



AVIAN CROP FUNCTION – A REVIEW*

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Abstract

The aim of this review is to present and discuss the anatomy and physiology of crop in different avian species. The avian crop (ingluvies) present in most omnivorous and herbivorous bird species, plays a major role in feed storage and moistening, as well as functional barrier for pathogens through decreasing pH value by microbial fermentation. Moreover, recent data suggest that this gastrointestinal tract segment may play an important role in the regulation of the innate immune system of birds. In some avian species ingluvies secretes “crop milk” which provides high nutrients and energy content for nestlings growth. The crop has a crucial role in enhancing exogenous enzymes efficiency (for instance phytase and microbial amylase, β -glucanase), as well as the activity of bacteriocins. Thus, ingluvies may have a significant impact on bird performance and health status during all stages of rearing. Efficient use of the crop in case of digesta retention time is essential for birds’ growth performance. Thus, a functionality of the crop is dependent on a number of factors, including age, dietary factors, infections as well as flock management. It is important to expand knowledge about the crop functions to use them effectively in poultry production. Furthermore, more scientific data is needed in the scope of immunological function of the crop as well as its microecosystem for a better understanding of the avian immune system and enhancing the health of the birds.

Key words: ingluvies, avian crop, crop anatomy, crop physiology, crop microbiology

Crop anatomy

Crop (ingluvies) is a tubular organ which is an enlarged part of the esophagus. Depending on its anatomy it is classified as rudimentary crop (e.g. Anseriformes), i.e. long and narrow, occupying a small space, either “false crop” – simple diverticulum of the esophagus (e.g. *Gyps fulvus*) or “real crop” (e.g. Galliformes) – well-developed and round-shaped bilobed enlargement (Farner, 1960). In the case of *Gallus*

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gallus var. *domesticus*, ingluvies is characterized by thin wall, 4.5–5.0 cm of length and 8–10 cm³ capacity. The crop wall is attached to the skin and to the clavicle (*clavicula s. furcular*) by the loose connective tissue as well as to the sternum by *musculus compressor ingluvialis* (Langenfeld, 1992). Furthermore, *m. cucullaris capitis pars clavicularis* forms a surface i.e. *m. levator ingluviei* which supports crop position (McLelland, 1993). Through the crop entrance (*ostium ingluviale*), the feed is transferred to the singular diverticulum (Galliformes) and then down to *fundus ingluvialis* (Kobryń and Kobryńczuk, 2004). Anatomical topography of the crop strictly depends on species. Ingluvies lies mainly to the right of the trachea, e.g. Galliformes and Falconiformes crop is located at the thoracic inlet; in Psittaciformes it is stretched transversely across the neck. Pigeons have two large lateral diverticula on both sides of the trachea and small enlargement in the median side (*diverticulum ingluviale sinistrum, dextrum et medianum*). In parrots crop lies at the caudal-cervical part of esophagus and has two pouches – bigger on the right and smaller on the left; the filled crop of some nectivoro-insectivorous birds as well as nestlings of *Chloris chloris* and *Taeniopygia guttata* is located dorsally over the vertebral column; *Opisthocomus hoazin* has the largest crop, which consists of cervical and thoracic parts of esophagus (Niethammer, 1933; Eber, 1956; McLelland, 1990; McLelland, 1993; Lumeij, 1994). A cross section through the entire chicken crop wall allows distinguishing the following parts: incompletely keratinized stratified squamous epithelium, lamina propria, mucous glands – *gll. ingluviales* (near esophageal area or their lack, depends on the authors), muscular mucosae, submucosa, inner circular muscle layer and longitudinal muscle layer (McLelland, 1990; Doneley, 2010). *Tunica mucosae ingluviei* contains *plicae et rugae ingluviei* (McLelland, 1993). The crops' muscular layer in *Strigops habroptila* and *Opisthocomus hoazin* is well developed and may play a role in mechanical grind of food (Szarski and Grodziński, 1987). Despite the fact that birds do not develop esophageal sphincters like mammals (Klasing, 1999), in the case of parrots and pigeons it is possible to identify a functionally similar structure which is located at the junction of the crop and the thoracic esophagus, which allows portioning of feed formation (Taylor, 2000).

The crop in different avian species

The size of the crop and its shape constitute species-specific features (Figure 1) (Godoy-Vitorino et al., 2008). This fact is determined by the birds' evolutionary adaptation to their diet, environment and behavior, i.e. through the rapid feed ingestion in stressful conditions and then digestion in a safety refuge (Gelis, 2006). Stevens and Hume (1998) point out that omnivores and herbivores, including granivorous birds, are characterized by a larger crop than carnivorous predators. Particularly noteworthy is the hoatzin (*Opisthocomus hoazin*), whose enlarged esophagus is the largest part of its digestive tract (Figure 2). Zheng et al. (2011), based on studies carried out on fossils at the Tianyu Museum of Nature, hypothesize that the development of the crop together with adaptation to the intake of a specific diet (e.g. gastroliths) had a significant impact on the reduction or total deprivation of teeth in birds from the Cretaceous period. However, not all present representatives of birds (Aves), for example, seagulls, penguins, geese and ostriches, have a developed esophagus

forming the crop (Table 1) (Denbow, 2000; López-Calleja and Bozinovic, 2000). On the other hand, some species, e.g. European goldfinch (*Carduelis carduelis*), developed an extensible esophageal pouch which is able to play a feed storage function like the crop (Klasing, 1999). Furthermore, esophageal diverticula or enlargements (*saccus esophagealis*) may be involved in courtship as resonating chambers and/or display devices, e.g. in several species of grouse, cranes and pigeons (Farner, 1960; Lumeij, 1994; Kobryń and Kobryńczuk, 2004). However, it should be noted that great bustard (*Otis tarda*), as well as frigatebird (*Fregata magnificens*) have a gular pouch which has the same function but another structure (Farner, 1960; Madsen et al., 2007).

