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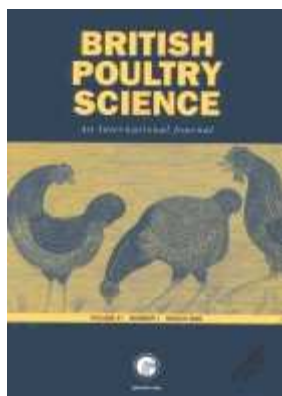
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Short-term feeding behaviour has a similar structure in broilers, turkeys and ducks

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Abstract. 1. This study is the first to quantitatively compare the structure of feeding behaviour of broilers, ducks and turkeys as recorded by electronic feeders. It tests the hypothesis that this structure is so similar that the same models would be suitable to group the feeding behaviour of these species into meals.

2. Visits to electronic feeders were recorded from 3470 broilers, 3314 turkeys and 480 ducks. The frequency distributions of the length of short intervals between visits to feeders varied between species as a result of differences in the number of visits within a feeding bout, the frequency of re-visits to the same feeder and probably in the likelihood of birds drinking within meals.

3. The lengths of longer day-time intervals between visits to feeders were all log-normally distributed. Disaggregation of these intervals by feeding strategy (meal frequency) showed that the probability of birds starting to feed increased with time since feeding last in all species, which is consistent with the satiety concept.

4. Two methods, one based on fitting a truncated log-normal, function, the other on observed changes in the probability of birds starting to feed with time since last feeding, gave very similar meal criteria estimates. These ranged from 1050 to 1200 s in broilers, 1650 to 1725 s in ducks and 1250 to 1320 s in turkeys.

5. There were large between-species differences in the average number of daily meals, intake per meal, and feeding rate. Despite this variation, the overall structure of feeding behaviour of broilers, ducks and turkeys was so similar that the same models were suitable for application in all three species. This would allow for standardised analyses of feeding behaviour of different avian species kept in different husbandry systems.

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INTRODUCTION

Analysis of feeding behaviour can not only improve our understanding of the mechanisms that underlie food intake regulation (LeMagnen 1985; Zorrilla *et al.*, 2005) but could also assist in identifying desirable traits for animal breeding programmes (Howie *et al.*, 2009b). Because of the importance of feed consumption in animal production systems, records of visits to feeders are increasingly being collected to measure daily intake in animals such as cattle (Tolkamp *et al.*, 1998b), pigs (Morgan *et al.*, 2000a) and poultry (Howie *et al.*, 2009a). Such data sets have also formed the basis for analyses of short-term feeding behaviour in each of these species (Friggens *et al.*, 1998; Hall *et al.*, 1999; Bley and Bessei 2008). It has been shown, however, that even small changes in feeder construction or software settings can have large effects on daily number of visits, median visit duration and intake per visit, without changing daily intake (Tolkamp *et al.*, 2000). It is, therefore, difficult to quantitatively compare analyses of short-term feeding behaviour between studies, even if the basic unit is measured in terms of visits to feeders in the same species. This is further complicated if data are collected with species-specific feeders or by other techniques, such as direct observation (Bokkers and Koene 2003) or recording pecks (Machlis 1977), that result in different definitions of the basic unit in which feeding is expressed.

In many species, feeding behaviour is organised in bouts and these bouts, or meals, are therefore considered a more biologically relevant unit for analyses of short-term feeding behaviour (LeMagnen 1985; Forbes 1995). The grouping of short feeding events, such as visits to feeders or pecks, into meals would allow a comparison of feeding behaviour, even when data are obtained with different techniques or different species. To do this, a meal criterion needs to be estimated (Slater and Lester 1982; Langton *et al.*, 1995). Because results of meal pattern analysis can be greatly affected by the value of the meal criterion estimate

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2
3 70 (Zorrilla *et al.*, 2005), it is important to demonstrate the biological basis of the meal definition
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6 71 and its suitability for the relevant species.
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8
9 72 Howie *et al.*, (2009b) concluded recently that there was sufficient similarity in the
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11 73 structure of short-term feeding behaviour of broiler chickens of different genetic lines to allow
12
13 74 robust estimations of reliable meal criteria by previously developed methods (Howie *et al.*,
14
15 75 2009a). The study also suggested that the underlying controls of food intake were unaffected
16
17 76 by intensive selection for production traits. For the current study we hypothesised that the
18
19 77 structure of short-term feeding behaviour of Pekin ducks and turkeys would be sufficiently
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21 78 similar to that of broilers so that the same methodologies for the estimation of meal criteria
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23 79 could be used. We tested this hypothesis with data that were collected in several separate
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25 80 experiments, with birds of different ages and under different conditions for the three species.
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27 81 In addition, we tested whether or not the main principle upon which the methodologies
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29 82 developed by Howie *et al.*, (2009a) are based, that is, a continuous increase in the probability
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31 83 of birds starting to feed with time since the last meal, applies to birds of each of these species.
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33 84 We also investigated how appropriate disaggregation of the data can aid in fully
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35 85 understanding the structure of feeding behaviour. Finally, we briefly describe the observed
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37 86 feeding behaviour of these three species after grouping it into meals.
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43 44 45 46 88 MATERIALS AND METHODS

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48 89 Records of visits to feeders of 3470 female broiler chickens (*Gallus gallus*), 3314 male
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50 90 turkeys (*Meleagris gallopavo*) and 480 male and female Pekin ducks (*Anas platyrhynchos*
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52 91 *domestica*) were available for analysis in this study (see summary in Table 1). The methods
53
54 92 and equipment for obtaining the basic duck and broiler data have been previously described in
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56 93 detail by Bley and Bessei (2008) and Howie *et al.*, (2009a), respectively, but data were
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58 94 analysed here using novel methods. The turkey data were collected from a set of 16 hatches.
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3 95 Each hatch, consisting of around 200 male birds, was housed from 18 to 22 weeks of age in a
4
5 96 single pen. The actual number of turkeys per pen varied slightly due to differences in the
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8 97 number of available birds per hatch.
9

