INTESTINAL PASSAGE AND ITS RELATION TO DIGESTIVE PROCESSES

Intestinal passage and digestion

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SUMMARY

Despite an effective nutrient retention , impaired digestibility is frequently observed. This review aims to give an overview of retention time of material through the digestive tract, in an attempt to reveal mechanisms relating flow and retention of material to the digestive process. The mean retention time based on marker content in the different segments of the digestive tract or measured as time of 50 % marker excreted is remarkably short at between 5 and 6 h, but varies considerably due to method used, diet composition and feeding pattern. Mean retention time in the small intestine is commonly reported to be around 3 h, with 1 h retention time in the tract proximal to Meckel's diverticulum, and is less affected by diet or feeding pattern. The mechanisms explaining a high nutrient digestion and absorption despite this astonishingly short time is still a puzzle. A selective flow and reflux of material throughout the small intestine seems to be a potential mechanism, but more research is needed in this important and fascinating area of poultry research.

DESCRIPTION OF THE PROBLEM

A short retention time in the digestive tract is one of the fascinating features of poultry. The short retention time allows for a high feed intake despite the limitations to volume of the digestive system. Although the digestive tract contents of broilers [1] can be estimated to represent more than twice the percentage of body weight compared to e.g. the 91 d old pigs [2], the difference in body weight makes such direct comparisons difficult. McWhorter et al. [3] states that when compared at a similar body weight, birds have a smaller digestive tract volume than mammals.

Despite this short retention time, domesticated birds do not seem to normally be compromising on nutrient digestibility, as digestibility of major nutrients such as fat, protein and starch are not lower in poultry as compared to e.g. pigs. This is particularly fascinating

for the starch fraction of the diet. Starch is the quantitatively most important fraction of the diet, and is largely present as intact starch granules in pelleted diets, which due to their semi-crystalline structure is hard to digest [4]. Starch is usually reported to have an ileal digestibility of more than 95 % in poultry, but a low digestibility has frequently been reported, e.g. of starch due to lack of structural components and/or due to the use of specific cereals such as wheat [5]. In addition to the economic consequences due to loss of nutrients, undigested nutrients may also have other harmful effects, such as being substrates for proliferation of potentially harmful microflora, or by facilitating wet litter problems.

Since retention time is an essential factor in intestinal digestion, this short review will attempt to describe the mechanisms governing the flow of material in the poultry digestive tract, and how this relates to digestive actions in relation to e.g. starch. In addition, knowledge gaps will be presented, as well as some suggestions for future research to fill those gaps. The review, while discussing flow of material in general, will focus on the small intestine, since this is where digestion and absorption mainly takes place. The importance of the crop [6, 7] and the gizzard [8] on digesta flow and digestion have been extensively reviewed previously, and will thus not be discussed in detail here. A very significant and complex flux and reflux processes, and degradation to absorbable nutrients via microbial activity, takes place in the ceca and colon [9], although this is also considered outside the scope of this review.

PASSAGE RATE AND MEAN RETENTION

Although retention time is the nutritionally relevant parameter, passage rate is the reciprocal value and is often measured and used interchangeably as expressions of the same. However, some methods of measuring passage rate are not really related to retention time, but are rather measurements of *minimum* time needed for ingested material to pass. A simple method is to

use an indigestible marker, and record the time needed for this marker to appear in excreta. For simplicity of recording this trait, the intensely red marker ferric oxide (Fe_2O_3) or the green marker chromium oxide (Cr_2O_3) have often been used, where passage rate can be visually determined by recording the time it takes for the conspicious colour of the excreta to appear. Typical minimum passage rates are presented in Table 1, and demonstrates a rather short minimum retention time, averaging close to 3 h. It is worth noting the large variation in values obtained, from less than 1 h to more than 5 h as an average for several birds within the same treatment. Probably, this reflects the inaccuracy of first appearance as a reliable measurement of passage, as will be discussed below.

For a more representative measure of retention time there are chiefly two methods in use, of which one is based on analysis of contents in the digestive tract, and the other is based on analyses of excreta. In the former method, a marker is added to the diet, and after a period of feeding to assure a steady state, where feed intake is also recorded, birds are killed and marker content in different segments of the digestive tract is determined. An estimate of retention time is calculated by dividing the content of marker in each segment with the marker intake per time unit. The method is particularly valuable due to the data often gained on retention time in different segments, but a potential weakness is the assumption of steady intake and flow of material. For example, although birds may eat frequently, data have shown that even ad libitum fed broiler chicken have distinct meals, eating in average twice per hour [21]. If birds are adapted to intermittent feeding, retention time may increase with many hours, since the birds are able to store large quantities in the crop, which will gradually be passed on to subsequent sections of the digestive tract [22].

