Reviews

The role of the crop in poultry production

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The importance of the crop is often underestimated in poultry production. In addition to storing ingested feed, it also can impact nutrient digestion by digesta softening and the initial activity of feed (endogenous and exogenous) and microbial enzymes. The crop represents the first major defence against poultry pathogens and zoonotic organisms with well established adaptive and innate immune function, and a lactobacilli dominated microbiota capable of reducing the passage of these organisms further along the digestive tract. However, the potential to improve bird productivity and health, as well as affect meat and egg safety, are influenced by the nature of the diet, and in particular feed entry and extended presence in the crop. This is required to promote lactobacilli fermentation, the production of lactic acid and other volatile fatty acids, and the lowering of crop pH. Management practices such as meal feeding and the use of lighting programs with extended dark periods encourage crop utilisation. Further, the use of feed additives such as prebiotics and probiotics may enhance crop function, which in turn contributes to well-being of the entire digestive tract. A healthy and functional crop, along with other segments of digestive tract, has increased importance in an era of reduced antibiotic use in poultry feeds.

Introduction

The digestive tract of vertebrate animals is complex and has evolved to serve its primary function of supplying nutrients to the host animal, while at the same time serving as a barrier to infection and harm from compounds within the digestive tract. As can be expected, functions of gastrointestinal tract (gut) segments are interdependent to provide for efficient digestion and other gut functions (Scanes and Pierzchala-Koziec, 2014).

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Evolution of the gut took place in a natural environment, where omnivorous chickens accessed a wide range of foods and were not always able to find the level of nutrients necessary for maximum growth and reproduction. The importance for gut segments would also change to match the nature of the feedstuffs being consumed. For example, the gizzard, and caeca and caecal fermentation would increase in importance in the presence of fibrous, poorly digestible materials that might be found in winter. It is well understood today that gut segments change to reflect diet changes and that communication mechanisms are in place between gut segments to optimize nutrient retention.

With increasing use of high quality ingredients in poultry feeding, the importance of all segments of the gut and their interrelationships has often been forgotten or neglected with emphasis instead being directed to delivery of digestible nutrients. However, more recently the importance of segments such as the proventriculus/gizzard and caeca has received renewed attention. A well-developed gizzard has been demonstrated to have relevance in digestion and gut health, and the caeca play a critical role in determining gut health and colonisation by zoonotic organisms. For reviews of these gut segments see Svihus (2011) and Svihus *et al.* (2013a). The crop has also been the subject of a wide range of research, but its importance in broiler feeding remains either poorly understood or neglected in research and poultry feeding. Based on the interdependence of gut segments and the relatively neglected crop, the objectives of this paper are to examine the digestive process that occurs in the crop, define its role in improving broiler nutrition and health, and then speculate on how it can be manipulated to benefit broiler production.

Crop anatomy

The crop is a thin walled diverticulum of the oesophagus and retains the basic structural pattern of the digestive tract (Hodges, 1974). Extending from the lumen are non-keratinised stratified squamous epithelium of the mucous membrane, *lamina propria* (connective tissue), *muscularis mucosae*, sub-mucosa (a layer of loose connective tissue), *muscularis externa* and the *serosa*. The structure of the crop is well innervated and vascularised implying potential for interaction with other gut segments, and possibly a variety of roles related to digestion and gut health. Mucous glands are found in the oesophagus and also at the interface between the oesophagus and crop, but are not found in the crop diverticulum (Fuller and Brooker, 1974). Similarly, structural differences have been noted between the oesophageal area of the crop (slightly convoluted surface with a high density of bacteria) and the apex of the diverticulum (flatter surface, numerous sloughing epithelial cells, and fewer bacteria) (Bayer *et al.*, 1975). The non-secretory nature of the crop suggests a limited capacity for digestion, but moisture and enzymes derived from consumption (water, feed), saliva and microorganisms play a role in initiating the digestive process. Demonstrated bacterial adhesion to starch granules is just one example of how digestion can occur in the crop (Bayer *et al.*, 1975). The importance of the crop in diet digestion will be affected by the proportion of the feed that enters the crop and the amount of time it spends there. Although the nature of the crop epithelium indicates less absorptive capacity than areas such as the small intestine, absorption by diffusion of organic acids such as lactic acid and DL-2-hydroxy-4(methylthio) butanoic acid has been suggested (Cutler *et al.*, 2005; Richards *et al.*, 2005). The possibility of transporter mediated absorption has not been evaluated in chickens, but since it occurs in other examples of stratified squamous epithelium (Connor *et al.*, 2010), this possibility can't be ruled out in the

avian crop. Again, residency time of feed and absorbable molecules in the crop impact this potential.