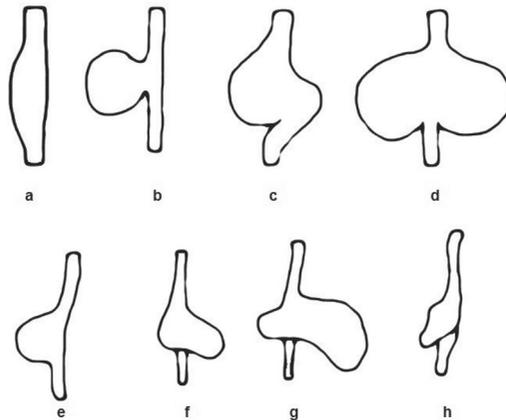


Figure 1. Shape of crop in selected bird species: a) cormorant (*Phalacrocorax carbo*) – rudimentary crop, b) peacock (*Pavo* sp.) – “true” crop, c) budgerigar (*Melopsittacus undulatus*), d) pigeon (*Columbidae*), e) “false” crop, e-h) different shapes of crop in Cacatuidae (King and McLelland, 1984)

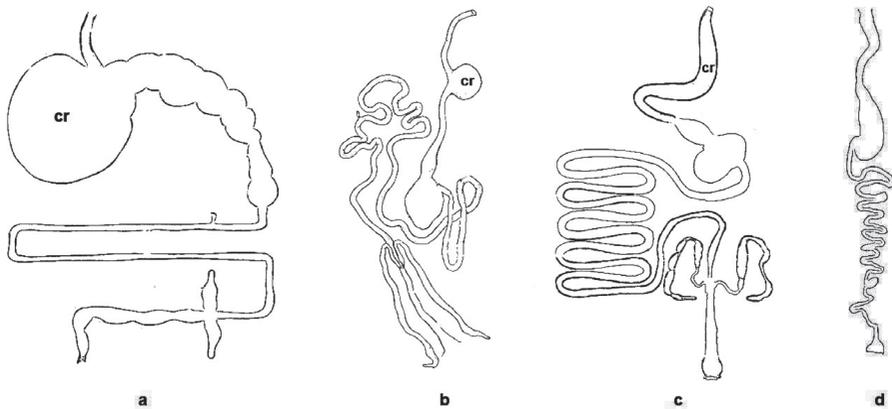


Figure 2. Diagram of the gastrointestinal tract: a) hoatzin (*Opisthocomus hoazin*), b) turkey (*Meleagris gallopavo*), c) goose (*Anser anser*), d) striated heron (*Butorides striatus*); cr – indicating the crop (based on Godoy-Vitorino et al., 2008; Montaner et al., 1997; Clemens et al., 1975; Duke, 1989)

Table 1. Presence of crop among the different taxa of birds

Order	Presence of the crop	Comments	Literature
Accipitiformes		With the exception of the bearded vulture (<i>Gypaetus barbatus</i>), which does not have the crop.	Duke (1997) Houston and Copsey (1994)
Anseriformes		Rudimentary crop.	Backues (2015) Taylor and Murray (1999)
Family: Apodidae	-	No caeca. There is a gall bladder.	Pye (2003) Sibley and Ahlquist (1990)
Caprimulgiformes			Charles (1995) Mayr (2010)
Charadriiformes		Crop and stomach are characterized by simple and often reduced structure.	McCain (2015)
Genus: <i>Ciconia</i>			Ziswiler and Farner (1972)
Columbiformes		Secretion of crop (i.e. crop milk) is produced by both males and females under the influence of prolactin.	Schultz (2003)
Falconiformes			Duke (1997) Aguilar et al. (2012)
Galliformes			Duke (1986)
Genus: <i>Gracula</i>	-	Ventriculus has a moderately muscular wall.	Dorresteijn (2009)
Gruiformes	-		Taylor and Murray (1999)
Musophagiformes	-	Relatively short gastrointestinal tract with a muscular glandular stomach (proventriculus) and thin-walled gizzard (ventriculus). Well-developed liver.	Johnston (1999)
Passeriformes		In most species the caecum is rudimentary or missing. The most characteristic feature of pelicans is a skin gular sac (gular pouch), which allows hunting and subsequent draining off the prey (not to be confused with crop).	Smith (2015)
Pelecaniformes	-	Proventriculus and ventriculus are thin-walled and flexible.	Redrobe (2015) Montaner et al. (1997)

Genus: <i>Phalarocorax</i>	Rudimentary crop	Ziswiler and Farmer (1972)
Phoenicopteriformes	Chicks are fed with high-energy secretion of crop, containing canthaxanthin, leukocytes and erythrocytes.	Lang (1963)
Procellariiformes		Hendriks et al. (2000) Miskelly et al. (2009) Padilla (2015)
Psittaciformes	Caeca are rudimentary or missing.	Taylor and Murray (1999)
Family: <i>Ramphastidae</i>		Leger et al. (2012) Del Hoyo et al. (2002)
Ratitae		Deeming (1999) Tully (2009)
Sphenisciformes	Glandular stomach (proventriculus) stores food, which is further used to feed the young.	Kirk Baer (1999)
Strigiformes	Food can be stored along the entire length of the esophagus.	McLelland (1979) Duke (1997)
Family: Tinamidae		Chikilian and de Speroni (1996)
Family: Trochilidae	Complete emptying of the crop takes approx. 4 minutes. No caeca or gall bladder. Presence of a thin-walled, flexible esophagus reaching up to 12 cm in length.	Karasow et al. (1986) Del Rio et al. (2001)
Trogoniformes	Cuban trogon (<i>Priotelus temnurus</i>) – has gizzard of considerable size (1.8 cm in diameter), also caeca measuring 18–26% of the total length of the intestines.	Wheelwright (1983) Clark (1918)