10 98 Pens for broilers were equipped with one and pens for ducks and turkeys with two
11
12 99 feeding stations. Each feeding station, previously described in detail for ducks (Bley and
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14
15 100 Bessei 2008) and broilers (Howie *et al.*, 2009a), consisted of 8 feeders and was linked to a
16
17 101 computer to allow automatic recording of visits. The feeding stations for turkeys were scaled-
18
19 102 up versions of the ones used to collect broiler data. Each feeder had a back bar and side plates
20
21 103 that were adjusted as the birds grew to allow entry of only one bird at a time. Each feeder
22
23 104 contained a feeding tray that was linked to electronic scales to record the weight of food at the
24
25 105 start and end of each visit. All birds were tagged with electronic wing bands and a radio
26
27 106 frequency antenna system was used to identify individuals entering and leaving the feeders.
28
29 107 Start and stop time, weight of food consumed, bird ID, visit duration, date, pen and feeder
30
31 108 number were recorded per visit and stored electronically in a database.
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36 109 Birds of all species were placed in their pens at least a few days before data collection
37
38 110 began to allow acclimatisation to the environment and feeding equipment. Birds had *ad*
39
40 111 *libitum* access to a species-appropriate pelleted feed throughout the data collection period.
41
42 112 Lighting regimes and stocking densities differed between the species, with turkeys having the
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44 113 most hours of darkness and ducks having the lowest stocking density (Table 1).
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48 114 *[Insert Table 1 around here please]*
49

50 115 **Analysis of feeding behaviour**

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52 116 The data were screened to remove visits where the wing band of the bird was not recorded,
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54 117 which affected less than 0.1% of the total number of broiler and turkey visits. Scale errors
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56 118 were also removed from the calculations of feed intake, but were included for other
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58 119 characteristics (less than 0.5% of all visits). On rare occasions, ducks were not properly
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3 120 identified by the feeders, which resulted in many short 'between-feeding' intervals which
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5 121 were removed before analyses.
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8 122 First the interval length between two consecutive visits to feeders of the same bird was
9
10 123 calculated. The frequency distributions of these interval lengths, as well as of \log_e -
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12 124 transformed interval lengths (measured in s), were plotted to assist in determining the
13
14 125 structure of short-term feeding behaviour and the estimation of meal criteria. On the basis of
15
16 126 previous experience, bin-widths of 5 min and 0.5 \log_e -units were selected to present the
17
18 127 clearest graphs.
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22 128 The effects of data pooling (Morgan *et al.*, 2000b; Yeates *et al.*, 2003) on the
23
24 129 distribution of interval lengths and on starting probabilities were investigated by
25
26 130 disaggregation of the data into sub-sets. First, 'day-time' data sets were produced for each
27
28 131 species that consisted of intervals that occurred entirely during the light period only. For each
29
30 132 species, day-time intervals of all birds were further disaggregated into two groups, that is, (i)
31
32 133 intervals between visits to the same feeder and (ii) intervals between visits to different
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34 134 feeders. After meal criteria were estimated (see below) three additional data sets were created
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36 135 of birds with similar feeding strategies in each species for further analyses. To that end, first
37
38 136 the mean number of daily meals was calculated per bird. For each species, data of three sub-
39
40 137 groups of 50 birds each were pooled. These sub-groups consisted of birds with a mean daily
41
42 138 meal number that was (i) around the average or (ii) the lowest or (iii) the highest of the total
43
44 139 population. To further investigate the structure of short-term feeding behaviour of ducks, we
45
46 140 calculated for each duck the number of intervals with an intermediate duration (between 1 and
47
48 141 10 min) as a proportion of all intervals between visits to feeders. Two data sets were created
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50 142 by pooling the data of 50 ducks each with either (i) the lowest or (ii) the highest proportion of
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52 143 such intermediate intervals.
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3 144 Two methods were used to estimate meal criteria per hatch. First a truncated log-
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5 145 normal model was fitted to the distribution of \log_e -transformed between-visit interval lengths
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8 146 using GENSTAT (VSN International 2008), as described in detail by Howie *et al.* (2009a).
9
10 147 The model was fitted to the lengths of day-time intervals longer than 7.5 \log_e units and has the
11
12 148 following probability density function (PDF):

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15 149
$$\text{PDF} = (1/\text{cunormal}((7.5-\mu)/\sigma))(1/(2.506628 \sigma))\exp(-((x-\mu)^2)/(2\sigma^2))$$

16
17 150 Where: cunormal = GENSTAT cumulative normal correction factor to allow for truncation, μ
18
19 151 and σ = mean and standard deviation of the log-normal distribution, and x = \log_e interval
20
21 152 length (in sec). The meal criterion was estimated at the interval length where the number of
22
23 153 observed intervals was twice that predicted by the model, as outlined by Howie *et al.* 2009a).
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27 154 Meal criteria were also estimated on the basis of the probability of birds starting to eat
28
29 155 in relation to time since last feeding (P_{start}). The probability of birds starting to feed within the
30
31 156 next 5 min at time t since feeding last was calculated as the number of intervals $> t$ and $\leq t + 5$
32
33 157 min divided by the number of intervals $> t$ min (Tolkamp and Kyriazakis 1999a). For the
34
35 158 estimation of meal criteria, these probabilities were also calculated with bin-width of 1 min.
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37 159 As described previously (Howie *et al.*, 2009a), the meal criterion is estimated as the time
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39 160 since feeding last where P_{start} is lowest, using a rolling average over 5-min intervals to reduce
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41 161 the effect of random variation in values.
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45 162 Meal criteria according to both methods were estimated per hatch. ANOVA was used
46
47 163 to test for an effect of methodology of estimation on resulting meal criteria estimates and the
48
49 164 associated meal characteristics.
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169 RESULTS

170 **Distribution of interval lengths between visits**

171 Figure 1 (top row) shows the relative frequency distributions of the length of intervals
172 between visits to feeders for all data pooled per species. Broilers, turkeys and ducks all
173 showed a rapid decrease in frequencies with increasing interval length to a minimum between
174 15 and 30 min. The frequencies then increased to a peak between 50 and 80 min, and then
175 gradually decreased to very low frequencies at long intervals. Although the values of the
176 minima and maxima varied between the species, all species show a similarly shaped
177 distribution of between-visit interval lengths. *[Insert Figure 1 around here please]*

