] \quad (4)
\]

with \( \log_e(t) = \log_e \)-transformed between-feeding interval length (measured in seconds) and \( c \) and \( α \) equal to the shape and scale parameter of the Weibull distribution.

First, a pdf consisting of two Gaussian functions, describing intervals within and between meals, was fitted to the observations (56):

\[
\text{pdf} = p \left\{ \frac{1}{σ₁ \sqrt{2π}} \right\} \exp \left[ - \left[ \log_e(t) - μ₁ \right]² / 2σ₁² \right] + (1-p) \left\{ \frac{1}{σ₂ \sqrt{2π}} \right\} \exp \left[ - \left[ \log_e(t) - μ₂ \right]² / 2σ₂² \right] \quad (5)
\]

Many animal species have been observed to drink in association with meals (6, 23, 79). For this reason, a third Gaussian function was added to the pdf to take account of observations of cows that drink during meals, which results in relatively long within-meal intervals (65):

\[
\text{pdf} = p \left\{ \frac{1}{σ₁ \sqrt{2π}} \right\} \exp \left[ - \left[ \log_e(t) - μ₁ \right]² / 2σ₁² \right] + q \left\{ \frac{1}{σ₂ \sqrt{2π}} \right\} \exp \left[ - \left[ \log_e(t) - μ₂ \right]² / 2σ₂² \right] + (1-p-q) \left\{ \frac{1}{σ₃ \sqrt{2π}} \right\} \exp \left[ - \left[ \log_e(t) - μ₃ \right]² / 2σ₃² \right] \quad (6)
\]

Subsequently, it was shown that the distribution of log-transformed long intervals was statistically better described by a Weibull than by a Gaussian function (75), which resulted in the following pdf’s, which differ only in the number of Gaussian functions:

\[
\text{pdf} = p \left\{ \frac{1}{σ \sqrt{2π}} \right\} \exp \left[ - \left[ \log_e(t) - μ \right]² / 2σ² \right] + (1-p)(c(\log_e(t))^{(c-1)/α}) \exp \left[ - (\log_e(t)/α)² \right] \quad (7)
\]

and

\[
\text{pdf} = p \left\{ \frac{1}{σ₁ \sqrt{2π}} \right\} \exp \left[ - \left[ \log_e(t) - μ₁ \right]² / 2σ₁² \right] + q \left\{ \frac{1}{σ₂ \sqrt{2π}} \right\} \exp \left[ - \left[ \log_e(t) - μ₂ \right]² / 2σ₂² \right] + (1-p-q) \left\{ c(\log_e(t))^{(c-1)/α} \right\} \exp \left[ - (\log_e(t)/α)² \right] \quad (8)
\]

The maximum likelihood procedure in GENSTAT (72) was used for model fitting. Model fit was compared by statistical analysis based on the likelihood values for the models. The higher the likelihood value, the better the model fits the data (37). Since likelihood values are very small, they are expressed in GENSTAT as minimum function values (MFV, i.e., twice the negative log-likelihood). Differences in MFV between models were tested for significance. If the models were nested (i.e., a model with \( n \) parameters is completely included into a larger model with \( >n \) parameters), a likelihood ratio test was used, assuming a \( χ² \) distribution of the test statistic (35). All other models were compared using Akaike’s Information Criterion, in which the MFV of models are compared directly, allowing for differences in the number of parameters. According to Akaike’s Information Criterion, a smaller MFV signifies a better fit if models with the same number of parameters are compared, even when the magnitude of these differences in MFV cannot be assigned a formal level of significance (4).

Probabilities of animals starting feeding (\( P_{\text{start}} \)) within \( x \) min at time \( t \) since feeding last were calculated as 1 minus the number of intervals \( \geq (t + x) \) divided by the number of intervals \( \geq t \). Similarly, probabilities of animals ending feeding (\( P_{\text{end}} \)) before consuming another quantity \( y \) of food after having consumed a quantity \( q \) were calculated as 1 minus the number of meals \( \geq (q + y) \) divided by the number of meals \( \geq q \).

**Results and Discussion**

Fig. 2A shows the log-survivorship plot and the fit of Eq. 1, i.e., a pdf consisting of two negative exponentials (after loge-transformation). The observed log-survivorship plot at longer intervals was not a straight line but a convex curve. This shows that the longer intervals did not have a negative exponential distribution, which implies that the probability of cows starting feeding is not independent of the time since feeding last (67). The meal criterion estimated according to Eq. 2 by the parameters of Eq. 1 was 8 min. Application of this criterion showed that (even if the assumptions underlying the model had been correct) a considerable proportion of estimated between-meal intervals was assigned to the wrong category, which would have restricted the proper identification of meals for subsequent analyses (67). The poor fit of the model shows, however, that such an estimate of the meal criterion has no clear biological meaning at all.

A plot of the frequency distribution of interval lengths (Fig. 2B) confirmed that longer (between-meal) intervals were not distributed as a negative exponential but as a skewed normal. Loge-transformation of interval lengths, measured in seconds, resulted in what first appeared to be two clearly separated populations (one within and one between meals), each with an approximately normal distribution (Fig. 2C). To obtain meal criteria, Eq. 5 was fitted to individual data and to data sets that were pooled across individuals (67; Fig. 2C). The two Gaussian functions in the model peaked at around 4.1 and 9.4 loge-units (i.e., median interval lengths around 1 min and 3.5 h, respectively). The number of intervals assigned to the wrong population is minimal when meal criteria are chosen at the interval lengths where the two Gaussian curves cross (67). This can be calculated from the model parameters as around 7.5 loge-units (corresponding to around 30 min).