Feed residency in the crop

The degree to which feed enters and the time it is resident in the crop is variable and highly dependent on the nature of bird feeding behaviour, feed presentation (*e.g.*, meal *vs*. ad libitum) and bird management (*e.g.*, periods of darkness). Estimates of crop retention time in birds given ad libitum access to feed and 24 hours of light per day are 7.4 and 24.6 minutes for broiler and White Leghorn chicks, respectively (Shires *et al.*, 1987). In this setting, it appears that feed is primarily directed to and accumulates in the gastric stomach and small intestine. The observation that broiler chickens eat very frequently, approximately every 30 minutes when having *ad libitum* access to feed, corroborates this (Svihus *et al.*, 2013b). Therefore, not only will crop residency be short, but it is also likely that most feed will not enter the crop (Chaplin *et al.*, 1992; Savory, 1985). An extreme contrast to this situation is broiler breeders fed on an every-other-day feeding schedule during the rearing period, where the crop does not empty until 20 hours after feeding (de Beer *et al.*, 2008). Similarly, the time feed spends in the crop can be affected by lighting programs with extended periods of darkness. In turkeys given a 14L:10D lighting program, digesta remained in the crop for 9 hours after the end of the photophase (Cutler *et al.*, 2005). Turkeys and chickens are diurnal and eat during the day if not limited by day length or other environmental factors such as high temperature. Feeding behaviour during the photophase has a daily pattern with the nature of the pattern dependent on the length of the dark period (Schwean-Lardner *et al.*, 2014). Feed intake may or may not be high immediately after lights come on, and increases again prior to lights going off (Buyse *et al.*, 1993; Schwean-Lardner *et al.*, 2014). Early morning feeding can be rationalised by hunger associated with the extended period of time during darkness, but when not seen may be attributed to the capacity of the crop to store feed for an extended period of time and therefore a lack of hunger (Scanes *et al.*, 1987). The late day increase in feed intake is anticipatory and takes time for birds to learn after first being exposed to a dark period. The rationale is that birds increase feed intake so that their nutritional needs are met for at least a portion of the dark period. Buyse *et al.* (1993) found that the crop contained only small quantities of ingesta during the photoperiod in a 14L:10D lighting program, in apparent agreement with Shires *et al.* (1987). However, the ingesta content of the crop increased dramatically (10.5-fold) at the beginning of the scotophase as a result of late day feeding. The crop content decreased gradually during the scotoperiod and of note feed transit time was longer during the night; this was also found by others (Cutler *et al.*, 2005; Duve *et al.*, 2011; Scanes *et al.*, 1987). These authors speculated that the storage of feed in the crop, its gradual release and the increased food transit time at night resulted in the majority of the bird's nocturnal energy needs being met. Anticipatory feeding appears to be affected by the length of the scotoperiod. In a comparison of 16L:8D and 13L:4D:3L:4D lighting programs, Duve *et al.* (2011) found that birds on the latter lighting program failed to display anticipatory feeding before either of the dark periods and suggested that its absence was caused by a lack of need to feed, rather than not predicting the dark period. This research plus other work (Schwean-Lardner *et al.*, 2013) suggest that dark periods of greater than four hours are necessary to induce anticipatory feeding behaviour. In conclusion, use of the crop as a feed storage device is minimal when highly nutritious feed is readily available and there are no constraints on feeding behaviour. However, birds utilize crop storage in response to hunger (*e.g.* food deprivation) or regular periods of darkness (Savory, 1985).