The crop functions

Crop in the case of nestlings' growth

In many avian species, crop plays an important role in the rearing of nestlings (e.g. pigeons, parrots, finches) (Lumeij, 1994). On the one hand, it stores initially ingested feed that is passed on or obtained directly by the young, and on the other hand in individual species, i.e. pigeons (Columbiformes) and flamingos (e.g. *Phoenicopterus ruber*), it secretes so-called crop milk (Studer-Thiersch, 1967; Gillespie et al., 2012). This substance is also produced by emperor penguins (*Aptenodytes forsteri*), however, it is synthesized through the esophagus due to the lack of an anatomically separated crop (Prévost et al., 1963; Kirk Baer, 1999).

The phenomenon of crop milk presence and secretion was first described by Hunter in 1786 (Hunter, 1840). It involves the secretion of prolactin causing hyperplasia of the mucosa (Riddle et al., 1933). Further, on account of the holocrine secretion, the exfoliating epithelium is mixed with the previously collected food forming a semi-solid substance (Kirk Baer, 1999). The composition of crop milk is species-specific (Table 2) and is characterized by a protein content of 50–60% (in dry matter), 32–45% of fat (including triglycerides, phospholipids, cholesterol, free fatty acids and cholesterol esters and diglycerides), and carbohydrates (1–3%) which, due to low concentration levels, are often overlooked (Davies, 1939; Desmeth and Vandeputte-Poma, 1980; Kirk Baer, 1999). Furthermore, this secretion is rich in keratinocytes and macroelements, i.e. calcium, phosphorus, sodium, and potassium (crude ash: 4.4–4.8%) (Davies, 1939). Due to the biology of short-term rearing of pigeon nestlings (10–40 days, depending on the species) the milk constitutes a food that is easily digestible, highly energetic and rich in immunoglobulin A (Goudswaard et al., 1979). In addition, this secretion contains bioactive substances such as: transferrin, glycoproteins (with the same sequence as lactoferrin) and a specific growth factor – Pigeon Milk Growth Factor (PMGF) (Frelinger, 1971; Shetty et al., 1992; Shetty and Hegde, 1993; Wally and Buchanan, 2007). It has been shown that this secretion, in the case of the flamingo, is characterized by the abundance of canthaxanthin, leukocytes and erythrocytes (Lang, 1963). It is also interesting that the introduction of substitute crop milk into chicks of pigeons led to their death or abnormal growth of young birds (Guareschi, 1936). This suggests the presence of immune-modulating factors such as immunoglobulins and cytokines, like in the case of mammals milk (Wagstrom et al., 2000; Stelwagen et al., 2009), which is necessary during post-hatching period.

Research work related to the supplementation of broiler chicken diets with pigeon crop milk resulted in an increased rate of growth when compared with the control group without its addition (Pace et al., 1952; Hegde, 1973). It is believed that the reason for this could be the higher energetic value of the feed and the beneficial effects of bacteria and bioactive substances contained in crop milk. The research of Gillespie et al. (2012) showed that pigeon crop milk supplemented to broiler chicken diet have a significant impact on their immune system by gene expression in the GALT (gut-associated lymphoid tissue), regulation of cytokine production and activation and proliferation of B-lymphocytes. Furthermore, the impact of crop milk was proven on beneficial diversification of the composition of the microbiota of chickens,

due to its pre- and probiotic properties. Therefore, it was suggested that crop milk is characterized by analogous properties to the milk secreted by mammals (Gillespie et al., 2012). At the same time, the fact of evolutionarily independent development process of the formation of this secretion is fascinating.

Table 2. Comparison of crop or esophagus secretion composition in selected species of birds (adapted from Campbell and Lack, 2011)

	Pigeon ¹	American flamingo (<i>Phoenicopterus ruber</i>) ²	Emperor penguin (<i>Aptenodytes forsteri</i>)
Protein	58.4	32.5	59.3
Fat	35.1	65.3	28.3
Carbohydrates	–	0.8	7.8
Minerals	6.5	1.4	4.6

¹Water content 74%.

²Water content 73%.

The role of the crop in scope of feed intake

Due to the relatively low volume of the glandular stomach and gizzard in comparison to body mass, birds (as the only vertebrates) developed an organ for transitional digesta storage. It was noted that up to 50% of the diet consumed in the morning and the afternoon goes directly to the crop of turkeys (Jackson and Duke, 1995). However, broiler chickens fed *ad libitum* do not use the maximum capacity of this organ due to a continuous manner of feed intake (Nielsen, 2004). It was experimentally documented by cropectomy that crop does not play a crucial role in controlling feed intake in *ad libitum* fed birds (Fisher and Weiss, 1956). Moreover, in the case of cropectomized Japanese quails (*Coturnix coturnix japonica*), birds may store feed in the esophagus at the same amount as a crop (Savory, 1985). Therefore, from the practical point of view, the crop acts as a storage of food in a situation when the feed is provided in an intermittent feeding system, but is not involved in the regulation of feed intake in a continuous manner (Jackson and Duke, 1995; Svihus et al., 2013). It must be noted that crop usage is linked with natural foraging behavior, e.g. least frequency and a large amount of feed intake (Savory, 1985), as well as day length (Irving et al., 1967). The same results of decreasing of filling crop were noticed in diluted diet with application of an indigestible filler (Fisher and Weiss, 1956; Slater, 1974). These data are contrary to reports discussing the impact of mechanoreceptors located in the wall of the crop as regulators of feed intake (Richardson, 1970; Hodgkiss, 1981). Explanation of this process should be traced, like in the case of other animals, including mammals, to the mechanism of stimulating the vagus nerve through the work of stomach muscles (Denbow, 1994), as well as humoral effects (ghrelin, gastrin, cholecystokinin) (Richards and Proszkowiec-Weglarz, 2007). Thus, the filling of the crop is closely dependent on the volume of food in the two-part stomach (proventriculus and ventriculus), whose capacity in chickens is estimated at up to 5–10 g of feed (Svihus, 2014). When this organ is filled up completely, storage of feed in the crop takes place (Jackson and Duke, 1995). After a while, when the gizzard is emptied, muscle contractions cause the passage of content to further sections