AJP-Regul Integr Comp Physiol • VOL. 301 • AUGUST 2011 • www.ajpregu.org
Some cows showed an additional, again log-normally distributed, population of between-feeding intervals. This third population consisted of within-meal intervals during which cows went to drink water (65, 75) (Fig. 2D) and peaked at around 6 loge-units (i.e., around 400 s). Eq. 6 seemed to give a good fit to such data sets (65). Later analyses showed, however, that the populations of within-meal log-transformed intervals could indeed be described well by Gaussian functions, but that the population of log-transformed long (i.e., between-meal) intervals was slightly skewed. Statistically, the latter could be described better by a Weibull than a Gaussian function (75; Fig. 2E), i.e., Eqs. 7 and 8. As expected, on the basis of the satiety concept, $P_{\text{start}}$ was observed to increase with time since the last meal (66, 75). This was predicted more accurately from the parameters of the fitted Weibull than from those of the fitted negative exponential or Gaussian function (Fig. 2F). Models that include such changes in $P_{\text{start}}$, i.e., semi-Markov, gave indeed better descriptions of cow feeding behavior than models that did not, i.e., Markov or latent Gaussian (3). The same models could be applied to cows on mixed diets with high or low forage-to-concentrate ratios (70) and with high or low protein content (69). These models have led to novel methods to analyze diurnal patterns in cow feeding behavior (70) and have successfully been applied to analyze data sets obtained with cows elsewhere (1, 19, 43, 50, 55).

Application to Other Species

Data description and analysis. We provide an overview (Table 1) and a brief description of the used data sets and refer for more details to earlier publications on pigs (48, 49, 74), dolphins (33), broilers (28, 29, 30), ducks (7, 30), turkeys (30), and rats (46). Data from pigs and avian species were collected day and night via electronic feeders that supplied ad libitum pelleted food and recorded visits of animals wearing a transponder. Time was recorded to the nearest second and feeder weight to the nearest 10 g (pigs), 1 g (ducks and turkeys), or 0.1 g (broilers). The 11 single zoo-housed dolphin calves obtained milk by sucking after “locking-on” to the mammary gland of their dams. Between-feeding intervals (in seconds) were calculated from data that were collected by observation during the day (33). Rats were housed individually in Techniplast metabolic cages (lights on from 0800 to 2000) and had ad libitum access to a feeder providing ground chow that was placed on scales linked to a computer that recorded feeding...
episodes (46). An episode started when the weight of the feeder became unstable and the unstable weight (to the nearest 0.1 g) and time (to the nearest 0.01 min) were recorded. The weight and the time were recorded again after the feeder had stabilized at the end of the episode. For intake calculation purposes, it was assumed that the stable final weight recorded in one episode was the start weight for the next episode.

Diurnal variation in feeding behavior was least evident for cows, and data were pooled across day and night. Birds showed almost no feeding activity during the dark (night) phase and pigs much less. Rats recorded little feeding activity between 0100 and 0900 (12% of daily intake) but consumed 48% and 40% of daily intake between 0900 (when fresh food was supplied) and 2000 and during the first part of the dark period (between 2000 and 0100), respectively. To avoid undesirable effects of pooling of data across nonuniform behavior caused by diurnal variation (28, 30, 49, 77), data collected during the night (avian species) or the second part of the night (rats), when feeding activity was extremely low, were not included in the analyses. For reasons discussed below, only the analysis of night-time pig data (74) are presented.

Results and Discussion

Frequency distributions of between-feeding interval lengths. In all species, the distribution of between-feeding interval lengths (Fig. 3) showed the highest frequency in the first bin (i.e., the shortest interval-class) and a (much) skewed normal distribution of longer intervals with a nadir in between. Longer (i.e., between-meal) intervals were not distributed as a negative exponential in any species. This is the null hypothesis underlying quantitative estimation of meal criteria on the basis of log-survivorship (61) or of log-frequency (37) plots. Thus, such methods are inappropriate for all these species.

Log-transformation of between-feeding interval lengths. We investigated for each species whether log-transformation of interval lengths would lead to distributions as seen in dairy cows and, therefore, allow applications of models in Eqs. 3–8 to estimate meal criteria. A double log-normal could be fitted to the frequency distribution of the lengths of between-feeding intervals observed in dolphin calves (Fig. 4B). In this data set pooled across 11 calves, a Gaussian function (Eq. 5) gave a better fit to the distribution of long (i.e., between-meal) intervals than a Weibull function (Eq. 6). Probable reasons for this will be discussed in more detail below. The fit was excellent (Fig. 4B) and resulted in a meal-criterion estimate of 161 s. This result demonstrates that a model originally developed for cows can be used to estimate meal criteria for animals of a nonruminant species that obtain food by drinking.

During the day, feeding behavior of pigs seemed random, as judged from the approximately negative exponential distribution of between-meal interval lengths, and this was not an effect of inappropriate pooling (74). The data were collected...
Fig. 4. Probability densities of loge-transformed interval lengths (all bin widths 0.5 loge-units) of cows with Eq. 7 fitted (A), dolphin calves with Eq. 5 fitted (B), pigs at night with a truncated Eq. 7 fitted (C), female broilers for all intervals (D), intervals between visits to the same feeder (E), and intervals between visits to different feeders with Eq. 5 fitted (F). The patterns observed in turkeys were very similar to those observed in broilers (30) and are not reproduced here; Pekin ducks for all intervals (G) and for two subsets of 50 birds each that showed many (H) or few (I) intervals of intermediate length (i.e., between 1 and 30 min), all with Eq. 6 fitted; Wistar rats, showing the distribution (J), the fit of truncated Eq. 8 to the data as a whole (K) and the fit in more detail for intervals around the meal criteria estimate (L). Gray bars represent the observed relative frequency (divided by bin width); thin lines denote individual populations, while thick lines denote the model as a whole, and arrows indicate estimated meal criteria.
from group-housed animals, with a single feeder per pen of 10 pigs, which contrasts with the experiments involving cows and avian species, in which animals had access to at least six feeders per group (Table 1). During the day, feeders were occupied most of the time, and pigs were frequently observed queuing in front of the single feeder that was occupied or blocked by a, likely more dominant, pig. Under such conditions, pigs cannot naturally structure their feeding behavior. During the night, however, feeders were unoccupied for long periods of time, and, for this reason, analyses of these data are shown. Between-feeding intervals shorter than 10 s were not recorded in this data set, as shown by the absence of intervals shorter than 2.5 log₁₀-units (Fig. 4C). This graph suggests that there is a population of longer (i.e., between-meal) intervals, separated from a population of shorter (i.e., within-meal) intervals, also in pigs. There is, however, slightly more overlap between these two populations than observed for cows and dolphin calves. This may well have been caused by an increase in some of the within-meal interval lengths as a result of unavailability of the feeder during some periods, even during the night. A model, consisting of a truncated Gaussian (28) and a Weibull distribution (essentially, Eq. 7) was fitted to intervals longer than 2.5 log₁₀-units (Fig. 4C). The model converged easily, and the model parameters predicted a meal criterion of 17.8 min, demonstrating that an adaptation of a model developed for cows can also be applied to free-feeding pigs.