The control of crop filling and emptying is complex, but the gizzard plays a central role (Chaplin *et al.*, 1992; Jackson and Duke, 1995) as it regulates passage of feed to the remainder of the digestive tract. Signalling includes neurological (vagus nerve; Denbow, 1989) and hormonal (*e.g.* ghrelin; Kaiya *et al.*, 2009; glucagon-like peptide-1, Tachibana *et al.*, 2003) mechanisms.

Bacterial populations and role in digestive tract health and pathogen colonisation

Lactobacilli dominate the bacterial community of the crop, but coliforms, streptococci and bifidobacteria have also been found (Abbas Hilmi *et al.*, 2007; Fuller, 1973; Fuller and Brooker, 1974; Fuller and Turvey, 1971; Guan *et al.*, 2003; Peinado *et al.*, 2013; Petr and Rada, 2001). At least some lactobacilli are capable of binding to the crop epithelium to form biofilm layers that are relatively uniquely found on non-secretory stratified squamous epithelium (Edelman *et al.*, 2002; Fuller and Turvey, 1971; Lebeer *et al.*, 2011). The nature of the adherence is not fully understood, but S-layer proteins may be responsible (Hagen *et al.*, 2005). Hagen *et al.* (2005) speculate that the diversity of S-layer proteins among *Lactobacillus gallinarum* strains may provide an opportunity for different strains to live together without direct competition for attachment sites on the crop epithelium. Adherence is vital for colonisation to prevent washout in intestinal compartments with continuous digesta passage. However, if only a small proportion of feed enters the crop, the low flow-through in the diverticulum may enable reproduction of bacteria that are not capable of resisting washout by adherence. Indeed, the crop could act as a natural fed-batch fermenter (like the caecum), seeding the intestine with metabolically active bacteria. The exact nature of the crop microbiota continues to increase in clarity as newer techniques of identification become available (Cousin *et al.*, 2012; Hammons *et al.*, 2010).

Bacterial colonisation of the crop is initiated either just prior to or after hatch (Barnes *et al.*, 1980). Colonisation is variable in young chicks immediately after hatch, and the speed and nature of crop bacterial colonisation is influenced by a variety of factors in the diet. Grains are naturally rich in lactic acid producing bacteria and unless toasted at extreme temperatures bacteria recover after rehydration (Apajalahti, unpublished). This is an important part of the bird's life as they also are most susceptible to colonisation by non-desirable pathogenic and zoonotic organisms at that time (Gast and Beard, 1989; Smith and Tucker, 1980). Factors affecting speed of lactobacilli colonisation include dietary introduction of competitive *Lactobacillus* strains, prebiotics and organic acids affecting their competitiveness, medication (Rada and Marounek, 1996), and the nutrient content of the feedstuffs themselves (Rubio *et al.*, 1998). It is worth noting that lactobacilli are fastidious bacteria with equally complex nutrient requirements as the host itself; they need to have access to simple sugars, amino acids and vitamins for growth. Lactobacilli can be eliminated by anti-bacterial agents such as penicillin and monensin, and when this occurs, the number of coliforms increases (Apajalahti and Kettunen, 2006; Rada and Marounek, 1996). Of note, *Escherichia coli* are capable of binding to crop squamous cells. Their colonisation can be inhibited by adhering strains of lactobacilli (ST1 *Lactobacillus crispatus*) because of shared adhesion sites (classic competitive exclusion), but not by those that are weakly adhesive (*L. crispatus* strain 134mi) (Edelman *et al.*, 2003). Similarly, lactobacilli are capable of inhibiting *Salmonella* colonisation of the gut (Gusils *et al.*, 1999). This ability to prevent colonisation can be attributed to a number of mechanisms including competing for adherence sites, stimulation of the immune system, antibacterial agents and lactic acid production

(direct inhibitory effect of lactate or indirect effect of lowered pH). These studies (and many others) support the concept that a stable and dominant position of lactobacilli in the crop is essential for gut health and the development and maintenance of a balanced crop microbiota (Fuller 1973; 1977).