178 Log_e -transformation of interval lengths resulted in the distributions shown in Figure 1
179 (centre row). From the data obtained with turkeys, it was evident that there was a population
180 of very long intervals, longer than approximately 10.5 log_e -units (corresponding to 10 h), that
181 was almost entirely separated from the remainder of the interval distribution. These very long
182 intervals all included at least part of the dark period. When the three data sets were
183 disaggregated by removing all intervals that included the entire dark period or parts thereof,
184 the separate distribution for very long intervals in turkeys completely disappeared (Figure 1,
185 bottom row). The same procedure also removed ‘blips’ that were previously observed in the
186 frequency distribution of long log_e -transformed intervals for broilers (around 9.6 log_e -units,
187 corresponding to 4 h) and ducks (compare centre with bottom row graphs in Figure 1). The
188 remaining distributions of the population of longer log_e -transformed intervals were
189 approximately normal in all species. Figure 1 shows that, apart from the approximately log-
190 normal distribution of a population of longer intervals, there is at least one additional
191 population of shorter log_e -transformed interval lengths for broilers and turkeys and there are
192 at least two for ducks. These are investigated in more detail below.

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194 **Changes in probabilities of birds starting to feed**

195 Figure 2 (top row) shows how the probability of birds starting to feed within the next 5 min
196 changed with time since birds fed last as estimated for the data pooled per species. An initial
197 decrease in P_{start} to a nadir between 20 and 30 min was followed by an increase to a plateau or
198 even a later decrease. As this may be an effect of pooling across day and night data (Morgan
199 *et al.*, 2006b), the intervals that included (part of) the night period were removed, resulting in
200 the probabilities depicted by the graphs in the middle row of Figure 2. The bottom row of
201 Figure 2 shows the effects of disaggregation by feeding strategy on P_{start} estimates. In contrast
202 with the trend seen in the pooled data, P_{start} generally continued to increase with time since
203 feeding last for birds with a given feeding strategy.

204 *[Insert Figure 2 around here please]*

205 **Effect of disaggregation of interval data by feeder visited**

206 For ducks, with few very short between-visit intervals, the sub-set of day-time intervals
207 between visits to the same feeder had virtually the same distribution as the sub-set of day-time
208 intervals between visits to different feeders (Figure 3). Disaggregation of data obtained with
209 broilers and turkeys, however, showed that very short intervals were recorded between visits
210 to the same feeder only (Figure 3, centre row graphs) and not between visits to different
211 feeders (Figure 3, bottom row graphs). For broilers, the frequency distributions of the log_e-
212 transformed length of intervals between visits to different feeders clearly showed two
213 overlapping populations that were both approximately log-normally distributed (Figure 3).
214 For turkeys, the data suggest that there is a population of shorter intervals, similar to that
215 observed in broilers but much smaller, that overlaps with the log-normally distributed
216 population of between-meal intervals.

217 *[Insert Figure 3 around here please]*

218 **Effects of disaggregation of duck data by individual feeding strategy**

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3 219 Duck data were examined in more detail in an attempt to find an explanation for the
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5 220 occurrence of three populations of intervals between visits to different feeders rather than the
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8 221 two that were observed in birds of the other two species. A preliminary inspection of interval
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10 222 distributions obtained with individuals showed that there was little variation between ducks in
11
12 223 the distribution of the populations of very short (with a peak around 2.75 \log_e -units
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14 224 corresponding to 15 s) and very long (with a peak between 8 and 9 \log_e -units, corresponding
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17 225 to 50 and 135 min) intervals. There was, however, considerable individual variation in the
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19 226 number of intervals between 1 and 10 min, corresponding to 4.1 and 6.4 \log_e -units, as a
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21 227 percentage of all intervals (from 1 to 46%). Figure 4 shows the observed frequency
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23 228 distributions of interval lengths pooled across the 10% of individuals with a low or a high
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25 229 proportion of intervals in the range of 1 to 10 min. The Figure demonstrates that a
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27 230 considerable proportion of ducks showed little evidence of a third population of intervals. At
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29 231 the same time, another considerable proportion of ducks produced a relatively large third
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31 232 population with 'intermediate' lengths (from around 1 to around 10 min) that was very clearly
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33 233 distinguished from the other two populations of intervals (Figure 4).

34 234 **Estimation of meal criteria**

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36 235 A truncated normal function describing all pooled \log_e -transformed day-time intervals longer
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38 236 than 7.5 \log_e -units gave a good fit to the data pooled across species (Figure 1, bottom row
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40 237 graphs). The model converged easily for all data sets and species-specific meal criteria could
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42 238 quickly be estimated (Table 2). Similarly, a clear trough in the plot of the probability of birds
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44 239 starting to feed in relation to time since last feeding (Figure 2, centre row) allowed an easy
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46 240 estimate of meal criteria for each species by this method. Meal criteria estimated per hatch in
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48 241 this manner were 150, 70 and 75 s shorter for broilers, ducks and turkeys, respectively, than
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50 242 estimates resulting from the truncated normal method. Because of the scarcity of intervals in
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52 243 this range, the effect of these shorter meal criteria on average number of daily meals (an
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3 244 increase with less than 0.1 in each species) and other meal characteristics was, however, very
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5 245 small. Meal criteria estimated by the truncated log-normal method were used to group visits
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8 246 into meals for further analyses (all between-feeding intervals shorter than the meal criterion
9
10 247 were ignored for the calculation of meals).

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13 248 *[Please insert Table 2 around here]*

14 249 **Meal characteristics**

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16 250 Broilers and ducks had a very similar average daily number of meals but turkeys consumed
17
18 251 their food in considerably fewer meals (Table 2). Ducks not only had the shortest meals but
19
20 252 also spent the smallest proportion of total meal duration feeding (24.1% vs. 70.6% and 81.8%
21
22 253 for broilers and turkeys, respectively). This resulted in ducks having by far the shortest daily
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24 254 feeding times (less than 12 min/d, compared with 34.2 and 63.6 min for turkeys and broilers,
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26 255 respectively; Table 2).