The frequency distributions of log-transformed interval lengths were very similar for broilers and turkeys (30) and, therefore, only the broiler data are presented here. Both species clearly showed a population of long (i.e., between-meal) intervals (30) (Fig. 4D). Fig. 4, E and F, shows the disaggregation into subsets of intervals between visits to 1) the same feeder or 2) to different feeders. In the latter, very short intervals are virtually absent (Fig. 4F), and the distribution of intervals appears as two slightly overlapping populations, both with an approximately log-normal distribution. The parameters of Eq. 5 fitted to this subset resulted in a meal criterion estimate of 17.9 min, similar to the estimates (ranging from 17.5 to 20.1 min) that were obtained (28) from the same data, using two other methods discussed below.

The distribution of log-transformed length of intervals between visits to the same feeder by broilers and turkeys deviated substantially (30) (Fig. 4E) from the distribution shown in Fig. 4F because of the many very short intervals (corresponding to interval lengths of one or a few seconds) in the former distribution. Part of these additional short intervals may be a result of the shorter time required for a bird to leave a feeder and to access the same (compared to another) again. However, no evidence for such a high frequency of birds leaving a feeder for very short periods was observed in video footage (28). It seems likely that temporary loss of contact between recording equipment and the transponder of birds remaining in the feeder caused the high frequency of short “intervals” shown in Fig. 4E. These intervals are all much shorter than the estimated meal criteria (30); a meal criterion based on the subset of intervals between visits to different feeders will then correctly identify within-meal intervals between visits to any feeders. This means that a model developed for cows can also be applied to broilers and turkeys.

There appears to be one population of log-normally distributed short intervals up to around 1 min (corresponding to 4.1 log₁₀-units) and one of approximately log-normally distributed intervals longer than, say, 7.5 log₁₀-units (corresponding to 30 min) in the duck data (Fig. 4G). There were, however, an excessive number of intervals between around 1 and 30 min (Fig. 4G). A subset of 50 ducks with many intervals in this range (>45% of all intervals) clearly showed three populations of intervals (Fig. 4H), each with an approximately log-normal distribution. In contrast, for another subset of 50 ducks with few (<10% of all) intervals in the intermediate population (Fig. 4I), intervals are almost entirely concentrated in the populations of very short or very long intervals. Equations 7 and 8 were fitted to the combined data displayed in Fig. 4, H and I. In these models, all parameters were estimated for the two subsets as a whole, except for the proportion of observations in each of the three populations, which were estimated per subset. The fit was best for the model consisting of three Gaussian functions (shown in Fig. 4, H and I). From the model parameters, meal criteria around 30 min were calculated, similar to the 28.8-min estimate for ducks that was obtained using one of the methodologies discussed below (30).

It is tempting to think that ducks, like dairy cows (Fig. 2, D and E), appear to be divided in subpopulations that drink frequently (Fig. 4H) or hardly at all (Fig. 4I) during meals. There may be a number of reasons why within-meal drinking would occur in ducks, while there is no evidence that it occurs frequently in broilers (28; Fig. 4) or turkeys (30). Ducks have higher water requirements per gram of food consumed than broilers (59). In addition, ducks had a much higher feeding rate than broilers or turkeys (30), which likely results from differences between species in bill shape. This may have contributed to an increased tendency to drink during meals. Drinking itself and the distance between feeders and drinkers (around 5 m) may thus well result in a separate population of within-meal intervals, although this hypothesis remains untested until data on drinking behavior of ducks become available for analysis.

The rat data show a large number of very short between-feeding episode lengths (Figs. 3F and 4J), and the unit in which time was recorded (0.6 s) was not fine enough to show its exact distribution. First, a model consisting of a truncated (at 0.6 s) Gaussian function for the short and a Weibull function for the longest intervals (essentially, Eq. 7) was fitted, but the addition of a second Gaussian function for an intermediate population of intervals (essentially, Eq. 8) was statistically highly significant (Fig. 4K). Fig. 4L highlights the fit of the model to the two populations of longer intervals. From the model parameters, the meal criterion was estimated at 6,472 log₁₀-units, corresponding with 647 s. The mean length of the population of intermediate interval was around 100 s, and this likely represents intervals during which animals drank (79). The graph demonstrates that the methodology can also be applied to singly housed laboratory rats.

The analyses illustrated by Fig. 4 show that log-transformation of between-feeding intervals allows identification of different interval populations. Disaggregation into subsets can be of great value to improve the understanding of the structure of short-term feeding behavior. Mixed models consisting of (truncated) Gaussian functions, sometimes including a Weibull function, which were originally developed for analysis of cow data, can be fitted to the distribution of log-transformed length of between-feeding intervals, and model parameters can subse-
ently be used to estimate meal criteria for all species analyzed here. The most suitable model to describe between-feeding intervals in these species depends on (1) the number (and sometimes truncation) of populations of within-meal intervals and (2) the best function (i.e., a log-normal or a log-Weibull) to describe the frequency distribution of between-meal intervals. The shape of the latter is determined entirely by the change in the probability of animals starting feeding in relation to time since the last meal and changes in $P_{\text{start}}$ will, therefore, be analyzed next.