When excreta is used to measure retention time, a diet without marker is commonly replaced by a diet with marker for a limited amount of time (normally 10 to 30 min), usually after a short feed withdrawal period to stimulate feed intake. Excreta is then collected at timed

intervals (normally at least once per hour for the first 8-10 h), and analysed for marker content. Feed intake of the diet with marker is also recorded. This method will measure total tract retention time based on passage of a major quantity of marker, with mean retention time usually measured as time of 50 % marker excretion (t50), or as mean retention time based on the product of marker excreted and time for passage, relative to total amounts of marker excreted (MRT). However, the feed withdrawal period prior to measurement may be a limitation if it is considerable, as a long feed deprivation time may affect passage rate, as will be discussed below. Alternatively, a marker can be provided directly to the birds, e.g. through a gelatine capsule, thus forsaking the need for a feed withdrawal period. In Table 2, retention times using the steady state or t50 method are presented.

As shown in Table 2, when Steady state or t50 were used as methods, the total tract retention time averaged slightly more than 5.5 h, which is a considerably longer time and with less variation than observed when minimum retention time is measured. Thus, first appearance is not a representative measure of retention time.

FACTORS AFFECTING RETENTION TIME

As discussed, mean retention time and not first appearance of marker in excreta, must be calculated to give a representative picture of retention time. However, measurements of mean retention time (MRT) using the equation of Coombe and Kay [34] is often reported to be much higher than the values presented in Table 2. Almirall and Esteve-Garcia [24] found twice as high mean retention times when measured using this method as compared to when t50 was used as a method, and Adeleye et al. [33] and Lázaro et al. [27] found values to be three times as high when MRT was calculated compared to t50. Duve et al. [31] also found MRT to be higher than t50, although here the retention time was only approximately 50 %

higher. Rochell et al. [32], however, only found a small increase in calculated retention time when MRT was used. The explanation for this large difference in observed values can be found in the method used to calculate retention time. The t50 method is based on the time when 50 % of the marker is excreted, and thus is based on the passage of the first 50 % of the marker, without the need to fully take the fate of the remaining marker into consideration. This would have given a valid estimate of mean retention time if marker flow followed a steady state over time, but this is not necessarily the case. The remaining fraction of the marker after 50 % of the marker has passed often stays in the digestive tract far longer than the first part. Thus, when retention time of this fraction is taken into consideration, the calculated mean retention time may become significantly longer. It is in this respect interesting to note that the small difference in values for t50 and MRT observed by Rochell et al. [32] was due to a very short collection period of only 12 h, as compared to the additional collections at 24, 36 and 48 h in the other studies. The smaller difference between t50 and MRT observed by Duve et al. [31] can likewise be explained by the fact that excreta was only collected for 24 h in this study.

In addition to the potential retention time in the crop as already mentioned, a significant cause for an uneven passage time of the marker is the extent to which material passes into the ceca, as material entering the ceca can remain there for at least 48 h [9]. It is in this respect interesting to note that Liu et al. [35] observed that it took 4 h for the marker to appear in the ceca after feeding. This indicates that the first passage will not be influenced by ceca retention. A potentially even more serious flaw in the calculation based on the method of Coombe and Kay [34], would be if all the material collected at 24, 36 and 48 h were dealt with mathematically as if they were all excreted during these times, while they in fact were excreted up to 12 h earlier. Coombe and Kay [34] corrected for this by using the mean time between collections as a measure of time, but it is uncertain whether this important principle

was followed in the work reported here, and anyway, it is logical to assume that excretion decreases over time, and thus that the mean passage rate would be less than this figure. Thus, this potential flaw in this calculation method and the fact that retention in the ceca may not be relevant to the extent to which potentially digestible nutrients may be digested (since the material has already passed the small intestine at this point), estimates of retention time based on MRT may not be relevant. In other words, retention time should be based on t50, and not on the method described by Coombe and Kay [34].

Another factor affecting results of measurements is the behaviour of the marker. When Rougiere and Carre [30] compared the use of a titanium marker (TiO_2) with the use of Cr-mordanted hay, the estimated retention time increased significantly, and in some cases to the double. Vergara et al. [36] also found that soluble Cr-EDTA passed much faster than insoluble Cr-mordanted rice hulls, and that a longer retention time in the gizzard was the major reason for this difference. This is related to the fact that large fibre particles are retained for a prolonged period in the gizzard, as demonstrated by Hetland et al. [37]. The particle size of the mordanted hay may thus be of importance, as retention of particles in the gizzard is related to size of the particles. Thus, the lack of difference in passage of Cr-mordanted hay and Cr-EDTA observed by Rodgers et al. [38] could be due to the fact that the hay was ground to a fine powder in this experiment. Retention time in the gizzard therefore will potentially have a significant influence on total tract retention time. In addition to particle size of the dissolved feed material, pelleting and other feed processing manipulations may also have an effect, either indirectly through affecting feed intake, or directly through particle reduction effects [8], but these topics are considered outside the scope of this review.