of the intestinal tract (Langenfeld, 1992). Therefore, the functions of the anterior digestive tract are closely linked, and affect the peristalsis of further sections of the digestive system. The time which is needed for the bolus to pass from the crop to the gizzard is around 5–30 seconds (Henry et al., 1933), moreover, the pressure used in this process (in laying hens) is in the range from 7 to 18 cm H₂O (Groebbels, 1932). Furthermore, it is possible, especially in the carnivorous birds (e.g. *Accipiter gentilis*) that the crop fills first, and after a few minutes the peristaltic movements push a prey into the stomach (Dedič, 1930).

In chickens the volume of the crop is closely related to body weight, gender, as well as its breed. It has been shown that with increasing body weight of laying hens (Quisenberry, 1971) and broiler chickens (Wehner and Harrold, 1982) its crop volume increases proportionally. Moreover, reduced sizes of this section have been observed in hens. Further, males of broiler chickens are characterized by a much higher crop volume when compared with the Single Comb White Leghorns (Table 3).

Table 3. Dependence of the crop volume on body weight, sex, and breed of chickens (adapted from Wehner and Harrold, 1981)

Type	Average body weight (kg)	Average crop volume (cm ³)	Crop volume to body weight ratio (cm ³ /kg)
SCWL laying hens	1.8	71.1 a	38.7 a
Lightweight roosters SCWL	1.9	95.8 b	51.2 b
Heavyweight roosters SCWL	3.2	169.3 c	52.9 c
Broiler cockerels	3.2	214.3 d	67.4 d

a, b, c, d – values differ at the significance level of $P \leq 0.05$.

SCWL – Single Comb White Leghorn.

Feeding *ad libitum* results in reduced physical use of the crop by chickens (Svihus et al., 2010) due to the fact of adjusting the frequency of feed intake (on average every half hour) to the rate of passage of the digesta (Svihus et al., 2013). Boa-Amponsem et al. (1991) confirmed that filling the crop in slow- and fast-growing chickens varies depending on the feeding system. It was also reported that the chickens adapting to environmental conditions (two feedings per day) could collect up to 40% of the daily dose at once, while using the crop, glandular stomach and gizzard as organs that store the feed (Barash et al., 1992; Buyse et al., 1993). In addition, free range farming caused an increase in the use of storage functions of the crop (Mwalusanya et al., 2002; Mekonnen et al., 2010). Therefore, it is possible that access to additional structural feeds results in increased feed intake, through which the crop is stimulated to intensified work. However, studies that were conducted on the use of various forms of physical feeds (pellets, coarsely ground, fine) for broiler chickens, did not show statistically significant differences in the impact of the structure of the diet on the mass of the crop content (Sacranie et al., 2012). The reduction in pH value was observed (5.1 vs. 5.6) in the crop of birds fed finely ground (1 mm) diet (Svihus

et al., 2013). It should be emphasized that in clinical condition (fluid therapy), the optimal amount of feed directly placed into the crop is within the 3–5% of bird's normal body weight (Quesenberry and Hillyer, 1994).

The crop and the efficiency of feed additives

Effective use of the crop organ is closely related to its filling and the rate of passage content. Therefore, the retention time of digesta during restrictive feeding of chickens should be noted. In an interval of 1 hour after the last feeding as much as 40 g DM of feed was observed in the crop. A significant amount of content was noticed even 4 or 5 hours after feeding, but it amounted to an average of 10 g (Buyse et al., 1993; Svihus et al., 2002). It is believed that due to the lack of endogenous enzymes secretion by the crop, it does not fulfill important functions in the digestion of feed. However, the study by Ponte et al. (2008) mentioned the possibility of synthesizing β -glucanase of bacterial origin in this segment, which may affect the activity of exogenous feed enzymes. In addition, the crop plays an important role in moistening the feed, which supports enzymatic degradation in subsequent sections of the digestive tract. At the same time, other substances activated by moistening, including exogenous feed enzymes, can potentially positively affect the nutrient's digestibility. The crop is the only part of the bird's gastrointestinal tract where the activity of digestive enzymes depends on the water content. Moreover, retention of a wet digesta takes prolonged time in comparison to short-term remaining of dry feed in the crop (Sturkie, 1976 a). Thus, the moistening time of feed is an important factor in determining the effectiveness of exogenous enzymes; however, this only applies to a situation where the crop is the place of their main activity. So, gradual moistening of the crop content in time was observed, increasing even by 50% within 60 minutes (Svihus et al., 2010). Furthermore, the light schedule changes from continuous to intermittent may enhance the effectiveness of exogenous enzymes by elongation of feed retention in the crop (Ao, 2005). Svihus et al. (2010) proved that the use of restricted feeding, thanks to the use of the crop by birds as a transitional feed storage, may have an impact on better growth performance of chickens. This is because of an increase in the efficiency of exogenous phytase. There was a 50% reduction in digesta phytic acid at 100 minutes retention of digesta in this segment of the gastrointestinal tract. In the *in vitro* experiment by Denstadli et al. (2006), degradation of phytic acid (IP6) reached up to 86% during 45 min of incubation in conditions similar to those in the crop. It has been repeatedly proven that the crop plays a major role in creating an environment for phytase activity synthesized, among others, by *Aspergillus niger*, *Mitsuokella jalaludinii* or *Peniophora lycii* (Liebert et al., 1993; Onyango et al., 2005; Lan et al., 2010).