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32 257 **DISCUSSION**

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35 258 The main objective of this study was to test the hypothesis that the same methods could be
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37 259 applied for the estimation of meal criteria in broilers, ducks and turkeys because of a similar
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39 260 structure of their feeding behaviour. The distribution of longer (that is, between-meal)
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41 261 intervals has a major effect on meal criteria estimates and this distribution is, therefore,
42
43 262 discussed first.

44 263 **Structure of feeding behaviour: the distribution of longer intervals**

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46
47 264 Plots of the frequency distribution of \log_e -transformed interval lengths between behavioural
48
49 265 events can reveal much about the structure of animal behaviour (Tolkamp *et al.*, 1998a;
50
51 266 Yeates *et al.*, 2001). Figure 1 shows that the distribution of interval lengths between visits
52
53 267 was clearly not consisting of just a single interval population in any of the three species,
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55 268 which is evidence for a bouted structure of behaviour. Most of the longer intervals in each
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57 269 species were part of a skewed normal distribution that could be normalised by \log_e -
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3 270 transformation of interval lengths. Diurnal species such as pigs (Morgan *et al.*, 2000b), cows
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5 271 (Yeates *et al.*, 2003) and chickens (Savory, 1980; Howie *et al.*, 2009a) have a much lower
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8 272 probability of feeding in dark than in light conditions. As a result, between-feeding intervals
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10 273 are on average longest when these include part or all of the dark period. In the present
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12 274 analysis, this was shown most clearly by the separate population of very long log_e-
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14 275 transformed interval lengths in turkeys (Figure 1). This probably relates to the comparatively
15
16 276 long dark period (10 h) that turkeys were subjected to, but the effect was also observed for
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18 277 ducks and broilers, exposed to dark periods of, respectively, 7 and 4 h only (Figure 1).
19
20 278 Because such long intervals will always exceed meal criteria, we disaggregated the data set
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22 279 for those analyses by removing intervals that included (part of) the dark period to facilitate
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24 280 model fitting.

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29 281 The remaining pooled longer intervals seemed to form a single, homogeneous and log-
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31 282 normally distributed population in ducks and turkeys (Figure 2), as was previously observed
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33 283 in broilers (Howie *et al.*, 2009a; b). This is further justification for the fitting of a log-normal
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35 284 function to the pooled population of long day intervals to estimate meal criteria.

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38 285 A log-normal distribution of intervals between specific behaviour can only be
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40 286 expected, however, if the probability of animals expressing that behaviour first increases but
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42 287 subsequently decreases with time since that behaviour was last expressed (Yeates *et al.*,
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44 288 2001). Such a decrease in starting probability at longer times is, however, in conflict with an
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46 289 expectation based on the satiety concept. (Metz, 1975; Simpson 1995; Yeates *et al.*, 2001).
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48 290 Pooling of between-feeding intervals across day and night or across individuals with different
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50 291 feeding strategies can obscure real changes in starting probability with time since the last
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52 292 meal for an individual at a given time (Morgan *et al.*, 2000b; Yeates *et al.*, 2003; Howie *et al.*,
53
54 293 2009a). For that reason, we investigated (Figure 2) the effects of disaggregation by feeding
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56 294 strategy on the change in P_{start} with longer times since feeding last. A bird with many daily
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3 295 meals has many short and very few long intervals between meals. In contrast, a bird with few
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5 296 daily meals will have few, mainly long, intervals between meals. This will result in a higher
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8 297 average P_{start} for the bird with many than for the bird with few daily meals at any time since
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10 298 the last meal. However, even if P_{start} increases for both animals with time since the last meal,
11
12 299 this may not be so when the data of the animals are pooled (Morgan *et al.*, 2000b). Since
13
14 300 young/small birds usually have more daily meals, and therefore a higher P_{start} , than
15
16 301 older/larger birds (Howie *et al.*, 2009a;b), disaggregation by age is in essence also a
17
18 302 disaggregation by feeding strategy. Figure 2 shows that in all species, when data were
19
20 303 properly disaggregated, P_{start} continued to increase with time since the last meal, in a manner
21
22 304 that can be expected on the basis of the satiety concept (Yeates *et al.*, 2001). In the pooled
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24 305 data set, however, the estimated P_{start} is consistent with a log-normal distribution of intervals
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26 306 between meals in broilers, turkeys and ducks and this resulted in similar distributions of
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28 307 longer between-feeding interval lengths in all three species.

308 *Estimating meal criteria*

309 There were large numbers of short intervals, especially for broilers and turkeys, that were
310 clearly not part of the log-normal distribution of the population of longer, that is, between-
311 meal, intervals (Figure 1). It was not immediately clear how many populations of short
312 intervals there were and how each of these was distributed. For such situations, Howie *et al.*,
313 (2009a) developed two methods that allow estimation of meal criteria on the basis of broiler
314 data. The method based on fitting a truncated log_e-normal model to the distribution of long
315 intervals only, suited the duck and turkey data as well (Figure 1). The second method
316 developed with broilers relies on estimation of the trough in starting probabilities calculated
317 from pooled data (Howie *et al.*, 2009a). Such a trough is also clearly observed in data
318 obtained with ducks and turkeys (Figure 2). Meal criteria that were estimated with this, rather
319 than the truncated log-normal method, resulted in similar predictions of daily meal number

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3 320 and other meal characteristics for all species. This result shows that both methods developed
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5 321 for broilers can be successfully applied to estimate meal criteria in turkeys and ducks.
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8 322 **Structure of feeding behaviour: the distribution of shorter intervals**