The probability that animals will start a meal. Fig. 5A shows the calculated $P_{\text{start}}$ within the next 15 min from simulated distributions (1,000,000 values each) for four common functions. Function parameters were selected to predict a similar $P_{\text{start}}$ of around 0.07 at 2 h after the last meal (as observed in cows, Fig. 2F). The negative exponential (threshold 0, mean 3.5) predicts a constant $P_{\text{start}}$. The normal distribution (mean 3 h, standard deviation 1 h, truncated at 0) is associated with a $P_{\text{start}}$ that first increases slowly and then fast and almost linearly. The $P_{\text{start}}$ associated with the log-normal distribution (based on intervals measured in seconds; mean 9.4, standard deviation 0.6 loge-units) first increases but then decreases at longer times. Finally, the log-Weibull (based on intervals measured in seconds; shape parameter 16.25, scale parameter 9.55 loge-units) is associated with a $P_{\text{start}}$ that continues to increase but at an ever decreasing rate.

![Fig. 5A: probability of animals starting a meal ($P_{\text{start}}$) within the next 15 min in relation to time since the last meal as predicted from 1,000,000 simulated data for each of four distributions of between-feeding intervals, i.e., a negative exponential (threshold 0, mean 3.5; +), a normal (mean 3 h, standard deviation 1 h, truncated at 0; ▼), a log-normal (based on intervals measured in seconds; mean 9.4, standard deviation 0.6 loge-units; ○) and a log-Weibull (based on intervals measured in seconds; shape parameter 16.25, scale parameter 9.55; •); the distributions were selected to predict similar $P_{\text{start}}$ around 2 h after the last meal. The observed $P_{\text{start}}$ in dolphin calves (B), pigs (C), broilers (D), ducks (E), Wistar rats (F), in pigs during the night (●), during the day (○) and for these data combined (+: all in G); $P_{\text{start}}$ in B to F show observed values as dots and values [as predicted by the parameters of the models (as fitted in Fig. 4)] as lines; the observed $P_{\text{start}}$ for a cow with many (●), or with few (○) daily meals is shown with the data combined (+: all in H). Subsets of 100 broilers with average daily number of meals when they were 2 (●), 3 (▼), or 4 (●) wk of age are shown with their data combined (+: all in I). G–I: symbols have been connected by lines, and $P_{\text{start}}$ has only been plotted for times longer than the meal criterion for clarity. $P_{\text{start}}$ observed in turkeys was very similar to those observed in broilers (30) and are not reproduced here.
A comparison of observed changes in $P_{\text{start}}$ with the ones expected for each of the simulated distributions (Fig. 5A) demonstrates that the observed $P_{\text{start}}$ was constant only when data obtained with individually housed pigs (48, 49) were pooled across day and night (Fig. 5G). For these pigs, however, $P_{\text{start}}$ increased during the day as well as during the night (Fig. 5G), indicating that a constant $P_{\text{start}}$ for the pooled data was an artefact, as expected from the satiety concept (49). For the other species analyzed here, $P_{\text{start}}$ is not constant, even when calculated from the pooled data (Fig. 5). The null hypothesis that the $P_{\text{start}}$ is independent of the time since the last meal (the basis of traditional quantitative log-survivorship and log-frequency analyses) can, therefore, be rejected for all species analyzed here. This is consistent with the shape of the distribution of longer intervals (Fig. 3), which is in the form of a skewed normal, not a negative exponential.

The $P_{\text{start}}$ observed in the pooled cow data (Fig. 2F) underestimates the average increase in $P_{\text{start}}$ for individual cows (77). Fig. 5H illustrates that $P_{\text{start}}$ at longer times is dominated by the (relatively low) $P_{\text{start}}$ of cows with few daily meals. A log-Weibull is, however, still the most suitable function to predict observed changes in $P_{\text{start}}$ for pooled cow data because the contrast in feeding behavior of cows between night and day and between individuals is limited (77). However, effects of pooling on the observed $P_{\text{start}}$ increase with increasing contrast in feeding behavior between day and night or between individuals (77). When the contrast is relatively small, the observed $P_{\text{start}}$ will still increase in the pooled data, as observed here in cows (Fig. 2F), in pigs during the night or during the day (Fig. 5, C and G), and in rats during the main feeding period (Fig. 5F). In such cases, a log-Weibull will give a good fit to the distribution of between-meal intervals (Figs. 2F and 4, C and L) and a good prediction of $P_{\text{start}}$ (77; Fig. 5). For dolphin calves and the three avian species, however, $P_{\text{start}}$, as estimated from pooled data, does not continuously increase (Fig. 5, B, D, E), even though these are based on daytime observations only. For avian species, this is mainly the effect of pooling across individuals with different feeding behavior, i.e., birds with few vs. birds with many daily meals (28, 30). Fig. 5I shows that even pooling of data across age of individuals with the same feeding behavior may distort the change in $P_{\text{start}}$ observed at a given age. To calculate this graph, a data subset was selected of 100 birds with an average number of daily meals during the observation period. Broilers grow very fast and, with age, tend to increase meal size but to decrease the number of daily meals, which is associated with an increase in between-meal interval lengths. $P_{\text{start}}$ increases with time since the last meal at all ages (Fig. 5I), but in the pooled data set, the increase stops, or even turns into a decrease at long times since the last meal, for the reason discussed earlier. The failure of $P_{\text{start}}$ to continuously increase in pooled data sets does, therefore, not necessarily invalidate the expectation based on the satiety concept that, for individuals with similar feeding strategy of a given age, at a certain time of day, $P_{\text{start}}$ will increase with time since the last meal. The typical pattern of $P_{\text{start}}$ in such data is consistent with the good fit of a log-normal to the frequency distributions of between-meal interval lengths (30) (Fig. 4). It is concluded, therefore, that the observed changes in $P_{\text{start}}$ are consistent with the satiety concept, although this may be distorted by pooling of nonuniform data.