The above illustrates a very important principle, which is that the flow of materials through the digestive tract is not even for all components of the diet, even when passage through the tract anterior to the ileo-ceco-colonic junction only, is considered. Thus, the measurement of

retention time is related to the specific behaviour of the indigestible component assessed, and not necessarily to the passage of the ingested feed as a whole. While Cr-EDTA may pass particularly fast, and Cr-mordanted fiber may pass particularly slowly, the insoluble but fine particles in the form of TiO_2 or Cr_2O_3 seem to pass at rather similar rates.

The large difference in passage rate of different fractions of the ingested material is illustrated elegantly when considering experimental data where birds have been starved to empty the digestive tract, and thereafter refed and killed at different times to quantify contents in various parts of the digestive tract. Doing so, it has been demonstrated that the part of the feed with the fastest passage will be found in the small intestine already within 25 min of commencement of feeding [39]. Svihus et al. [40] even demonstrated that the jejunum was full and operating at maximum capacity 30 min after feeding, as indicated by the fact that marker content in the jejunum did not increase over time after 30 min. Such a rapid passage would indicate literally no retention time in the anterior digestive tract. For the crop, this is not surprising, as Chaplin et al. [41] clearly established the important principle that material will bypass the crop when the gizzard is not full. In addition, there are no significant digestion processes taking place in the crop, and thus it would be logical to bypass the crop in such a situation. For the gizzard, however, this rapid passage is surprising, since retention time in the gizzard is important for the digestive processes taking place there. As already discussed, a selective retention is taking place in the gizzard. Thus, although experimental data is lacking, it is logical to assume that the material which bypasses the gizzard is the most finely ground fraction of the feed, where there is no need for further grinding in the gizzard. However, the lack of time for chemical degradation through hydrochloric acid and pepsin is puzzling. A rapid passage of material into the small intestine is neither dependent on using starved birds. Svihus et al. [17] gave broiler chickens a capsule containing Cr_2O_3 without feed withdrawal, and found that a majority of the marker had passed into the small intestine within

45 min, without any considerable differences in marker content in the jejunum and the ileum. Slightly slower passage rates were observed by Liu et al. [35], when a contrast agent were added without prior feed withdrawal, and the exposed digestive tract were assessed by x-ray scanning. In this experiment, no significant amounts were observed in the ileum before after 1 h. Interestingly, no marker was detected in the small intestine after 15 min in this experiment, but large amounts were observed in the jejunum after 30 min. Also Vergara et al. [36] found extremely fast passage into the small intestine even for ad libitum fed birds. When the soluble marker Cr-EDTA was administered using a capsule, 22 % of the marker had entered the small intestine already after 5 min.

Thus, as the above discussion has demonstrated, the passage of material through the digestive tract is not even, but varies due to selective retention in different segments, which again is affected by both physical characteristics of components in the feed and the feeding pattern. For example, the above seems to indicate a mechanism where material is rapidly passed into the small intestine when this segment is not full, possibly to maximize the digestive processes to compensate for a short retention time.

In addition to the experimental implications, such as being aware of that nutrient digestibility values obtained by the use of markers assumes that the nutrient and the marker has a similar passage pattern, this fact also has implications for understanding the interaction of intestinal retention time and the digestion process, as will be discussed in the next section.

RETENTION TIME IN THE SMALL INTESTINE

A pertinent question is the time available for digestion in the small intestine. This is obviously related to retention time in this segment, and this important question has been assessed in several experiments where birds have been killed and dissected following marker administration. Some results from such assessments are summarized in Table 3 below.

As Table 3 shows, retention time in the jejunum is most commonly reported to be around 1 h, although some authors report up to 2 h retention time. Retention time in the ileum is longer than retention time in the jejunum, often approaching 2 h or more. Although the weight of the jejunum is higher than the ileum [30, 38]) and the holding capacity of the ileum is smaller than the jejunum [1, 22], a longer retention time in the ileum is a logical consequence of the reduced amount of digestible components, which will allow for a slower flow. A retention time in the small intestine of about 3 h fits well with studies of flow of material through the small intestine, carried out by timed killing of birds after feeding a marker [40, 35].

Surprisingly, retention time seems to be rather insensitive to a number of factors assumed to have an important role. In the publications presented in Table 3, a number of different diets and fasting times have been used, although no clear pattern seems to be apparent in regards to small intestinal retention time. As already discussed, retention in the crop due to intermittent feeding or retention in the gizzard due to structure can affect total tract retention time, but passage through the small intestine seems to be rather insensitive to diet or feeding manipulations.