The acidic environment of the crop is crucial to optimal efficacy of the exogenous enzymes added to the chicken diets. It is well-documented that bacterial or fungal enzymes show the highest activity at pH 4.0–6.0 (Coughlan, 1985; Ademark et al., 2001; Beauchemin et al., 2003; Greiner and Konietzny, 2011). In the situation where pH value is above 6.5 (up to 3 h after feeding) the enzymes activities are decreased to 10–15% of effectiveness at pH 4.5 or 5.5 (Baas and Thacker, 1996). Thus, the crop allows for a thorough utilization of exogenous enzymes by decreasing the

pH value of digesta through the *Lactobacilli* fermentation. It should be noticed that disturbances of microbial composition may be a limiting factor for maximizing the enzyme activity.

Another feature of ingluvies, through the blood vessels presence, is absorption of nutrients (Bolton, 1965). This property is frequently overlooked due to the fact of minimal intensity of this process or its absence. Some authors indicated that glucose (Bolton, 1965; Pritchard, 1972), threonine (Teekell et al., 1967) and β -carotene (in the presence of bile) (Sibbald and Hutcheson, 1959) could be absorbed directly from the crop. In contrast to that, botulinus toxin is not absorbed through the crop (Leasure and Foltz, 1940).

The environment of the crop and its functioning

The digesta in crop is characterized by a high variability of pH (Table 4), which according to various scientific reports of healthy birds ranges from 4.0 to 7.8 (*Gallus gallus* var. *domesticus*) (Herpol and van Grembergen, 1967; Józefiak et al., 2008, 2011, 2014). In the case of sour-crop the pH value can be as low as 3.7 (Bolton, 1965). Feeds for nonruminants usually have pH values around 6.0 (Ao, 2005). Therefore, it may be assumed that when the content begins to be stored, the pH will be formed at a similar level (Ao et al., 2008). However, prolonged retention is associated with a significant increase in the fermentation activity of the endogenous microbiota. Organic acids synthesized by the bacteria effectively reduce the pH value (Hilmi et al., 2007). Thus, the different storage time of the content is associated with a different intensity of fermentation, and hence the concentration of hydrogen ions and other products of microbial activity. Bolton (1965) confirmed that the pH value decreases with prolonged retention time of feed in the crop, but it concerned only broiler chickens. In the case of laying hens similar effects were not observed due to the high dietary content of limestone characterized by a high buffering capacity. Moreover, the addition of acidifiers (formic and propionic acids) to the diets for laying hens did not affect pH change in the crop. In contrast, it had negative effects by reducing the number of lactic acid bacteria and decreased the concentration of short-chain fatty acids (Thompson and Hinton, 1997). Besides, addition of 25 g/kg of the propionate ion to the hen diet resulted in chronic damage of the crop epithelium (Bolton and Dewar, 1965). Insufficient activity of the fermentation of carbohydrates by lactic acid bacteria in the crop, for example, through lack of feeding during transport, reduces their population and the concentration of the product, i.e. lactic acid.

It has to be emphasized that complete emptying of the crop in broiler chickens takes less than four hours (May and Deaton, 1989), although this may be dependent on feeding and management. This affects the sudden drop in bacterial activity and, consequently, an increase in pH. The most preferred conditions for the reproduction of *Salmonella* sp. are in the range of pH 6.0–7.5, for the remaining Enterobacteriaceae, including *E. coli*, this range is slightly wider, i.e. from 6.0 to 8.0 (Banwart, 1979). In this case, the crop's ability to resist pathogen invasion significantly decreases. This allows the colonization and stabilization of Enterobacteriaceae and *Salmonella* spp. in the gastrointestinal tract of the host (Fuller, 1977).

To conclude, the functionality of the crop will be dependent not only on the feeding system of animals and their behavior, but also on alimentary factors, as well as the presence of buffering substances.

Table 4. The crop pH value in selected avian species and poultry breeds

Breed	pH value	References
Broiler chickens		
ROSS 308	4.5–5.8	Józefiak et al. (2012) Svihus et al. (2013) Amerah et al. (2014)
COBB-Vantress male broiler	3.4–6.8	Ao et al. (2009) Fonseca et al. (2010) Alali et al. (2013)
COBB 500	4.3–5.1	Rubio-García et al. (2015) Józefiak et al. (2005)
Feed withdrawal broilers	5.3–6.5	Hinton et al. (2000 a) Hinton et al. (2000 b)
Laying hens		
Hy-Line® W-36	4.1–5.9	Gordon and Roland (1997) Moore et al. (2004)
Single Comb White Leghorn hens	4.1–6.0	Kubena et al. (2005) Woodward et al. (2005)
Medium-weight hens (Warren)	4.8–6.0	Mongin (1976)
Indigenous Venda chickens	4.9±0.210	Mabelebele et al. (2014)
Laying hens fed molt diet	4.6–6.2	Donalson et al. (2008)
Turkey		
	5.3–6.2	Farner (1942) Bennett et al. (2002) Giannenas et al. (2014)
Duck	4.8–5.1	Farner (1942)
Goose	4.1–5.0	Clemens et al. (1975)
Others:		
Pigeon	4.1–4.4 6.3	Farner (1942) Sturkie (1976 b)
Pheasant	5.6–6.0	Farner (1942)
Hoatzin	6.0–6.8	Grajal et al. (1989) Grajal (1995)