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10 323 In previous analyses of large data sets of feeding behaviour obtained with broilers it was not
11
12 324 well understood what caused the observed distribution(s) of intervals shorter than the
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14 325 estimated meal criterion (Howie *et al.*, 2009a,b). The hypothesis that disaggregation of data in
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16 326 subsets of intervals in which drinking did or did not occur would assist model fitting proved
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18 327 to be wrong for broilers (Howie *et al.*, 2009a). In the present study we further explored the
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20 328 use of disaggregation of pooled data into subsets, which showed that very short intervals were
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22 329 not recorded between visits to different feeders. It will take more than a few seconds for a bird
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24 330 to leave a feeder and access another one (certainly if adjacent feeders are occupied by other
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26 331 birds), which explains the absence of very short intervals between visits to different feeders. It
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28 332 is not immediately clear, however, what caused the considerable number of very short
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30 333 intervals between visits to the same feeder in broilers and turkeys (Figure 3). A temporary
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32 334 loss of contact between the tag on the bird and the RFI antenna system for certain positions of
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34 335 a bird that remained in a feeder seems a more plausible explanation. Until that is validated
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36 336 (for example by means of video recordings during an experiment), this suggestions remains,
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38 337 however, speculative.
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46 338 In the duck data collection, such very short intervals had already been removed from
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48 339 the data set that was available for analysis, but they occurred only sporadically. This could
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50 340 well have been caused by a difference between feeder systems in the sensitivity of continuous
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52 341 bird identification. In the pooled duck data, log-transformation of interval length suggested
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54 342 that there were three populations of between-feeding intervals (Figure 1). Inspection of
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56 343 individual data showed that one log-normal distribution of short intervals and one log-normal
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58 344 distribution of long day intervals (with a peak between 1 and 2.5 h) occurred in all birds. A
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3 345 proportion of birds, however, showed another clear population (consisting of up to almost half
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5 346 of all intervals) with an intermediate length between approximately 1 and 10 min that was
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7 347 very rare in other birds (Figure 4). This suggested clear individual differences between ducks
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9 348 in the structure of short-term feeding behaviour. A similar individual variation in the number
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11 349 of populations of between-feeding intervals has been observed in cows. (Tolkamp and
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13 350 Kyriazakis, 1999b). Similarly, Zorrilla *et al.* 2005) concluded that in rats meal criteria can
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15 351 only be properly estimated if the occurrence of within-meal drinking pauses is taken into
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17 352 account. Unfortunately, no observations on drinking behaviour were made during data
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19 353 collection with ducks. There may be a number of reasons why within-meal drinking would
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21 354 occur in ducks while there is no evidence that it occurs frequently in broilers (Howie *et al.*,
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23 355 2009a) or turkeys. Ecological differences in the original habitats of the involved species
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25 356 would suggest that dry food (as fed during these experiments) may have been less common in
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27 357 the feeding environment of ducks compared to birds of the other species. There was also a
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29 358 considerable difference between species in feeding rate. Whereas the age and body weight of
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31 359 the ducks overlapped with that of broilers and duck age and weight was certainly lower than
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33 360 that of turkeys (Table 1), ducks showed by far the highest feeding rate. This may well be a
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35 361 direct result of the differences between species in bill-shape. Duck bills are especially suited
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37 362 to scoop up large quantities of dry food pellets in a short period of time, which may have
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39 363 stimulated drinking behaviour during meals. Ducks were also estimated to spend the lowest
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41 364 proportion of total meal time feeding (less than a quarter compared with more than 70% in
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43 365 broilers and turkeys). This would be consistent with part of the ducks using some of the
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45 366 within meal intervals for drinking, which would result in a separate population of intervals for
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47 367 those individuals. Until data on drinking behaviour in relation to feeding in ducks become
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49 368 available for analysis, however, the suggestion we developed here must remain tentative.
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3 370 **Meal patterns**
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5 371 On average, turkeys consumed their daily intake in only half the number of meals compared
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7 372 with broilers and ducks and many of these meals consisted of a single visit only. Because the
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9 373 turkey data were obtained from birds that were more mature than the birds from the other two
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11 374 species, this may not be solely a species effect. Howie *et al.* (2009a; b) observed a trend of
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13 375 fewer and larger meals from electronic feeders in broiler lines as birds increased in age and
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15 376 weight and this will have affected any comparisons of meal patterns across species here. In
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17 377 addition, birds of all species consumed most of their feed during the light period, which was
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19 378 shortest in the experiment involving turkeys. This will have stimulated turkeys to consume
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21 379 their daily intake in a shorter time, which must have resulted in a relatively higher bird
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23 380 pressure per feeder in turkeys compared to other species than suggested by the data in Table
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25 381 1. Such an increase in pressure per feeder may well have contributed to increased visit and
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27 382 meal sizes, as has been observed in other species (Nielsen *et al.*, 1995).
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34 383 In conclusion, the same methodologies can be applied to investigate the feeding
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36 384 behaviour of the three bird species included in this study. The frequency distribution of
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38 385 longer, between-meal, intervals was very similar in broilers, ducks and turkeys. This was a
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40 386 direct result of similar changes in the probability of birds starting to feed with time since last
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42 387 feeding, which could be estimated accurately because very large data sets of feeding
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44 388 behaviour were available for the present study. As a result of this similarity, methods that
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46 389 were developed for the estimation of meal criteria in broilers, based on fitting a truncated log-
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48 390 normal function or on analysis of changes in P_{start} , could be applied to data obtained with
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50 391 turkeys and ducks. This was despite considerable differences between species in the
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52 392 distribution of shorter, that is, within-meal, intervals. Disaggregation of data that were
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54 393 originally pooled across day and night, across all individuals and across visited feeder
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56 394 numbers provided a powerful tool to further the understanding of the structure of short-term
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3 395 feeding behaviour as measured with electronic feeders in the poultry species considered here.
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6 396 This revealed that the feeding behaviour of all three avian species is underpinned by the same
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8 397 principle, that of satiety. The quantitative analysis of such behaviour will not only improve
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10 398 our understanding of the role of hunger and satiety in food intake regulation but could also
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12 399 provide additional traits for selecting the most desirable future genotypes of domestic poultry
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15 400 species.