THE RELATION BETWEEN RETENTION TIME AND DIGESIVE FUNCTION

With 3 h retention time in the small intestine, this means that the digestion process must be completed and nutrients must have been absorbed within that short time period. However, since the digestive and absorptive capacity is not considered to be equal throughout the small intestine, the effective time available could be shorter. It is well established that the anterior digestive tract is very active in digestion and absorption. Since the retention time in the duodenum is reported to be only a few min [42, 43, 44, 26, 29], the quantitative effect of the duodenum would be thought to be limited. However, Sklan et al. [48], reported that 95 % of

241 the fat was enzymatically degraded by the end of this segment, and Riesenfeld et al. [49]
242 concluded that the duodenum was the major site for starch degradation and glucose
243 absorption. Zimonja and Svihus [50] found that between 30 and 70 % of the starch had been
244 digested and absorbed in the duodenum, and Gutierrez de Alamo et al. [45, 46] found that
245 around 50 % of the starch had been digested by the proximal jejunum.

246 Although no comparative studies surprisingly have been found, e.g. whether the amylase
247 secreted by the chicken is particularly effective in digesting starch, a particularly effective
248 system for digestion and absorption of nutrients would be thought to be an important cause
249 for a high digestibility despite a short retention time.

250 Although no histologically distinct segments exist posterior to the duodenum, the remainder
251 of the digestive tract is conveniently divided into the jejunum and ileum using the remnant of
252 the yolk sac (Meckels diverticulum) as a demarcation. The length of the villi, however,
253 decreases throughout the small intestine [51], indicating reduced digestive capacity as the
254 digesta passes down the intestine. Thus, the duodenum and the jejunum are obviously the
255 most important sites for digestion and absorption, where a large majority, usually reported to
256 be higher than 75 %, of the starch is digested and absorbed [49, 52, 45, 46, 50]. The retention
257 time of perhaps 1 h in these segments taken into consideration, this high rate of digestion is
258 truly remarkable. Even more remarkable is the fact that the mechanisms governing this high
259 rate of digestion and absorption within a very short time is still poorly understood, as
260 discussed in a previous review [53]. The issue of a high digestion rate despite a low retention
261 time was also discussed extensively by McWhorter et al. [3]. A high paracellular absorption
262 was presented as one possible contributing factor, although it was pointed out that more
263 research is needed in this fascinating and important area.

As already discussed, the retention time in the small intestine posterior to Meckels diverticulum is longer than in the jejunum, and thus could contribute significantly to the digestion and absorption process, although the extent to which this segment of the digestive tract is able to digest and absorb nutrients has been questioned [54]. As there are villi below Meckels diverticulum as discussed above, this at least partly can explain the significant starch digestion taking place posterior to Meckels diverticulum [49, 50]. Ferrer et al. [55] even found the lower ileum, defined as the segment of the ileum attached to the ceca, to be able to absorb glucose, although the capacity was lower than more anterior segments. Gutierrez de Alamo et al. [45, 46] assessed starch digestibility in the proximal and distal portions of the jejunum and the ileum, and demonstrated that although half the starch was digested by the proximal jejunum, considerable amounts of starch was digested in the distal jejunum and the proximal ileum. However, little further digestion took place at the distal ileum. A similar pattern was observed for protein, although only a small part of the protein was digested by the proximal jejunum. These observations indicate that little digestion takes place in the distal ileum. However, the cause for this could simply be that the remaining part of the diet reaching the distal ileum is not digestible. It is in this respect interesting that Yamauchi [56], in his review of own and other's work on functionality of the small intestine, noted that when the jejunum was resected, the ileum resumed a considerable digestive and absorptive capacity, resulting in normal digestion in the resected birds. Thus, it is possible that a large part of the ileum is able to take part in digestion and absorption if needed.

As discussed above, material may pass very rapidly into the small intestine. Sacranie et al. [22] starved birds for 16 h to empty the digestive tract, and observed that within 1 h of refeeding, both the jejunum and the ileum (using Meckels diverticulum as demarcation) contained its maximum content of DM. Equally fascinating, the starch content in the ileum was very high after 1 h of feeding, and slowly levelled off during the subsequent hours. In

289 fact, the content of the ileum contained more than 30 % starch 1 h after refeeding for the diet
290 which contained no gizzard-stimulating structural components. Although starch digestion
291 may take place in the ileum as already discussed, another mechanism facilitating digestion in
292 this situation is reflux. Clench and Mathias [57] observed a unique mechanism of contraction
293 throughout the small intestine in starved chickens, with about one-third of these being
294 refluxing contractions. Thus, Basha and Duke [58] demonstrated a considerable reflux of
295 material from as far as the proximal ileum to the duodenum and gizzard. Although these
296 refluxes were observed during starvation, they also seem to be taking place during normal
297 feeding. Sacranie et al. [59] injected a marker into the cloaca of intermittently and ad libitum
298 fed broiler chickens, and 2 h later found significant quantities of this marker throughout the
299 small intestine and in the gizzard, without significant differences between feeding regimes.
300 Although these data need to be confirmed in further experiments, they demonstrate a
301 considerable reflux throughout the digestive tract. In recent unpublished research from our
302 lab, very little starch was observed to be excreted despite a rather high starch content in the
303 ileum within 1 h after refeeding starved broiler chickens. Reflux seems to be a plausible
304 mechanism explaining this effect. Thus, the surprisingly high digestion rates observed in the
305 proximal jejunum and even in the duodenum as discussed above, may be due to the fact that
306 this section of the digestive tract contains significant amounts of digesta refluxed from the
307 ileum. However, if reflux is indeed an important process taking place even in high-
308 performing birds, a mechanism of selective retention would be necessary to avoid a negative
309 effect of reflux on feed intake, which needs to be high in these birds. Studies needs to be
310 undertaken to study e.g. whether large fibrous particles are passing fast and without being
311 refluxed, while e.g. starch granules are retained and even refluxed until digested.