The crop microbiota composition and its properties

The environment of ingluvies is favorable to bacterial growth, it is maintained at a temperature of 40°C, as well as essentially anaerobic conditions (Bolton, 1965). The microbiota of bird crops develops together with age and the changing diet (Godoy-Vitorino et al., 2010). The majority of the microbiome inhabiting the crop are bacteria assigned to the *Lactobacillus* spp. (Table 5, 6) (Salminen et al., 1993; Mackie et al., 1997). The most frequently isolated representatives of this type include *Lactobacillus salivarius*, *L. fermentum*, *L. reuteri* and *L. acidophilus*. However, for *L. acidophilus*, due to reclassification two homologous groups have been separated (A and B) containing six species, i.e. *L. acidophilus* (A1), *L. crispatus* (A2), *L. amy-*

lovorus (A3), *L. gallinarum* (A4) *L. gasseri* (B1) and *L. johnsonii* (B2) (Lauer et al., 1980; Fujisawa et al., 1992; Jensen et al., 1993). Flora is very stable and permanently attached to the crop, as evidenced by the colonization of these bacteria in just 1 hour after hatching. At the same time, there were no effects of the diet and rearing conditions on the process of bacterial colonization in the first hours of life (Fuller, 2001). In addition, the crop is also inhabited by the representatives of *Bifidobacterium*, *Enterococcus*, and *Enterobacter* (Yeoman et al., 2012). Generally, bacteria in the crop are concentrated at a high level of about 10^9 /g (Figure 3) (Oakley et al., 2014).

Table 5. Identification of bacterial isolates (n=300) from the crop of broiler chickens through partial sequencing the 16S RNA gene (Hilmi et al., 2007)

Species	Number of isolates	% of isolates	Number of isolates detected in 8 crop samples
<i>L. acidophilus/L. johnsonii</i>	5	1.7	4
<i>L. crispatus</i>	56	18.7	7
<i>L. gallinarum</i>	1	0.3	1
<i>L. helveticus</i>	1	0.3	1
<i>L. pentosus</i>	1	0.3	1
<i>L. reuteri</i>	99	33.0	7
<i>L. salivarius</i>	40	13.3	7
<i>Lactobacillus</i> sp. oral clone CX36	6	2.0	3
<i>Lactobacillus</i> sp. strain CLE-4	1	0.3	1
<i>Lactobacillus</i> spp. ^a	83	27.7	8
<i>P. acidilactici</i>	7	2.3	2
Total	300	100	8

^a Bacteria of the genus *Lactobacillus* not assigned to species.

In the case of adult individuals of *Opisthocomus hoazin*, the microbial content of the crop closely resembles the rumen of ruminant animals and is dominated by Bacteroidetes, Firmicutes and Proteobacteria (Godoy-Vitorino et al., 2012). In addition, there are relatively high concentrations of Spirochaetes, Synergistes or Acidobacteria, and for the first time for vertebrates Aquificae, Coprothermobacteria, Thermodesulfobacteria and Caldithrix (Godoy-Vitorino et al., 2010). In the critically endangered (126 individuals) (IUCN, 2015), endemic for New Zealand, flightless and heaviest of parrots – kakapo (*Strigops habroptilus*), bacterial flora of the crop is limited to Gammaproteobacteria and Firmicutes (Waite et al., 2012). Moreover, in 95% of cases, the microbiome of the gastrointestinal tract of this species belongs to the genera *Escherichia* and *Streptococcus* (Waite and Taylor, 2015). It is believed that this difference is caused by the specific behavior of food intake consisting in the “chewing” of plant material and then leaving out the fibrous fraction (Horrocks et al., 2008). However, not all parrots are characterized by such a little differentiated microbiota of the gastrointestinal tract. For the green-rumped parrotlet (*Forpus passerinus*) the crop is populated by gram-positive bacteria of the genera *Lactobacillus*, *Streptococcus*, *Enterococcus*, *Pediococcus* and *Propionibacterium*, and gram-negative, i.e. *Enterobacter*, *Klebsiella*, and *Escherichia coli* (Pacheco et al., 2004).

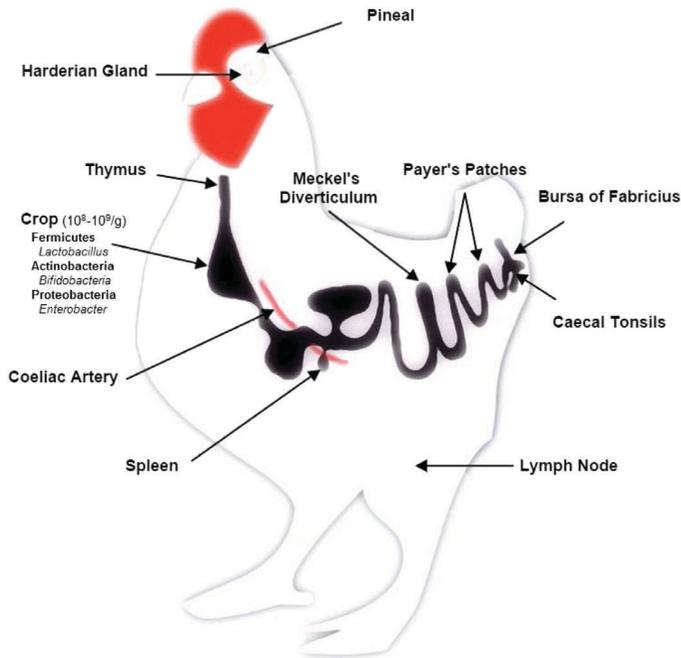


Figure 3. Primary and secondary immunological tissues, indicating the crop (based on Glick, 2000; Yeoman et al., 2012)