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4 474 **Figure 1.** *Frequency distributions of (\log_e -transformed) interval lengths between visits to*
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6 475 *feeders recorded with broilers, turkeys and ducks. The top row graphs show plots of the*
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8 476 *frequency distributions of all interval lengths for each species, using a bin-width of 5 min;*
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10 477 *please note the broken Y-axis and the high frequencies for the first bin. The centre row shows*
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12 478 *histograms of all log-transformed lengths of intervals between visits to feeders; bars are the*
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14 479 *observed relative frequencies (bin-width 0.5 \log_e -units). The bottom row shows the frequency*
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16 480 *distribution of \log_e -transformed lengths of intervals between visits after removal of intervals*
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18 481 *that include (part of) the dark period; bars are the observed frequency distribution divided by*
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20 482 *bin-width (0.5 \log_e -units), with solid bars for data to which the truncated probability density*
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22 483 *function (see text) was fitted, shown here in bold lines.*
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32 486 **Figure 2.** *Probability of birds starting to feed within the next 5 min (P_{start}) in relation to the*
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34 487 *time since they fed last for the pooled data of broilers, ducks and turkeys (top row graphs);*
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36 488 *The centre row graphs show the data for the three species pooled across intervals occurring*
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38 489 *during the light period only. Please note the broken Y-axis and the high frequencies for the*
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40 490 *first bins in the top and middle row graphs. The graphs in the bottom row show the species-*
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42 491 *specific P_{start} (within 10 min, to accommodate the lower number of observations) that were*
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44 492 *calculated for groups of 50 birds after data were disaggregated by feeding strategy (Δ = few*
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46 493 *daily meals, \circ = average number of daily meals ∇ = many daily meals and \bullet = data*
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48 494 *combined).*
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4 498 **Figure 3.** *Frequency distributions of pooled log-transformed interval lengths between visits*
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6 499 *to feeders recorded with broilers, turkeys and ducks after deleting intervals that include (part*
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8 500 *of) the dark period (all bin widths 0.5 log_e-units). The graphs show the frequency distributions*
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10 501 *of the pooled log_e-transformed intervals (top row), intervals between visits to the same feeder*
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12 502 *only (centre row) and intervals between visits to different feeders only (bottom row).*

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17 504 **Figure 4.** *Frequency distributions of log_e-transformed intervals between visits to feeders that*
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19 505 *were observed in ducks (bin widths 0.5 log_e-units). Graphs show the distribution of all data*
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21 506 *pooled (left-hand graph) and of data pooled across 48 birds (10% of the total) with a number*
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23 507 *of intervals between 1 and 10 min that, as a proportion of all intervals, was either lowest*
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25 508 *(from 0.01 to 0.04; n = 12,303; centre graph) or highest (from 0.21 to 0.48; n = 22,865;*
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27 509 *right-hand graph).*
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Figure 1