From the above, a logical conclusion seems to be that the whole small intestinal tract is involved in digestion and absorption, and that reflux mechanisms may contribute further to an effective digestion process despite a short retention time.

CONCLUSIONS AND APPLICATIONS

1. The retention time in the digestive tract of poultry is remarkably short, averaging between 5 and 6 h.
2. The retention time in the small intestine is usually around 3 h, of which 1 h is in the duodenum and jejunum.
3. While total tract retention time will be affected by feeding system and the extent to which material enters the caeca, the average retention time in the small intestine seems to be much less affected by such factors.
4. Selective rapid passage of material from the gizzard to the small intestine seems to be an important mechanism which may increase digestion capacity when time available for digestion is a limited factor.
5. Reflux of material from the distal to the proximal small intestine is another mechanism which could contribute to increased digestive capacity, although this hypothesis needs experimental substantiation.
6. More research is certainly needed to understand the high digestion capacity despite a short retention time, which is a hallmark trait of our successful commercial bird species.

REFERENCES AND NOTES

1. Hetland, H., and B. Svihus. 2001. Effect of oat hulls on performance, gut capacity and feed passage time in broiler chickens. Br. Poult. Sci. 42: 354-361.
2. Overholt, M. F., J. E. Lowell, E. K. Arkfeld, I. M. Grossman, H. H. Stein, A. C. Dilger and D. D. Boler. 2016. Effects of pelleting diets without or with distillers' dried grains with solubles on growth performance, carcass characteristics, and gastrointestinal weights of growing–finishing barrows and gilts. J. Anim. Sci. 94:2172-2183.
3. McWhorter, T. J., E. Caviedes-Vidal and W. H. Karasov. 2009. The integration of digestion and osmoregulation in the avian gut. Biol. Rev. 84:533-565
4. Svihus, B., A. K. Uhlen, and O. M. Harstad. 2005. Effect of starch granule structure, associated components and processing on nutritive value of cereal starch: A review. Anim. Feed Sci. Technol. 122: 303-320.
5. Svihus, B. 2011. Limitations to wheat starch digestion in growing broiler chickens: a brief review. Anim. Prod. Sci. 51:583–589.
6. Classen, H. L., J. Apajalahti, B. Svihus and M. Choct. 2016. The role of the crop in poultry production. World's Poult. Sci. J. 72:459-472.
7. Kieronczyk, B., M. Rawski, J. Dlugosz, S. Swiatkiewicz and D. Jozefiak. 2016. Avian crop function – a review. Ann. Anim. Sci. 16:653-678.
8. Svihus, B. 2011. The gizzard: function, influence of diet structure and effects on nutrient availability. Worlds Poult. Sci. J. 67: 207-223
9. Svihus, B., M. Choct and H. L. Classen. 2013. Function and nutritional roles of the avian caeca: a review. World's Poult. Sci. J. 69:249-263.
10. Washburn, K.W. 1991. Efficiency of feed utilization and rate of feed passage through the digestive system. Poult. Sci. 70:447-451.

11. Barash, I., Z. Nitsan, and I. Nir. 1992. Metabolic and behavioural adaptation of light-bodied chicks to meal feeding. Br. Poult. Sci. 33: 271-278.
12. Buyse, J., D. S. Adelsohn, E. Decuypere, and C. G. Scanes. 1993. Diurnal-nocturnal changes in food intake, gut storage of ingesta, food transit time and metabolism in growing broiler chickens: a model for temporal control of energy intake. Br. Poult. Sci. 34: 699-709.
13. Ritz, C. W., R. M. Hulet, B. B. Self and D. M. Denbow. 1995. Effects of protein level and enzyme supplementation upon growth and rate of digesta passage of male turkeys. Poult. Sci. 74:1323-1328.
14. Son, J. H., Y. Karasawa and K. H. Nahm. 2000. Effect of caecectomy on growth, moisture in excreta, gastrointestinal passage time and uric acid excretion in growing chicks. Br. Poult. Sci. 41:72-74.
15. Amerah, A. M., V. Ravindran, R. G. Lentle, and D. G. Thomas. 2008. Influence of feed particle size on the performance, energy utilization, digestive tract development, and digesta parameters of broiler starters fed wheat- and corn-based diets. Poult. Sci. 87: 2320-2328.
16. Hughes, R. J. 2008. Relationship between digesta transit time and apparent metabolisable energy value of wheat in chickens. Br. Poult. Sci. 49:716-720.
17. Svihus, B., A. Sacranie, V. Denstadli, and M. Choct. 2010. Nutrient utilization and functionality of the anterior digestive tract caused by intermittent feeding and inclusion of whole wheat in diets for broiler chickens Poult. Sci. 89: 2617-2625.
18. Kim, J. H., S. Seo, C. H. Kim, J. W. Kim, B. B. Lee, G. I. Lee, H. S. Shin, M. C. Kim and D. Y. Kil. 2013. Effect of dietary supplementation of crude glycerol or tallow on intestinal transit time and utilization of energy and nutrients in diets fed to broiler chickens. Livest. Sci. 154:165-168.