In the case of most birds, including chickens (*Gallus gallus* var. *domesticus*), helmeted guinea fowl (*Numidia meleagris*), great bustard (*Otis tarda*) and North African ostrich (*Struthio camelus*), the main fermentation of carbohydrates takes place in the caeca (Józefiak et al., 2004, 2005, 2007, 2010). Species collecting plant food and not having this organ had to develop alternative mechanisms. The green-rumped parrotlet (*Forpus passerinus*) uses the ability of microorganisms naturally present in the crop (*Lactobacillus* and *Streptococcus*) for the production of amylase which decomposes starch into maltose, maltotriose and glucose (Champ et al., 1983; Kotarski et al., 1992). This process greatly simplifies the distribution of carbohydrates in the subsequent sections of the digestive tract. In addition, glucose may simultaneously be absorbed by the mucous membrane of the crop or used as a substrate for the production of volatile fatty acids (*E. coli*, *Klebsiella* spp., and *Enterobacter*), which constitute one of the sources of energy for the bird and maintains an acidic environment (Soedarmo et al., 1961; Stevens and Hume, 2004). Due to the hard-digestible diet of the parrotlet, the retention time of the content will play an important role in increasing the efficiency of the microbiota. Moreover, due to the intake of feed poor in protein, the flora of the crop takes part in increasing the level of this nutrient in the diet (Pacheco, 2000, Ph.D. dissertation).

Table 6. Identification of bacterial isolates from the crop of laying hens using the fragments V6-V8 and V2-V3 of the 16S rRNA gene sequence (Janczyk et al., 2009)

V6-V8		V2-V3	
Species	No.	Species	No.
<i>Acinetobacter</i> sp.	EF111248	<i>Lactobacillus salivarius</i>	AJ508721
<i>Aeromonas hydrophila</i> ssp. <i>hydrophila</i>	AY422755	<i>Lactobacillus vaccinosternus</i>	DSM 20634; AJ417735
<i>Bacillus subtilis</i> ssp. <i>subtilis</i>	AJ288302	<i>Lactobacillus suebicus</i>	DSM 5008; AJ417734
<i>Lactobacillus amylovorus</i>	AJ241720	<i>Lactobacillus paracasei</i>	MBRG 1.4; AJ508362
<i>Lactobacillus crispatus</i>	EF439685	<i>Lactobacillus mucosae</i>	AJ508724
<i>Lactobacillus gasseri</i>	AY339167	<i>Lactobacillus jensenii</i>	5L08; DQ317562
<i>Lactobacillus helveticus</i>	FJ749687	<i>Lactobacillus ingluviæi</i>	JCM 11423; AB289169
<i>Lactobacillus plantarum</i>	FJ604851	<i>Lactobacillus iners</i>	AM117145
<i>Lactobacillus salivarius</i>	DSM 20555; DQ901733	<i>Lactobacillus gasseri</i>	BJ H36-3b; AY339179
<i>Pseudomonas putida</i>	KCTC1639; AY750859	<i>Lactobacillus gallinarum</i>	JCM 1036; AB289121
<i>Staphylococcus delphini</i>	EU157199	<i>L. gallinarum</i>	ATCC 33199; X97898
<i>Staphylococcus saprophyticus</i> ssp. <i>saprophyticus</i>	EU816968	<i>Lactobacillus frumenti</i>	JCM11122; AB289119
<i>Uncultured bacterium</i>	AY667924	<i>Lactobacillus fermentum</i>	AJ617543
<i>Uncultured bacterium</i>	DGGE gel band 10; AY509585	<i>Lactobacillus delbrueckii</i> ssp. <i>bulgaricus</i>	ATCC 11842; AJ414693
		<i>Lactobacillus crispatus</i>	180; AJ421225
		<i>Lactobacillus casei</i>	AJ507644

The crop as the first barrier to the colonization of microbiota is particularly important in terms of integrity and homeostasis of the microbiome of further sections of the gastrointestinal tract. Bayer et al. (1974) due to the structure of the mucosa and biodiversity of the microbiome, compares the crop of chickens to the rumen. Microbiota of the digestive tract and crop are divided into two groups in terms of their environmental niche: bacteria residing in its lumen, and bacteria closely associated with the mucosa (Dubos et al., 1965). The close link between endogenous microorganisms and the host causes it to have a significant impact on bird's metabolism and health. This thesis is confirmed by the fact that bacteria, e.g. *Escherichia coli*, to cause pathological conditions, must first bind to the host's epithelial mucosa (Fuller and Brooker, 1974). The same situation was observed for *Vibrio cholerae*, which even in substantial numbers in the intestinal lumen did not cause disease symptoms (Freter, 1969).

The concentrations and biodiversity of different microbiota populations are significantly correlated with filling the crop. Fasting chickens before being transported to the slaughterhouse may contribute to the growth of bacteria of the genus *Salmonella* in the crop and caeca (Hargis et al., 1995; Ramirez et al., 1997). Subsequently, during technological processes there is a high probability of contamination of chicken carcasses (Hinton et al., 2000 b). The natural defense of the host against the colonization of Enterobacteriaceae is competitive exclusion by populations of probiotic commensal bacteria, as well as decreasing the pH by the increase in the activity of microbial fermentation (Hinton et al., 1990). However, fasting may cause physical, chemical and microbiological changes in the crop of broiler chickens, which will reduce the natural resistance of birds to the potentially pathogenic bacteria. However, it should be emphasized that some representatives of Enterobacteriaceae (e.g. *E. coli*) are an integral part of the microbiota of the digestive system of animals and only in certain situations, when homeostasis wavers, negative effects on health status of their presence occur.