The absence of feed, such as during withdrawal prior to slaughter or moulting procedures, results in a shift in the bacterial community and predisposition of the crop to *Salmonella* and *Campylobacter* spp. colonisation. Feed withdrawal increases the potential for pathogen presence as a result of decreased lactobacilli colonisation and consequent weakened barrier of entry for pathogens. Among other changes, decreased lactobacilli numbers result in decreased production of lactic and acetic acid (the ratio of which is a species specific feature; Hammes and Vogel, 1995), and increased pH (Durant *et al.*, 1999; Hinton *et al.*, 2000a). The presence of *Salmonella* and *Campylobacter* spp. in the crop of broilers at slaughter represents a human disease risk because of the higher potential of carcass contamination at slaughter from the crop than caecal rupture (Corrier *et al.*, 1999; Hargis *et al.*, 1995; van Gerwe *et al.*, 2010). This emphasizes the need to reduce *Salmonella* spp. colonisation during grow-out and maintaining this status during the feed withdrawal period. Inclusion of organic acids or fermentable growth substrates for lactobacilli in water can reduce the *Salmonella* and *Campylobacter* spp. contamination of crops and broiler carcasses (Byrd *et al.*, 2001 (lactic acid); Chaveerach *et al.*, 2004 (acidified drinking water); Hinton *et al.*, 2000b (glucose); 2002 (sucrose)).

Feed withdrawal during moulting in laying hens also markedly increases the survival of *Salmonella* spp. in the crop (Humphrey *et al.*, 1993) and may provide an environment that increases the expression of genes necessary for intestinal invasion (Durant *et al.*, 1999). In comparison to feed withdrawal, providing low calcium, low calcium and zinc, or low energy by-product diets have been shown to reduce *S.* Enteritidis infection, and maintain lactobacilli in the crop and a lower crop pH (Ricke *et al.*, 2004; 2013; Seo *et al.*, 2001).

The presence of pathogens harboured in the crop and additional organisms that pass through to the lower gut suggest the need for expression of both adaptive and innate immune responses in the crop. Research has confirmed this logic with the demonstration of well-developed lymph nodules in the upper alimentary tract in the form of oesophageal tonsils (Arai *et al.*, 1988). A further demonstration of immune competency in the crop is the development of lymphoid aggregates in crop walls following challenge with *S. enterica* ser. Enteritidis (Seo *et al.*, 2003; Vaughn *et al.*, 2008a; 2008b) and the presence of secretory immunoglobulins (IgA) that specifically bind to *S. enterica* ser. Enteritidis antigens (Seo *et al.*, 2002; 2003). The high expression of β-defensin gallinacin-6 (Gal-6) in the oesophagus and crop, and the demonstration of its antimicrobial activity against food-borne pathogens, demonstrates that the crop can play a role in chicken innate host defence (Hong *et al.*, 2012; van Dijk *et al.*, 2007). Another innate immune function is indicated by Thaxton *et al.* (2006) who found an increase in crop nitrate content after gavaging turkeys with *S.* Typhimurium. The authors suggest that the results are indicative of the activation of inducible nitric oxide synthase in resident macrophages. Taken together, these findings suggest an influence of the crop in local and total digestive tract health and pathogen colonisation.

The crop forms part of the acidic barrier formed by the crop and gizzard, which reduces passage of bacteria including pathogenic *Clostridium* spp. and representatives of zoonotic genera such as *Salmonella* and *Campylobacter* spp. to the distal gut (Sekelja *et al.*, 2012). The modulation of crop bacteria may affect caecal microbiota, as demonstrated by experiments using dietary butyric acid in an unprotected and partially protected form to study *S. enterica* ser. Enteritidis colonisation in the crop and caeca (Fernández-Rubio

et al., 2009). Both sources of butyric acid reduced crop and caecal colonisation, but the unprotected butyric acid was more effective in the crop and less effective in the caeca as expected. Unprotected butyric acid in the diet is taken up by the small intestinal epithelium and hardly reaches the caeca. However, the still important effect of the diet amended with unprotected butyric acid in the caeca suggests that controlling colonisation in the crop benefits the entire digestive tract.