19. Yamanaga, M. and M. Furuse. 2014. Preference and passage through the gastrointestinal tract of paddy rice in young chicks. J. Poult. Sci. 51:47-51.
20. dos Santos, T. T., H. V. M. O'Neill, G. Gonzalez-Ortiz, D. Camacho-Fernandez and C. Lopez-Coello. 2017. Xylanase, protease and superdosing phytase interactions in broiler performance, carcass yield and digesta transit time. Anim. Nutri. 3:121-126.
21. Svihus, B., V. B. Lund, B. Borjgen, M. R. Bedford, and M. Bakken. 2013. Effect of intermittent feeding, structural components and phytase on performance and behaviour of broiler chickens. Br. Poult. Sci. 54: 222-230.
22. Sacranie, A., X. Adiya, L. T. Mydland and B. Svihus. 2017. Effect of intermittent feeding and oat hulls to improve phytase efficacy and digestive function in broiler chickens. Br. Poult. Sci. 58:442-451.
23. Salih, M. E., H. M. Classen and G. L. Campbell. 1991. Response of chickens fed on hull-less barley to dietary β-glucanase at different ages. Anim. Feed Sci. Technol. 33:139-149.
24. Almirall, M. and E. Esteve-Garcia. 1994. Rate of passage of barley diets with chromium oxide: Influence of age and poultry strain and effect of β-glucanase supplementation. Poultry Science 73:1433-1440.
25. Dänicke, S., O. Simon, H. Jeroch and M. Bedford. 1997. Interactions between dietary fat type and xylanase supplementation when rye-based diets are fed to broiler chickens. 1. physicochemical chyme features. Br. Poult. Sci. 38:537-545.
26. Dänicke, S., W. Vahjen, O. Simon, and H. Jeroch. 1999. Effects of dietary fat type and xylanase supplementation to rye-based broiler diets on selected bacterial groups adhering to the intestinal epithelium, on transit time of feed, and on nutrient digestibility. Poult. Sci. 78: 1292-1299.

27. Lázaro, R., M. Garcia, P. Medel and G. G. Mateos. 2003. Influence of enzymes on performance and digestive parameters of broilers fed rye-based diets. Poult. Sci. 82:132-140.
28. Sieo, C. C., N. Abdullah, W. S. Tan and Y. W. Ho. 2005. Influence of β-glucanase-producing *Lactobacillus* strains on intestinal characteristics and feed passage rate of broiler chickens. Poult. Sci. 84:734-741.
29. Chee, S. H., P.A. Iji , M. Choct , L.L. Mikkelsen and A. Kocher. 2010. Functional interactions of manno-oligosaccharides with dietary threonine in chicken gastrointestinal tract. III. Feed passage rate. Br. Poult. Sci. 51:677-685.
30. Rougiere, N., and B. Carré. 2010. Comparison of gastrointestinal transit times between chickens from D+ and D- genetic lines selected for divergent digestion efficiency. Animal 4: 1861-1872.
31. Duve, L. R., S. Steenfeldt, K. Thodberg and B.L. Nielsen. 2011. Splitting the scotoperiod: effects on feeding behaviour, intestinal fill and digestive transit time in broiler chickens. Br. Poult. Sci. 52:1-10.
32. Rochell, S. J., T. J. Applegate, E. J. Kim, and W. A. Dozier III. 2012. Effects of diet type and ingredient composition on rate of passage and apparent ileal amino acid digestibility in broiler chicks. Poult. Sci. 91:1647-1653.
33. Adeleye, O. O., A. D. Ologhobo and B. T. Oje-Adetule. 2016. Influence of carbohydrate source on digesta kinetics and postprandial glucose responses of broiler chicks. Livst. Sci. 188:37-42.
34. Coombe, J. B. and R. N. B. Kay. 1965. Passage of digesta through the intestines of the sheep. Br. J. Nutr. 19:325-338.