It has been reported many times that both gram-positive and gram-negative organisms are capable of secreting bacteriocins (Józefiak and Sip, 2013). Bacteriocins are ribosome-synthesized peptides not exceeding the molecular weight of a dozen kDa, which are characterized by antimicrobial properties (Stern et al., 2006). Jack et al. (1995) and Montville et al. (1995) classify microorganisms naturally present in the crop, i.e. *Lactobacillus*, *Bifidobacterium*, *Enterococcus*, and *Enterobacter* to bacteriocinogenic bacteria. This activity effectively limits potentially pathogenic strains in the crop of the bird host. Stern et al. (2006) observed that bacteriocin produced by *Lactobacillus salivarius* (NRRL B-30514) reduces the number of four strains of *Campylobacter jejuni*. It has been shown that Bifidocin B (*Bifidobacterium bifidum*) may exhibit antagonistic activity towards *Listeria*, *Enterococcus*, *Leuconostoc* and *Pediococcus* (Yildirim and Johnson, 1998). Bacteriocinogenic activity of *Enterococcus faecium* results in the inhibition of growth of *Listeria monocytogenes* (Strompfova and Laukova, 2007). Lauková et al. (1993) observed that Enterocin A (*E. faecium*) effectively limits the concentration of *Salmonella dusseldorf* SA31 in the gastrointestinal tract of Japanese quail.

The crop is the most important GIT segment for bacteriocins activity due to the specific environment and lack of endogenous proteolytic enzymes such as pepsin or trypsin (Józefiak et al., 2013). However, bacteriocins are not the only antimicrobial factors present in this section of the gastrointestinal tract. *Lactobacillus reuteri*, by far the most numerous bacteria of the genus *Lactobacillus* in the crop, i.e. 33% of the total, due to anaerobic fermentation of glycerol, is able to produce reuterin (Axelsson et al., 1989). Reuterin is resistant to degradation with the use of endogenous proteolytic and lipolytic enzymes; its activity remains in a wide pH range and it dissolves in water (El-Ziney et al., 1999). Its biocidal mode of action includes the reduction of gram-positive and gram-negative bacteria, yeasts, molds, protozoa and viruses (Axelsson et al., 1989; Casas and Dobrogosz, 2000).

In the available literature there is information concerning the biocidal effects of β -defensin on *Salmonella enterica* serovar typhimurium and *Clostridium perfringens*. The latter is responsible for the pathogenesis of necrotic enteritis in poultry annually generating the greatest financial losses globally (2 billion USD) (Van Immerseel et al., 2009). In the case of chickens gallinacin-6 (*AvBD9*) plays an important role in the bird's innate immunity to the pathogens of the gastrointestinal tract (van Dijk et al., 2007). The research of the team Hong et al. (2012) suggests that the crop can perform the function of local expression of β -defensins (*AvBD1*, 7, 9) towards *Eimeria maxima* and *C. perfringens*. However, further research is needed for a detailed understanding of the host-pathogen relationship in this aspect.

The immunological function of the crop

The composition of the specific immune system of birds includes primary lymphoid tissues, i.e. the thymus and bursa of Fabricius. The secondary, peripheral tissues include, among others, the spleen (Gallego et al., 1993), Harderian gland (Olah et al., 1996), esophageal and glandular stomach tonsils (Matsumoto and Hashimoto, 2000), Peyer's patches (Befus et al., 1980), Meckel's diverticulum (Olah et al., 1984) and lymphoid follicles in the cecum (Olah and Glick, 1979), as well as lymphoid tissues of the gastrointestinal tract, i.e. GALT (gut-associated lymphoid tissue) (Glick and Olah, 1981) and BALT (bronchial-associated lymphoid tissue) (Figure 3) (Bienenstock and McDermott, 2005). Furthermore, studies by Holt et al. (2006) clearly indicate the possibility of immunological response of the crop in the presence of *Salmonella enterica* serovar Enteritidis (strain SE89-8312). The experiment was carried out with White Leghorn line raised gnotobiotically (specific pathogen free). During infection of chickens (1 ml *per os*, 9×10^6 *S. enteritidis*), an increase of IgA specific for the used pathogen in the crop was observed. At the same time, there was the presence of lymphoid aggregates within the lamina propria of mucous membrane of the crop (Holt et al., 2002). In many cases it was shown that immunoglobulins A have an inhibiting effect towards bacteria present in the gastrointestinal tract of animals (Michetti et al., 1992; Iankov et al., 2002). Moreover, they are defined as the first line of immunological defense by limiting the adhesion of pathogens to the mucosal epithelium and its penetration (Michetti et al., 1994). In the lymphoid tissue of the crop, plasma cells and lymphocytes-B were also isolated. So, the local humoral immunity located in the crop may constitute a specific diagnostic indicator used to

detect disease of the gastrointestinal tract of chickens (Seo et al., 2003). Simultaneously, it is a cheap method, non-invasive and simple in execution (Vaughn, 2007, Ph.D. dissertation).

Conclusions

In conclusion, feed storage is a basic and direct role of the crop. However, from the point of view of productivity and the health of birds, the most important functions of this organ are: feed moistening and creating a favorable environment for the development of probiotic microbiota. Indirectly, the crop is involved in the suppression of potentially pathogenic bacteria and reduces contamination of further sections of the gastrointestinal tract by substances with antimicrobial properties and those regulating the digesta pH. However, the composition of the microbial populations of the crop may change under the influence of dietary factors (Knarreborg et al., 2002; Hammons et al., 2010), age (Hilmi et al., 2007), antibiotics (Knarreborg et al., 2002) and other feed additives (Józefiak et al., 2011; Józefiak et al., 2012; Ptak et al., 2015) supplementation or infection (Kimura et al., 1976). Therefore, it is necessary to better understand the different processes occurring in the crop in order to use it as efficiently in poultry production.

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