Crop pH and fermentation

The acidity of the chicken crop can vary with values ranging from well below pH 5 to greater than pH 6 (Bowen and Waldroup, 1969; Hinton *et al.*, 2000a; Józefiak *et al.*, 2006; Rynsburger, 2009; Svihus *et al.*, 2013b). The pH varies with the degree of crop fermentation primarily by lactobacilli and by the production of lactic acid together with weaker acetic acid (Cutler *et al.*, 2005; Józefiak *et al.*, 2006). In turn, fermentation is influenced by factors such as the presence of substrate (feed or prebiotic) and again colonisation by lactobacilli (Barnes *et al.*, 1980; Fonseca *et al.*, 2010). The pH of the crop can also be impacted by other non-fermented components of the diet. Feed ingredients have been found to have differing acid binding (buffering) capacity that can affect crop pH with mineral ingredients having the highest capacity followed by protein ingredients and then energy sources (Lawlor *et al.*, 2005). Considering the high calcium levels in laying hen diets, one would expect that crop pH values would be high. Although this has been reported to be the case (Bolton, 1965), an examination of pH values for hens fed on an *ad libitum* basis from 17 research trials averaged pH 4.91 with a range of 4.29 to 6.00 (Durant *et al.*, 1999, 2000; Gordon and Roland, 1997; Kubena *et al.*, 2005; Moore *et al.*, 2004; Nahashon *et al.*, 1994; Ricke *et al.*, 2004). Of interest, the values for hens being moulted by feed withdrawal averaged pH 5.91 with a range of 5.42 to 6.96. These values suggest that considerable fermentation occurs in the crop of laying hens and in turn the reduction in pH can affect its microbial community.

As noted above, extended dark periods result in anticipatory eating and crop storage (Cutler *et al.*, 2005). In turkeys provided with a 14:10D lighting program, feed gradually emptied from the crop for 9 hours after the beginning of darkness and during that time pH decreased from 5.9 to 5.0; at the same time levels of lactic acid and other short chain fatty acids were increasing. This demonstrates that the presence of feed in the crop for an extended time enhances fermentation. In a second experiment, Cutler *et al.* (2005) found that the number of *S. enterica* ser. Typhimurium in crop digesta decreased from 7.1 to 4.9 (log10)/gram of crop digesta over an eight hour period starting after the end of the photophase. This research confirms the beneficial effect of fermentation on crop pH and subsequently bacterial colonisation.

The low pH has direct inhibition effects against a variety of pathogenic and zoonotic organisms and also enhances the impact of butyric acid when it is used in water or broiler feed. The effectiveness against these organisms increases at lower pH because butyric acid in its undissociated form can cross bacterial membranes and acidify the bacterial cell cytoplasm. Therefore, unprotected free sodium butyrate should be more effective against bacteria when converted to protonated butyric acid at the acidic pH of the upper portion of the digestive tract (Van Immerseel *et al.*, 2006).

Pendulous crop

Loss of tone in muscle can result in pendulous crop. The condition is more prevalent in turkeys, but can be found in broiler chickens and occasionally occurs at relatively high levels (Ebling *et al.*, 2015). Despite the usually low incidence, research on pendulous crop may provide clues on management and nutrition required to produce a 'healthy' crop. The etiology of pendulous crop is not clear, but incidence has been linked to genetic, environmental and nutritional influences (Asmundson and Hinshaw, 1937; Wheeler *et al.*, 1960). In a comparison of feeding glucose monohydrate or starch to turkeys, a high incidence of pendulous crop was found for the birds fed glucose monohydrate and none were found for birds fed starch. In addition, abnormal fermentation was found as a result of yeast and fungi colonisation of the pendulous crop birds. Evidence from turkey lighting research (Vermette *et al.*, 2016) has found a higher incidence of pendulous crop in hens given 23 in contrast to those receiving 14, 17 and 20 hours per day. It may be that crop feed storage is required to maintain a scheduled flow of feed through the crop and maintenance of a desired lactobacilli biofilm on crop epithelium, thereby preventing abnormal colonisation by other microbiota.