35. Liu, J. D., S. A. Secrest and J. Fowler. 2017. Computed tomographic precision rate-of-passage assay without a fasting period in broilers: More precise foundation for targeting the releasing time of encapsulated products. Livest. Sci. 200:60-63.
36. Vergara, P., C. Ferrando, M. Jimenez, E. Fernandez and E. Gonalons. 1989. Factors determining gastrointestinal transit time of several markers in the domestic fowl. Quart. J. Exp. Physiol. 74:867-874.
37. Hetland. H., B. Svihus, and M. Choct. 2005. Role of insoluble fibre on gizzard activity in layers. J. Appl. Poult. Res. 14: 38-46.
38. Rodgers, N. J., M. Choct, H. Hetland, F. Sundby, and B. Svihus. 2012. Extent and method of grinding of sorghum prior to inclusion in complete pelleted broiler chicken diets affects broiler gut development and performance. Anim. Feed Sci. Technol. 171: 60-67.
39. Jackson, S. and G. E. Duke. 1995. Intestine fullness influences feeding behaviour and crop filling in the domestic turkey. Phys. Behav. 58:1027-1034.
40. Svihus, B., H. Hetland, M. Choct, and F. Sundby. 2002. Passage rate through the anterior digestive tract of broiler chickens fed on diets with ground or whole wheat. Br. Poult. Sci. 43: 662-668.
41. Chaplin, S. B., J. Raven, and G. E. Duke. 1992. The influence of the stomach on crop function and feeding-behavior in domestic turkeys. Physiol. Behav. 52: 261-266.
42. Shires, A., J. R. Thompson, B. V. Turner, P. M. Kennedy, and Y. K. Goh. 1987. Rate of passage of canola meal and corn-soybean meal diets through the gastrointestinal tract of broiler and white leghorn chickens. Poult. Sci. 66: 289-298.
43. van der Klis, J. D., M. W. A. Verstegen, and W. de Wit. 1990. Absorption of minerals and retention time of dry matter in the gastrointestinal tract of broilers. Poult. Sci. 69: 2185-2194.

456 44. Noy, Y., and D. Sklan. 1995. Digestion and absorption in the young chick. Poult. Sci.
457 74: 366-373.
458 45. Gutiérrez del Álamo, A., P. Pérez de Ayala, L. A. Den Hartog, M. W. A. Verstegen
459 and M. J. Villamide. 2009a. Wheat starch digestion rate in broiler chickens is affected
460 by cultivar but not by wheat crop nitrogen fertilisation. Br. Poult. Sci. 50:341-349.
461 46. Gutiérrez del Álamo, M. W. A. Verstegen, L. A. Den Hartog, P. Pérez de Ayala and
462 M. J. Villamide. 2009b. Wheat starch digestion rate affects broiler performance.
463 Poult. Sci. 88:1666-1675.
464 47. Sydenham, C. J., H. H. Truong, A. F. Moss, P. H. Selle and S. Y. Liu. 2017. Fishmeal
465 and maize starch inclusions in sorghum-soybean meal diets generate different
466 esponses in growth performance, nutrient utilisation, starch and protein digestive
467 dynamics of broiler chickens. Anim. Feed Sci. Technol. 227:32-41.
468 48. Sklan, D., S. Hurwitz, P. Budowski, and I. Ascarelli. 1975. Fat digestion and
469 absorption in chicks fed raw or heated soybean meal. J. Nutr. 105: 57-63.
470 49. Riesenfeld, G., D. Sklan, A. Bar, U. Eisner, and S. Hurwitz. 1980. Glucose absorption
471 and starch digestion in the intestine of the chicken. J. Nutr. 110: 117-121.
472 50. Zimonja, O., and B. Svihus. 2009. Effects of processing of wheat or oat starch on
473 technical pellet quality and nutritional value for broilers. Anim. Feed Sci. Technol.
474 149: 287-297.
475 51. de Verdal, H., S. Mignon-Grasteau, C. Jeulin, E. Le Bihan-Duval, M. Leconte, S.
476 Mallet, C. Martin and A. Narcy. 2010. Digestive tract measurements and histological
477 adaptation in broiler lines divergently selected for digestive efficiency. Poult. Sci.
478 89:1955-1961.

52. Zimonja, O., A. Stevnebo and B. Svihus. 2007. Nutritional value of diets for broiler chickens as affected by fat source, amylose level and diet processing. Can. J. Anim. Sci. 87:553-562.
53. Svihus, B. 2014. Function of the digestive system. J. Appl. Poult. Sci. 23:306-314.
54. Osman, A. M. 1982. Amylase in chicken intestine and pancreas. Comp. Biochem. Physiol. 73B:571-574.
55. Ferrer, R., M. Gil, M. Moreto, M. Oliveras and J. M. Planas. 1994. Hexose transport across the apical and basolateral membrane of enterocytes from different regions of the chicken intestine. Plügers Arch. 426:83-88.
56. Yamauchi, K. 2007. Review of a histological intestinal approach to assessing the intestinal function in chickens and pigs. Anim. Sci. J. 78:356-370.
57. Clench, M. H. and J. R. Mathias. 1992. A complex avian intestinal motility response to fasting. Am. J. Physiol. 262:G498-G504.
58. Basha, M. E. and G. E. Duke. 1999. Effect of fasting on small intestinal antiperistalsis in the Nicholas turkey (*Meleagris gallopavo*). J. Exp. Zool. 283:469-477.
59. Sacranie, A., B. Svihus, V. Denstadli, B. Moen, P. A. Iji, and M. Choct. 2012. The effect of insoluble fiber and intermittent feeding on gizzard development, gut motility, and performance of broiler chickens. Poult. Sci. 91: 693-700.