The frequency distribution of within-meal intervals. Traditional quantitative methods for the estimation of meal criteria, such as log-survivorship and log-frequency analysis, describe the frequency distribution of within-meal interval lengths with a negative exponential. We have argued (67) that there will be relatively few very short intervals between feeding events if an appropriate unit of time is used for data collection. For instance, if visits are the recorded feeding event for broilers, birds require some minimum amount of time to move between feeders. If time is recorded in an appropriate unit (in this case, 1 s), few very short within-bout intervals will be recorded (Fig. 4F), and a negative exponential will not be the most appropriate model to describe its frequency distribution. Machlis (40), who recorded time in units of 0.1 s, found fewer short within-bout pecking intervals than expected in data obtained with chickens for the same reason. Additional examples of such a “shortage” of very short within-bout intervals may be found in work on licking behavior of rats (54) and feeding behavior of cows (67) and zebra finches (58). Therefore, if an appropriate unit of time measurement is used for data collection, very short intervals between feeding events, whatever their nature, are not possible “for mechanical reasons” (58), and then a negative exponential will be unsuitable to describe the data. Figure 4 shows that for cows, dolphin calves, and ducks, the populations of within-meal intervals are not distributed as negative exponentials but as log-normals. This has been observed before for pecking chickens (40) and for drinking rats (54). This could not be established with certainty for the pig data set because intervals shorter than 10 s were not recorded or for rats because the measurement time-scale was too crude to describe precisely the distribution of the many very short intervals in this data set. This raises the question why log-normals give such a good description of the distribution of intervals within feeding or drinking bouts in so many species.

For intervals between meals, a log-normal distribution may result from pooling of nonuniform data (Fig. 5). To investigate whether pooling also affected the distribution of within-meal intervals, we first disaggregated data with respect to the distance between feeders that were visited immediately before and after the recorded interval that were obtained with cows, broilers, turkeys, and ducks (Fig. 6). Graphs for turkeys are not shown because they were very similar to those for broilers; because of the manner in which the data were collected, this disaggregation was not possible for pigs, dolphins calves, or rats. The frequency distribution of between-meal intervals was essentially unaffected by feeder distance in all these species, as could be expected (Fig. 6, A–C). Within-meal intervals as proportions of all intervals decreased with feeder distance in all species, which is because the probability of animals accessing a feeder near the last-visited one will be higher within than between meals. In addition, the peak of the distribution occurs at interval lengths that increase systematically with feeder distance. Again, this is to be expected because it will take more time to move from one feeder to the next the farther they are separated. The frequency distributions of the disaggregated data sets of intervals in these graphs do not seem to deviate from log-normal ones, with two exceptions: 1) intervals between visits to the same feeder by broilers and turkeys (for reasons discussed above) and 2) intervals between visits to the same feeder by cows, which show a slightly truncated distribution (because visits to the same feeder within 10 s were not
The observed changes in $P_{\text{restart}}$ with time are consistent with log-normal distributions. The calculations of $P_{\text{restart}}$ were based on the assumption that intervals shorter than 1,801 or 61 s represented the first population of within-meal intervals for cows and Pekin ducks, respectively. Because of the considerable overlap between interval populations in broilers, it was estimated (from Fig. 6B) that 12, 16, and 25% of all intervals occurred within meals for intervals between adjacent feeders, between feeders separated by one or two other feeders or between feeders separated by three or more other feeders, respectively. To avoid the disturbing effect of a second population of within-meal intervals, cow data were restricted to individuals with no evidence of within-meal drinking (75). In all cases, $P_{\text{restart}}$ first increases and then decreases with time since feeding last (Fig. 6, D–F), which is characteristic of log-normal interval distributions (29) (Fig. 5A). The log-normal distributions of within-meal intervals in Fig. 4 are, therefore, not a result of pooling of subsets of intervals that differ as a result of feeder distance.

Fig. 6. Effects of disaggregation of data sets on the relative frequency distribution of log-transformed interval length and the probability of animals continuing their meal ($P_{\text{restart}}$) in relation to time since feeding last. Shown are effects on this distribution of intervals between visits of cows to the same feeder (A; n = 7,585, symbol ●), adjacent feeders (n = 8,203, symbol ▲), two or three feeders away (n = 6,397, ○) or more than three feeders away (n = 7,555, +). B: intervals between visits of 3-wk-old broilers to the same feeder (n = 327,203, ●), adjacent feeders (n = 9,542, ▲), two or three feeders away (n = 62,283, ○) or more than three feeders away (n = 104,209, +). C: intervals between visits of Pekin ducks to the same feeder (n = 29,003; ●), adjacent feeders (n = 42,043, ▲), two or three feeders away (n = 6,397, ○) or more than three feeders away (n = 49,703, +). Effects of feeder distance on $P_{\text{restart}}$ (within 10 s) for cows, broilers, and ducks are shown in D, E, F, respectively (with symbols corresponding to those in the top row). Shown are also effects of disaggregation in subsets of four cows with short (●) or long (○) within-meal interval medians (G), subsets of 100 broilers with short (●), average (▲) or long (○) within-meal interval medians (H), and subsets of 100 ducks with short (○), average (▲), or long (○) within-meal interval medians (I).
Both subsets of within-meal intervals obtained with cows during the day and during the night were log-normally distributed with their associated characteristic change in $P_{\text{restart}}$ with time (data not shown). Likely as a result of less crowding, $P_{\text{restart}}$ was significantly higher during the night than during the day (paired $t$-test, $n = 19$, $P < 0.01$), but the differences in $P_{\text{restart}}$ were very small (mean $= 0.006$, SE $= 0.0019$). The log-normal distribution of within-meal intervals in cows was not an artifact that resulted from pooling of data across day and night.