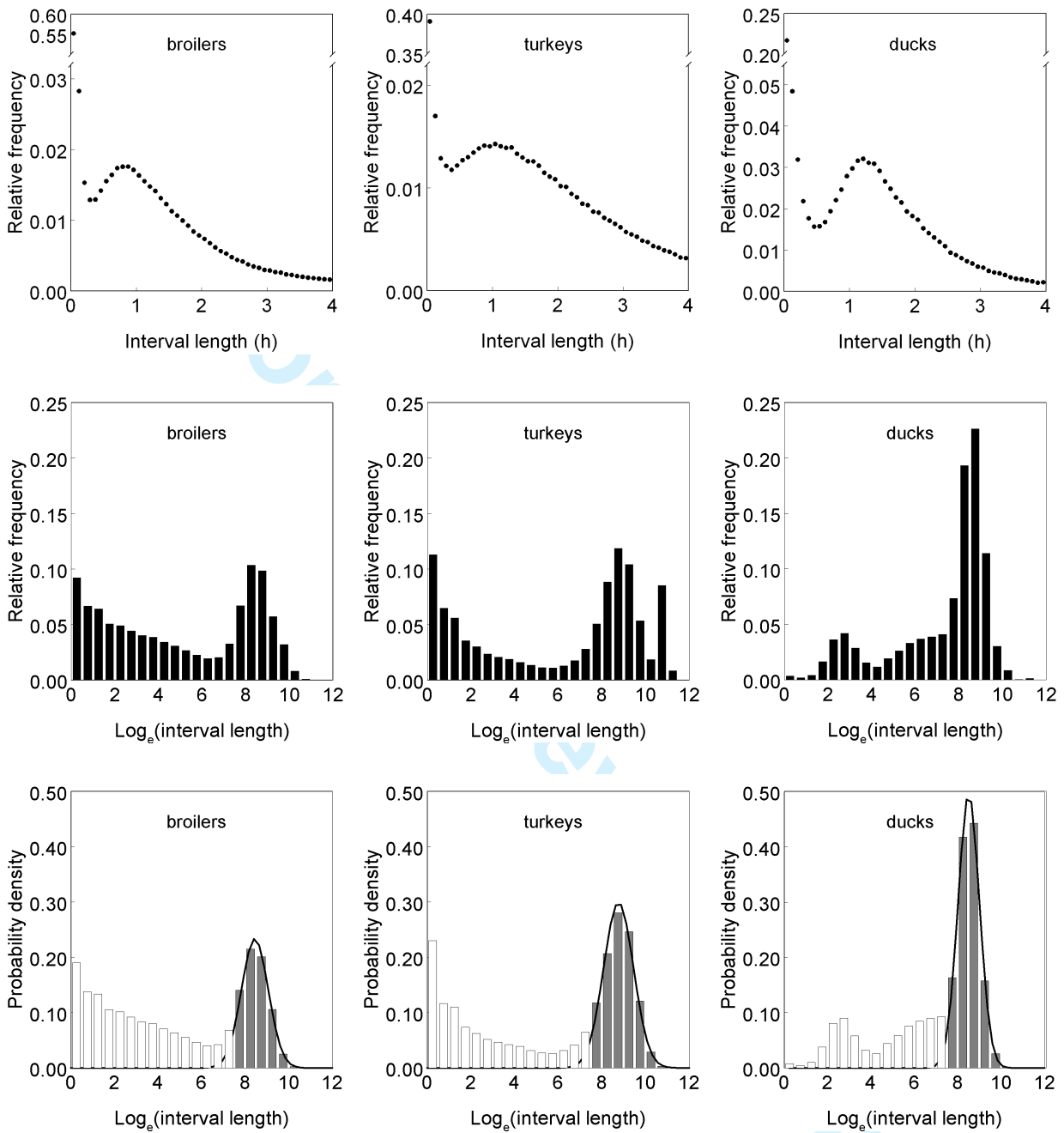


Figure 2

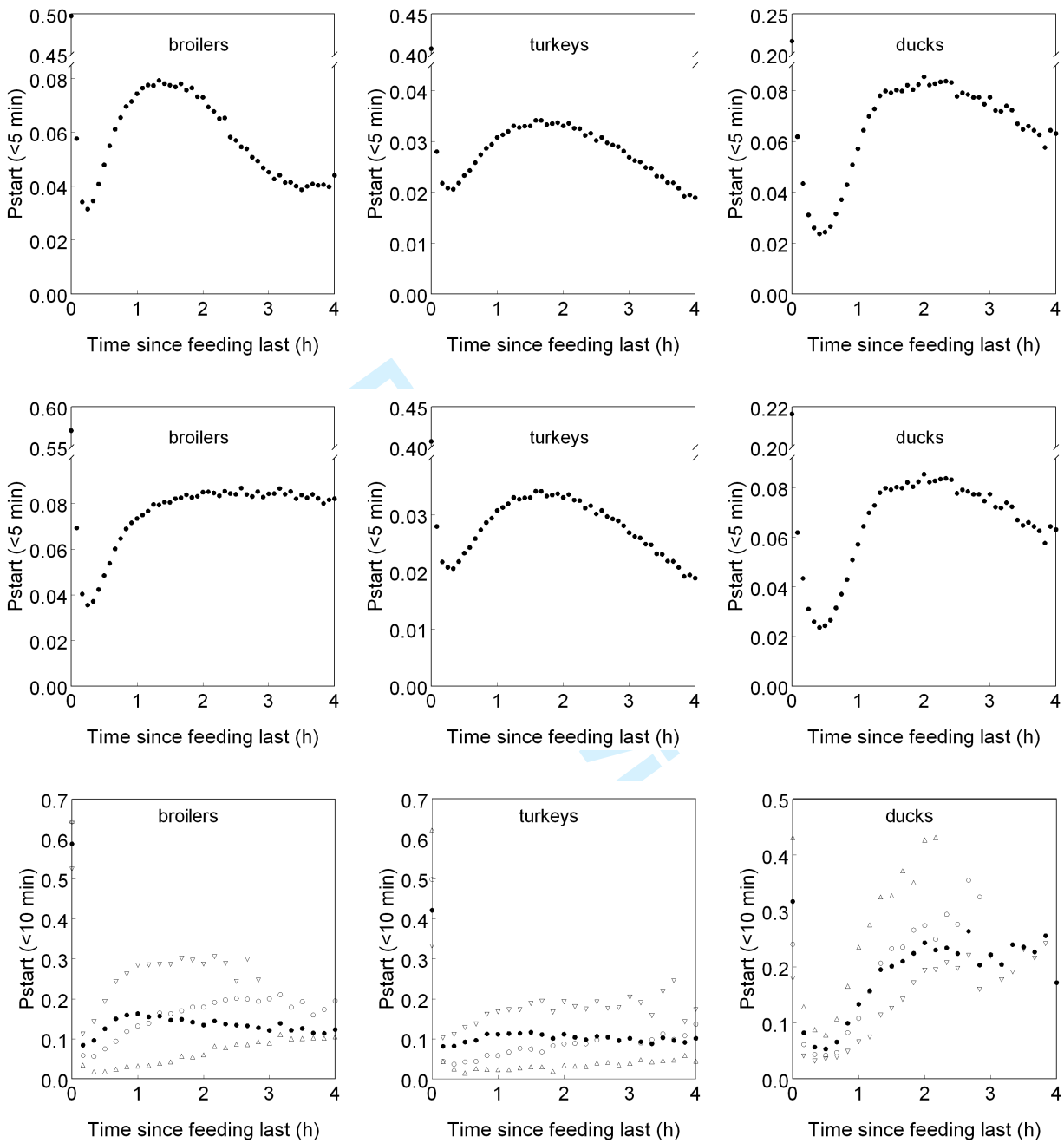


Figure 3

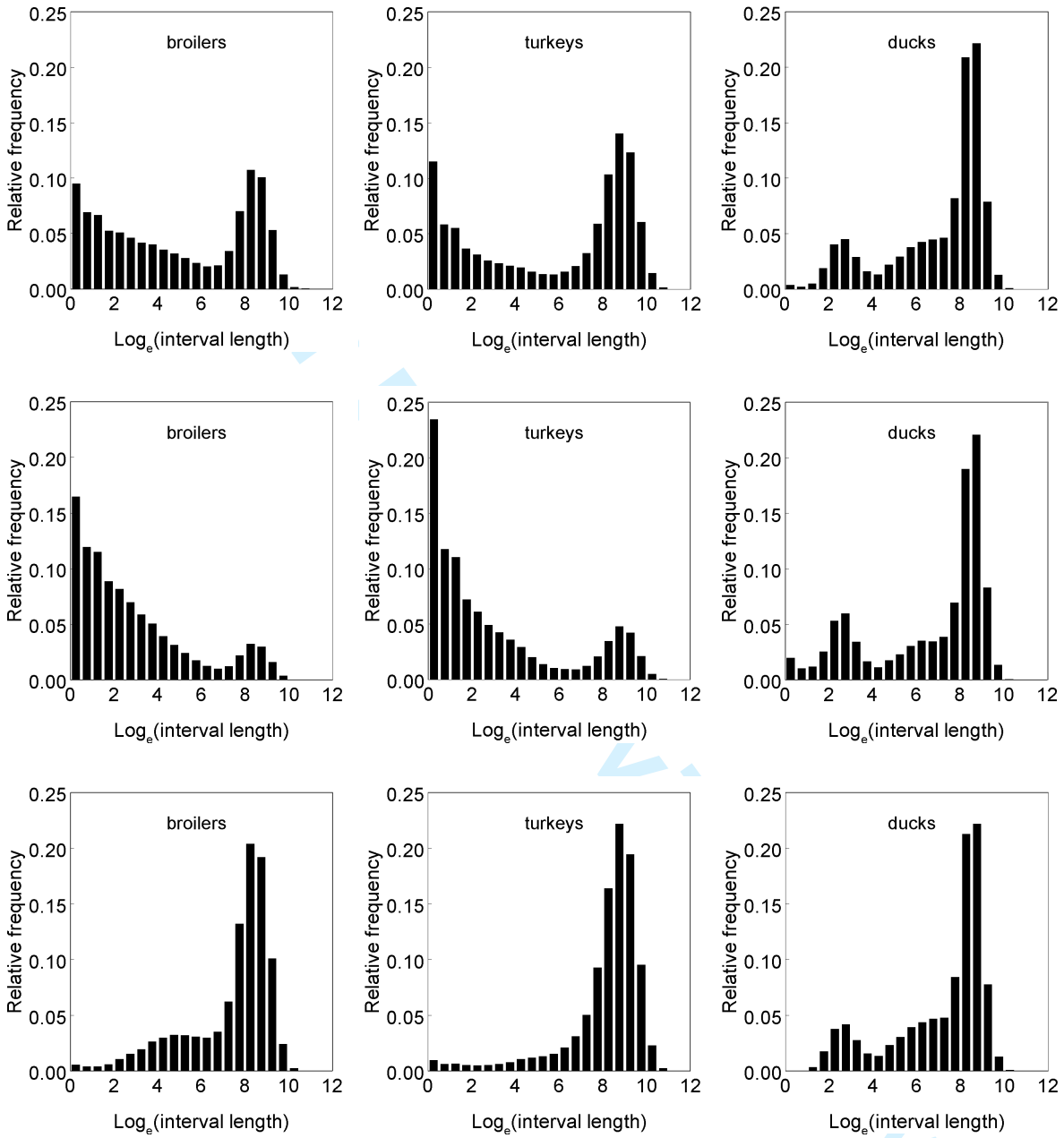
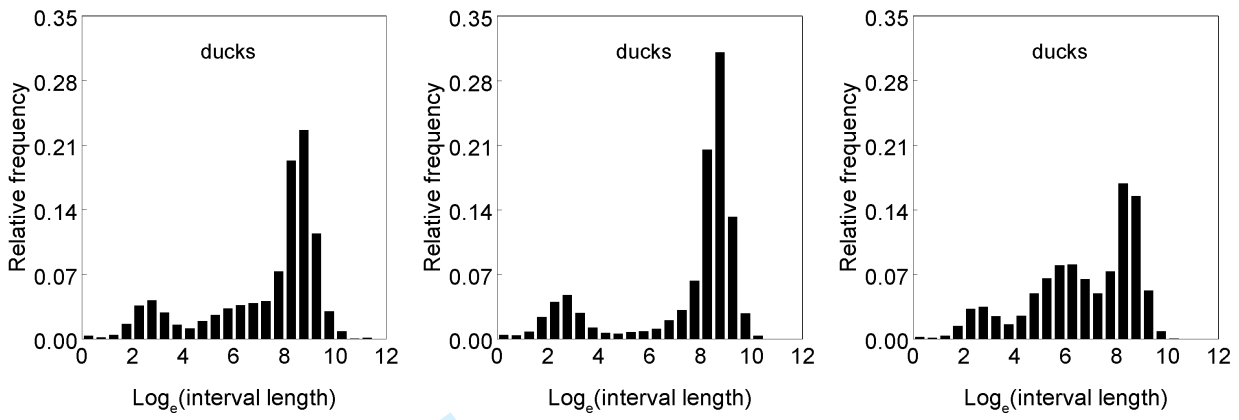


Figure 4



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Table 1. *Details of experimental setup for the collection of short-term feeding behaviour data of the three poultry species.*

	Broilers	Turkeys	Ducks
Total number of recorded visits	1 941 822	851 513	209 309
Total number of birds	3470	3314	480
Bird sex	♀	♂	♀ + ♂
Number of hatches	12	16	1
Bird ages (weeks)	2 to 5	18 to 22	3 to 7
Mean start weight (kg)	0.474	21.67	1.062
Mean end weight (kg)	2.275	26.34	3.033
Pen area (m ²)	8.1	127	32
Mean birds per pen	116	207	160
Birds per feeder	14.5	12.9	10
Lighting regime (h light : h dark)	20:4	14:10	17:7

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3 542 **Table 2.** Summary of mean (\pm standard error) meal characteristics for broilers, ducks and turkeys.

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6 543 Meal criteria were estimated per hatch using the truncated log-normal model.

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	Broilers	Turkeys	Ducks
Meal criterion (s)	1200 \pm 40.4	1320 \pm 78.0	1725
Meals per day	12.2 \pm 0.05	6.2 \pm 0.04	12.2 \pm 0.11
Meal duration (min)	7.38 \pm 0.05	6.47 \pm 0.07	4.02 \pm 0.08
Meal size (g)	12.2 \pm 0.05	140 \pm 0.82	19.31 \pm 0.20
Time spent feeding per meal (min)	5.21 \pm 0.02	5.29 \pm 0.02	0.97 \pm 0.08
Feeding rate (g/min)	2.55 \pm 0.01	30.3 \pm 0.21	20.73 \pm 0.21
Visits per meal	2.43 \pm 0.02	1.87 \pm 0.02	1.53 \pm 0.01
Daily intake (g)	140 \pm 0.26	804 \pm 3.60	227 \pm 1.43
Time spent feeding per day (min)	63.6 \pm 0.13	34.2 \pm 0.18	11.8 \pm 0.17

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