502 Table 1. Typical passage rates (min) based on timed feeding and visual observation of first
503 appearance of marker in excreta. All values presented are averages for a treatment with
504 replicates.

Method used	Species and age	Minimum	Maximum	Average	Reference
12 h feed withdrawal, fluorescent dye in capsule	Broilers, 28-56 d	166	267	200	[10]
Fe_2O_3 in diet	Layer chicks, 25 d	Approx. 240	Approx. 240	Approx. 240	[11]
Fe_2O_3 and Cr_2O_3 in diet	Broilers, 28 d	173	215	192	[12]
Fe_2O_3 in capsule	Turkey, 7, 14, 21 and 28 d	98	161	136	[13]
24 h feed withdrawal, Cr_2O_3 in diet	Layers, approx. 20 d	114	130	122	[14]
2 h feed withdrawal, Cr_2O_3 in diet	Broilers, 15 d	136	142	139	[15]

Fe_2O_3 in capsule	Broilers, 26 d			206	[16]
Fe_2O_3 in capsule	Broilers, 24 d	218	253	232	[17]
Cr_2O_3 and Fe_2O_3 in diet	Broilers, 26-31 d	112	137	123	[18]
Red dye in diet	Layers, 8-9 d	50	220	120	[19]
30 min feed withdrawal, Fe_2O_3 in diet	Broilers, 21, 28, 35, 42 d	149	339	237	[20]
Average				177	

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516 Table 2. Typical total tract retention times (min) observed assuming steady state flow of diet
517 and analysis of marker content in the digestive tract (Steady state), or cumulative excretion
518 and time of 50 % marker excretion (t50). All values presented are averages for a treatment
519 with replicates.

Method used	Species and age	Minimum	Maximum	Average	Reference
2 h feed withdrawal, Cr_2O_3 in diet, t50	Broilers, 14, 28, 42 and 56 d	359	455	397	[23]
8 h feed withdrawal, Cr_2O_3 in capsule, t50	Broilers, 14 d	329	533	431	[24]
8 h feed withdrawal, Cr_2O_3 in capsule, t50	Leghorn Cocks, 1 y	203	289	246	[24]
Overnight feed withdrawal, TiO_2 in diet, t50	Broilers, 15 d	401	503	449	[25]

Steady state, TiO_2 in diet	Broiler 24 d	378	498	419	[26]
TiO_2 in capsule, t50	Broilers, 15 d	284	314	302	[1]
8 h feed withdrawal, Cr_2O_3 in capsule, t50	Broilers, 20 d	253	388	321	[27]
12 h feed withdrawal, Cr_2O_3 in diet, t50	Broilers, 7, 14 and 21 d	250	409	358	[28]
12 h feed withdrawal, TiO_2 in diet, t50	Broilers, 16 d	348	392	373	[29]
Steady state, TiO_2 in diet	Broilers, 9 and 29 d	155	339	251	[30]
Cr_2O_3 in diet, t50	Broilers, 29 d	Approx. 240	Approx. 300	Approx. 270	[31]
2 h feed withdrawal, TiO_2 in diet, t50	Broilers, 18 d	268	298	286	[32]

12 h feed withdrawal, Cr_2O_3 in capsule, t50	Broilers, 21 d	252	372	320	[33]
Average				340	

536 Table 3. Typical small intestinal retention times (min) observed assuming steady state flow
537 and analysis of marker content in the digestive tract. All values presented are averages for a
538 treatment with replicates.

Marker used	Species and age	Duodenum+jejunum	Ileum	Total small intestine	Reference
Ruthenium-labeled TRIS	Broilers and leghorn cockerels, 16-86 d	65 – 67	73 – 86		[42]
Cr_2O_3	Broilers, 44 d	76	90		[43]
Cerium-141	Broilers, 10 – 21 d			Approx. 115 – 120	[44]
TiO_2	Broilers, 24 d	92 – 128	104 – 140		[26]
CrO_2	Broilers, 30 d	45 – 53[1]	104 – 124	149 – 177	[45]
CrO_2	Broilers, 30 d	42 – 56[1]	94 – 114	145 – 170	[46]
TiO_2	Broilers, 21 d	60 – 69	100 – 122		[29]

TiO_2 and Cr-mordanted hay	Broilers, 9 and 29 d	42 – 69	44 – 83		[30]
Acid-insoluble ash	Broilers, 28 d	81 – 123[1]	118 – 172	199 - 291	[47]

[1]Excluding duodenum