$P_{\text{restart}}$ within meals was calculated for additional subsets of cows, broilers, and ducks with recorded short, average, or long median within-meal intervals. In all cases, $P_{\text{restart}}$ first increased and subsequently decreased with time since feeding last (Fig. 6, $G$–$I$), showing that these subsets had log-normal distributions as well. It is highly unlikely, therefore, that the log-normal distributions of within-meal interval length (Fig. 4) are a result from inappropriate pooling of data across day and night, across individuals with different feeding strategies, or across different distances between the feeders that were visited. Log-normal distributions of intervals may be expected if a number of conditions must be met before an event can occur, each with their own (change in) probability (47). The probability that a cow will continue her meal after ending a visit may well increase with time but be, on average, lower when access to feeders is blocked by a dominant cow than when access is free. Similarly, the probability of a bird continuing its meal may well increase with time since the last visit but be lower if the animal encounters another bird and engages in social contact than when that is not the case. Under both conditions, the initial increase in $P_{\text{restart}}$ observed in the whole data set will be dominated by the probability associated with nondistracted animals, which will be relatively high; the probability at long times, however, will only be observed if animals are distracted, which is associated with a relatively low $P_{\text{restart}}$ (effects similar to those depicted in Fig. 5, $G$–$I$). The data sets that we analyzed do not have the information that would allow disaggregation on the basis of such criteria. We conclude, however, that the log-normal distribution and the associated characteristic change in $P_{\text{restart}}$ observed here likely results, again, from data pooling across nonuniform behaviors.

The probability of animals ending a meal. It is generally assumed that animals start a meal when satiety levels are low and that they continue to feed until satiation causes the animal to end a meal (45). This leads to the expectation that the probability of animals ending a meal ($P_{\text{end}}$) will increase with the amount of food already consumed. The probability of cows ending a meal, indeed, increases almost linearly with the amount of food consumed (Fig. 7A) (66), which is consistent with this expectation and also with a (truncated) normal distribution of meal size (Fig. 7D). In broilers, the probability of birds ending a meal increases with amount already consumed,

![Fig. 7. A: probability of cows stopping feeding before consuming another 0.5 kg of food in relation to amount already consumed during a visit (▲) or during a meal (●). B: probability of 3-wk old broilers stopping feeding before consuming another 1 g of food in relation to amount already consumed during the visit (▲) or the meal (●); C: probability of Wistar rats stopping feeding before consuming another 0.2 g of food in relation to the amount already consumed during the visit (▲) or the meal (●); the relative frequency distributions of meal size in cows (D), 3-wk old broilers (E), and Wistar rats (F). To avoid negative values after log-transformation for broilers, the amount of food consumed was expressed in the units it was measured, i.e., 0.1 g.](http://ajpregu.physiology.org/)

AJP-Regul Integr Comp Physiol • VOL 301 • AUGUST 2011 • www.ajpregu.org
at first fast but then gradually slower (Fig. 7B), which can be expected for a log-Weibull type of frequency distribution of meal size (Fig. 7E). For rats, the probability of animals ending a meal increases continuously with the amount already consumed, which is associated with an almost normal (be it slightly truncated) distribution of meal size (Fig. 7F).

The differences between cows, broilers, and rats in changes of $P_{\text{end}}$ in relation to amount of food already consumed during the meal and in meal size distribution is related, again, to the existing variation in the pooled data. While cows change their meal pattern very little during lactation (70) and also the meal patterns of mature rats are expected be stable (25), broilers gained considerable weight and changed their feeding behavior during the observation period (30). Initially, young animals consumed small meals, but the size of their meals increased considerably during the measurement period (30). For reasons addressed above, the pooling of such nonuniform data may give the impression that the probability of animals ending a meal does not continuously increase with meal size. However, limiting the data set for analyses to 3-wk-old broilers abolished the decline in $P_{\text{end}}$ observed in the data pooled across age in that species (Fig. 7B). It shows that, for animals at a certain age and/or with a given feeding strategy, $P_{\text{end}}$ does increase with amount already consumed, which is consistent with expectations based on the satiation concept. The $P_{\text{end}}$ and distribution of meal size for the pooled turkey and duck data sets were similar to those observed in broilers, and these graphs are, therefore, not reproduced here. No intake data were collected with dolphin calves.

The probability of animals ending a visit was higher than $P_{\text{end}}$ for meals at low amounts of food consumed in all species (Fig. 7). This probability is affected little by the amount consumed during the visit (Fig. 7A) and remains higher for visits than for meals (Fig. 7A) in cows because meals of cows generally consist of many visits (67, 70). In contrast, the probability of broilers and rats ending a visit is initially higher than $P_{\text{end}}$ for meals, but the two probabilities become much closer after larger amounts of food have been consumed (Fig. 7, B and C). Observations for ducks and turkeys were similar to those in broilers and are not shown. This is consistent with the observation that, especially in the avian species, a single long visit during which a considerable amount of food is consumed can constitute a meal in itself. As a result, the character of visits and their associated $P_{\text{end}}$ changes with the amount consumed in these species and the $P_{\text{end}}$ associated with long visits is similar to that for meals after the same intake. Thus, these data are consistent with satiation gradually increasing during meals, which is associated with a rise in the probability of animals ending a meal.

**General Discussion and Conclusions**

Animals are expected to finish a meal when they are satiated. As a result of satiety, the probability of animals starting a meal immediately after finishing one is expected to be low. As the time since the last meal increases, satiety is expected to wear off and hunger/feeding motivation is likely to increase. The probability of animals starting feeding is, consequently, expected to increase with time since the last meal. Such an increase was observed in all species analyzed here, at least when inappropriate pooling of data was avoided (Fig. 5). In addition, the probability of animals ending a meal increased with amount of food already consumed, again when effects of inappropriate pooling were avoided (Fig. 6). These observations are consistent with the idea that the temporal structure of feeding behavior for an animal with free and continuous access to food is caused by changes in satiety and satiation and the associated changes in the probability that the animal will start and end meals.