Potential effects on bird performance

Exposing birds to darkness and meal feeding both promote crop storage of feed, and can improve feed efficiency (Schwean-Lardner *et al.*, 2012; Su *et al.*, 1999; Svihus *et al.*, 2010; 2013b). The improvement in feed efficiency in these cases has been attributed to factors such as altered metabolism during darkness (Apeldoorn *et al.*, 1999), a more concave growth curve (Buyse *et al.*, 1996b), and improved nutrient retention (Buyse *et al.*, 1996a; Svihus *et al.*, 2013b). An argument can be made that increased food softening and acid exposure, the initiation of the digestive process due to endogenous and exogenous enzymes, and slower digesta transit (at least during darkness) as a result of feed presence in the crop may result in improved nutrient digestibility and feed efficiency. Svihus *et al.* (2013b) speculated that improved gizzard digestion as indicated by reduced gizzard pH contributed to the improvement in feed efficiency seen with intermittent feeding. Of interest, in a comparison of graded levels daylength (14, 17, 20, 23 hours), gizzard size increased and jejunum and ileum weights decreased with shorter days, which result in improved feed efficiency (Classen, Schwean-Lardner and Fancher, unpublished).

As mentioned above, lactobacilli require simple sugars and amino acids in their growth. Why then does the utilisation of dietary substrates and nutrients by the crop lactobacilli not reduce the feed conversion efficiency of the host? The effect of this apparent competition for nutrients between the host and the upper intestinal microbiota (in the crop and small intestine) on bird performance depends on i) the extent to which the host can benefit from the produced microbes and their metabolic products, ii) other nutritional and health benefits provided by the growing intestinal lactobacilli, and iii) the proportion of feed entering the crop and becoming utilised by its microbes. Lactobacilli have anaerobic metabolism, and therefore are able to extract only little energy from carbohydrates such as glucose. In their metabolism, homofermentative species produce mainly lactic acid, but heterofermentative species also to a varying extent produce acetic acid and ethanol (Hammes and Vogel, 1995). The acids and ethanol are central metabolic intermediates and excellent substrates for the host and, provided that they are readily taken up from the digestive tract, cellular dehydrogenases convert them into intermediates that enter the citric acid cycle and subsequent ATP-producing electron

transport chain. If lactobacilli converted 100% of glucose to lactate, acetate, or ethanol and the metabolites would be completely absorbed, the energy deficit for the bird would be only 5% (calculation based on ATP yield from glycolysis, citric acid cycle and aerobic respiration).

In a crop with lower pH as a result of fermentation, conditions are optimised for some enzymes, both endogenous and exogenous (Zeller *et al.*, 2016). In particular, it is well established that phytate hydrolysis in the crop can be extensive (Lan *et al.*, 2010; Onyango *et al.*, 2005; Svihus *et al.*, 2010; Zeller *et al.*, 2015; 2016). Increased crop hydrolysis does not necessarily lead to differences in terminal ileum phytate disappearance (Zeller *et al.*, 2015). However, reducing phytate's ability to bind minerals and protein at this early stage of the digestive process should reduce its negative effects on nutrient digestibility (Yu *et al.*, 2012). Of interest is the finding that β-glucanase supplementation of broiler diets containing oats or barley increased the lactic acid concentration and lowered the pH in the crop (Józefiak *et al.*, 2006). This demonstrates that exogenous enzymes are active in the crop and as a consequence influence conditions in the lower gut that beneficially affect production characteristics. In the latter research, enzyme use improved performance criteria, but it is not possible to relate this improvement to effects in the crop. Unfortunately, the lighting program used was not identified so it is also not possible to know whether increased crop storage would enhance the β-glucanase effect. The potential for enzyme activity in the crop will be affected by the match between the crop environment and enzyme activity requirements, as well the time of substrate exposure.

Developing and maintaining a healthy crop

The crop, though often relegated to being just a storage organ, can play a role in broiler health and nutrient retention, as well as colonisation by zoonotic organisms. Positive effects of the crop on broiler health, nutrient retention, as well as colonisation by zoonotic organisms appear to relate to regular utilisation of the crop for feed storage. Because of the susceptibility to colonisation by undesirable organisms in newly hatched birds, early promotion of crop lactobacilli colonisation is highly desirable.