As a result of the gradual increase in $P_{\text{start}}$ with time since the last meal, all species show a distinct population of longer (i.e., between-meal) intervals (Fig. 3). The frequency distribution is in all cases a (sometimes extremely) skewed normal, which can be converted into an approximately normal distribution by log-transformation (Fig. 4). The distribution is never in the shape of a negative exponential, except when data are inappropriately pooled (49) or when animals do not have free access to food, as in daytime group-housed pigs (74). There is more variation in the frequency distribution of shorter (i.e., within-meal) intervals, within species, as well as between species or methods of data collection. This relates to both the number of populations of such intervals and their distributions. For several species, such as dairy cows (65) (Fig. 2) and rats (67), within-meal drinking can result in an additional within-meal interval population, and it is hypothesized here that this may also be the case for other species (such as ducks; Fig. 4). For the species analyzed here, none of the within-meal interval distributions was in the shape of a negative exponential. Similar results have been obtained by other authors for rats (79) and zebra finches (60) before. This means that there is no biological basis for any methodology that relies on fitting a model consisting of two or more negative exponentials to the (cumulative) frequency distribution of between-feeding intervals.

Our method for meal criteria estimation consists of fitting a mixed model of log-normals and (sometimes) a log-Weibull, to the frequency distribution of between-feeding interval lengths (Eqs. 5–8). Inspection of graphs as plotted in Fig. 4 give a first impression of which model might be most appropriate for a given data set. After fitting these models, the best meal criterion estimate (65) is the interval length where the functions describing the frequency distribution of between-meal intervals and the nearest population of within-meal intervals is equal (the arrows in Fig. 2 and Fig. 4). This interval length can be calculated from the parameters of the fitted model (67, 75). At this interval length, the predicted total number of intervals is, by definition, double that predicted by the function describing the frequency distribution of between-meal intervals. If the fit of the model is good, the observed number of intervals at this length will also be (approximately) twice the frequency predicted by the fitted function. This observation helped to develop the first of two alternative methods to estimate meal criteria from data sets that do not clearly show $J$ how many within-meal interval populations there are or 2) what the most appropriate function is or functions are to describe these distributions (or both).

The first alternative requires only that the appropriate distribution of between-meal intervals is known. Howie et al. (28) fitted a truncated function (i.e., a log-normal or a log-Weibull) to the frequency distribution of between-feeding intervals that were long (i.e., certain to be between-meal intervals). The model parameters were subsequently used to find the interval
length at which the observed interval frequency was twice that predicted by the fitted function. This resulted in meal criteria estimates that were similar to those estimated from the parameters of models described by Eqs. 5–8.

The second alternative does not even require knowledge of the most appropriate function to describe the frequency distribution of between-meal interval lengths. It is based, instead, on observations as depicted in Figs. 2F and 5, A–F. These graphs show that, with increasing time since feeding last, \( P_{\text{start}} \) first decreases sharply, reaches a nadir, and then (at least initially) increases sharply. At very short times since feeding last, the calculated \( P_{\text{start}} \) is dominated by \( P_{\text{restart}} \) because most of these short intervals are ended by animals going from one to the next feeding event within a meal. Obviously, at long times since feeding last, \( P_{\text{start}} \) is determined entirely by animals starting another meal. The nadir is then an estimate of the interval length where the major effect on \( P_{\text{start}} \) switches from \( P_{\text{restart}} \) to \( P_{\text{start}} \) proper. Meal criteria estimated by this method are similar to (but tend to be slightly shorter) than those estimated by the other methods (28, 29). In our view, the fitting of Eqs. 5–8 is the best method of estimating meal criteria, but the described alternatives can be useful when the number of interval populations or the best functions to describe their distributions is unknown.

The methodology proposed here differs from that recently developed on the basis of nocturnal data obtained with rats. Zorrilla et al. (79) calculated the effect of increasing the length of arbitrarily chosen meal criteria on “meal” duration. The choice of an arbitrary but very short criterion will result in many meals being split in shorter feeding bouts (which were still called meals). Subsequent arbitrary increases in the criterion will initially reassign many intervals to the within-meal population, resulting in a considerable increase in average “meal” duration. An increase in the arbitrary criterion around the interval length where the nadir in the interval frequency distribution occurs (Fig. 3) reassigned only a few intervals to the within-meal population and has, therefore, very little effect on average “meal” duration. A further increase in the arbitrary criterion at longer interval lengths, however, will increasingly identify bouts that may include more than one meal. This will, again, have a considerable effect on average “meal” duration. The interval length at which an increase in arbitrary meal criterion had the least effect on average “meal” duration was then selected as the final meal criterion. Although the estimates obtained by this method seem very reasonable, we consider the methods proposed here 1) more biologically correct (because the estimated criteria are close, but not always identical, to the nadir in the interval frequency distribution) and 2) less cumbersome than the method proposed for rats (79). In addition, the definition of “interval” used by these authors and by others (e.g., 12) slightly differs from intervals as analyzed in the current paper. For the seven species analyzed here, animals had no access to food in the recorded intervals, i.e., these were real between-feeding intervals. In the aforementioned studies with rats, however, intervals between pellet removal were analyzed (12, 79). These are not between-feeding intervals proper, as in most intervals, rats will consume the pellet as well. This means that some (short) “intervals” probably consist of feeding only (when a rat removes a pellet, consumes it, and immediately removes another pellet). In other “intervals”, both feeding and nonfeeding behavior likely occurs. This may not distort the frequency distribution of between-meal intervals, but it may have some effect on the distribution of short (within-meal) intervals. It seems likely, however, that (an adapted version of) the models proposed here should also be suitable to analyze such data sets.

Electronic tagging in combination with computerized feeders allows collection of individual feeding behavior data of group-housed animals. Animals had access to between 6 and 16 feeders in the experiments using cows and the avian species (Table 1), and our analyses show that one or more feeders were accessible during most of the day and night. Dolphin calves also had continuous access to their dams. In contrast, group-housed pigs were frequently queuing in front of the single feeder during the day, and then feeding behavior seemed entirely random. Under such conditions, it is not useful to try to group feeding behavior into bouts. Although the rat data contained many more very short intervals than those from the other species (Fig. 4), the distribution at interval lengths around the estimated meal criterion (i.e., at the nadir) and longer was very similar. This makes the proposed models eminently suitable as well for such data obtained with singly housed animals.

The meal criteria estimated by the methods proposed here are usually longer than those resulting from traditional log-survivorship or log-frequency analyses or estimates based on other (frequently arbitrary) considerations. For cows, for instance, many estimates (frequently based on analysis of log-survivorship or frequency plots) are 8 min or less (e.g., 13, 22), shorter than our meal criteria estimates of around 30 min (70, 77; Fig. 2). Similarly, the estimate obtained after fitting our model to the dolphin calf data (161 s) was also longer than the 107.7 s estimated on the basis of the (poor) fit of a log-frequency model (33). For pigs, we estimated (on the basis of night data only), a meal criterion of around 18 min, while much shorter estimates generally result from log-survivorship analyses, e.g., 10 min (6), 5 min (17), and 2 min (52). Our meal criteria estimates range from 1,050 to 1,210 s (29) for four different broiler lines, while estimates of around 1,700 and 1,300 s were obtained for ducks and turkeys, respectively (30) (Fig. 4). This contrasts sharply with the much shorter earlier estimates for domestic avian species, such as an arbitrary 10-s (8), or 36- to 70-s, based on inspection of log-survivorship plots (11, 56). We question the validity of such very short meal criteria (e.g., 10 s) not only on the basis of the applied methodology. If animals terminate a meal when they are satiated, as generally assumed, a meal criterion of 10 s implies that such a short period is considered sufficient to transform a satiated animal into a hungry one. We doubt that this will be the case and question whether bouts that are identified by such short criteria are meals. As a direct result, the validity of conclusions about meal patterns and associated measurements such as preprandial and postprandial correlations that are calculated on the basis of such bout criteria (8) is questionable.

A large variation in meal criteria that are used to analyze rodent data was already observed almost four decades ago (60), and this can still be observed in the literature over the past two decades. For instance, some analyses are performed on the basis of meal criteria as short as 2 min (12, 14), while other groups use criteria such as 4 or 5 min (e.g., 42, 73, 78), 10 min (e.g., 32, 51), 14 min (18), 15 min (e.g., 20, 39, 53), and 20 or longer (e.g., 5, 41). Had we used a 2-min criterion (instead of the estimated 647 s), we would have identified one-third more meals in the rat data set, which shows the large effect that
different criteria can have. Many criteria, however, fall in the 5- to 15-min range and also the estimates made on the basis of careful analyses of the actual feeding structure, such as 11 min (this article), 14 min (18), and 5 or 14 min (79), fall in the same range. Even then, a correct meal criterion choice may be highly relevant because in some data sets, more than 40% of all intervals can fall within the 10- to 20-min range (e.g., 18). It is evident that the most reliable conclusions of meal pattern analysis can only be drawn if a criterion is estimated on the basis of the actual observed structure of feeding behavior.

Analysis of the temporal structure of short-term feeding behavior produces the most biologically relevant information if it is based on the main functional unit in which animals organize their feeding behavior (69). Animals of most species cluster their feeding behavior into meals, which requires the estimation of meal criteria before proper analysis of feeding behavior can occur. Zorrilla et al. (79) showed elegantly that unless an appropriate method is used to estimate meal criteria, interpretation of the structure of short-term feeding behavior can be severely biased. For instance, using an inappropriately short meal criterion suggested that temporary food restriction was followed during refeeding by an increase in meal frequency (and not meal size), while a meal criterion estimate based on a proper analysis showed the opposite to be the case (79). Similarly, the use of an inappropriate short meal criterion will split meals into smaller bouts, separated by short intervals. This may well affect subsequent correlations between bout size and the length of preceding and following intervals (18), which cannot then be interpreted as preprandial and postprandial correlations, as we suspect has happened. As highlighted by Geary (24), an appropriate method to identify meals is, therefore, a prerequisite for any meaningful analyses of the structure of short-term feeding behavior.

Perspectives and Significance

The methodology proposed here is based on a detailed analysis of large data sets of feeding behavior obtained with seven different species and highlights the similarity in the observed structure in birds, as well as ruminants and nonruminating mammals. This structure results from the alternating decrease in satiety between meals and increase in satiation during meals, which is associated with corresponding increases in the probability of animals starting and ending meals, respectively. This contrasts sharply with the assumption of random behavior that underlies traditional methods for estimating meal criteria, such as log-survivorship analysis. Because the mechanisms associated with satiety/satiation are functional in species ranging from birds to small and large mammals, the proposed models may be useful for the analysis of the structure of feeding behavior of animals from other species as well. We highlighted the bias that can result from pooling of nonuniform data sets, especially when contrasts in feeding behavior are large. Nonuniformity may result if data sets are obtained during the day and the night or from individuals at different ages or with different feeding strategies. Disaggregation of such data sets may be required before the true structure of feeding behavior can be elucidated and valid conclusions about the controls of feeding behavior can be drawn.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the contributions of the Biotechnology and Biological Sciences Research Council (United Kingdom), the Scottish Government (United Kingdom), BOCM PAULS (United Kingdom), Georg Schelle (Germany), the Institute for Pig Genetics (The Netherlands), and AVIAGEN (United Kingdom) to parts of the work that generated data analyzed here.

Present addresses: T. A. G. Bley, Cherry Valley Farms, Rothwell, Market Rasen, LN7 6BJ, UK; J. A. Howie, Faculty of Life Sciences, Michael Smith Building, University of Manchester, Oxford Road, Manchester, M13 9PT, UK; T. B. Jacobsen, Frue Kirkestraede 5B, DK-5000 Odense C, Denmark; D. P. N. Stolle, Intercontinental, Wijn de koevenstraat 35, 5831AX Boxmeer, The Netherlands; S. Wilkinson, The Roslin Institute and Royal (Dick) School of Veterinary Studies, University of Edinburgh, Easter Bush, EH25 9RG, UK; M. P. Yeates, Bridge Farm, Glastonbury, Somerset, BA6 8LU, UK.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

REFERENCES