Providing birds with darkness is an easy method of stimulating crop utilisation. However, the use of continuous or near-continuous light is predominant in the early part of a broiler's life with introduction of more substantial periods of darkness no earlier than four days and most often seven or more days of age. The degree of crop utilisation during this period is not known, but it is common to judge crop fill on the day after placement, with a recommendation that ~90% of birds will have feed in their crop. This degree of fill may relate to it being the first meal, and as feeding behaviour acclimatizes to continuous light the degree of crop storage may be decreased. It is possible that earlier provision of darkness would increase crop storage of feed. Intermittent lighting post-hatch has been recommended for broilers to synchronize flocks and provide young chicks with rest (Malleau *et al.*, 2007). Similarly, day-of-placement introduction of darkness (4 x 4L:2D) is also recommended for laying hen pullets (Lohmann Tierzucht, 2016).

During the rearing period of broilers, turkeys and laying hens, a longer dark period could be initiated to encourage anticipatory feeding prior to the scotophase. A longer dark phase would appear to be appropriate because of the evidence that four hours of darkness is required to develop anticipatory feeding behaviour. Alternately, a longer dark period could be combined with intermittent lighting during the 'photophase'. Simulating dawn and dusk would be recommended for both intermittent and diurnal phases of the broiler life cycle to provide a stronger signal of the upcoming dark period.

Near slaughter age, it is not uncommon for broilers to be returned to near continuous light to increase ease of bird handling and preparation for feed withdrawal. This may reduce crop lactobacilli numbers and make the crop more susceptible to *Salmonella* and *Campylobacter* spp. colonisation, a situation that will worsen during feed withdrawal. Maintaining a longer dark period until marketing and then planned feeding prior to broiler harvesting may reduce this problem by maintaining a healthy crop, and provide feed longer in the crop (with fermentation and low pH) during withdrawal. Concerns regarding digesta contamination at slaughter because of feed in the crop may not be warranted if the feed withdrawal process is properly managed.

Feed withdrawal stimulates enhanced crop use, and this can readily be accomplished by planned meal timing or simply allowing feeders to empty on one or more occasions during a day (Svihus, 2015). This type of feeding could also be used to enhance crop use in broilers exposed to a diurnal lighting program (one light and one dark period per day). Meal feeding during the mid portion of the photophase would ensure crop use for a longer portion of the total day period, and complement crop use after lights come on and during anticipatory feeding before lights go off.

Enhancing the maturation of the crop microbiota after hatch may provide a less susceptible environment to pathogenic load, and appropriate probiotics (Beasley *et al.*, 2004; Abbas Hilmi *et al.*, 2007), and carbohydrates and other nutrients targeted for lactobacilli may be useful to accomplish that goal (Lebeer *et al.*, 2011). Although *in ovo* application of probiotics would seem appropriate to ensure earliest possible bacterial colonisation (Edens *et al.*, 1997), the authors are unaware of successful applications.

Conclusions

The crop is often not considered in making broiler nutrition or management decisions. However, there is evidence that a functional crop can play a role in bird performance and health, and the safety of poultry meat and eggs. For this to happen, the early establishment of lactobacilli in the crop and providing substrate for fermentation by ensuring regular crop feed storage are essential. Commercial probiotics in the marketplace today have not been optimised for the specific requirements of the crop habitat and the substrates of the undigested feed slurry. Indeed, cocktails of multiple, site specific bacterial strains would be needed to extend beneficial effects throughout the intestinal tract. It seems logical that combinations of nutritional and management techniques are required to achieve a functional crop, including use of probiotics, prebiotics, organic acids, exogenous enzymes, meal feeding and lighting programs. This paper has focused exclusively on the crop, but in the larger picture, all segments of the gut should be considered when planning for successful broiler production. Therefore, in addition to decisions on the crop, nutrition that stimulates gizzard size and activity, diets that provide ingredients digested at rates that provide for efficient production and maintenance of the small intestine, and dietary constituents that fuel healthy caecal fermentation may be an important method of improving broiler performance and health in an antibiotic free era.

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