

Anatomy and digestive physiology of the neonatal ostrich (*Struthio camelus*) in relation to nutritional requirements

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Summary

The demand for ostrich meat and other products is increasing. The primary problem facing the industry is a lack of information on the nutrient requirements of these birds, particularly neonatal birds. This may be partly responsible for the high mortality of chicks and the lack of expansion of the industry. Knowledge of the development of the ostrich's anatomy and digestive function is limited. This review collates current knowledge on these aspects and suggests a way forward for the development of ostrich nutrition.

Keywords: Digestive physiology, feeding strategies, fermentative digestion, nutritional requirements, ostrich

standards began about 20 years ago in South Africa (Swart and Kemm 1985). Recently, research has been conducted to define the nutritional requirements of this species, but there is still a lack of information on the requirements of the neonatal chick. Knowledge of nutrient requirements for this phase of development is critical because it may alleviate the high incidence of mortality in ostrich chicks. This paper reviews current knowledge on the digestive anatomy of the ostrich in relation to nutrient requirements. Recent research on the development of gastrointestinal function is highlighted to define a direction for research on nutrient requirements of the neonatal ostrich.

Introduction

There is increasing demand for ostrich meat and hides, worldwide. Between 1996 and 2001, there was a six-fold increase in the consumption of ostrich meat. The rising demand for ostrich meat is attributed to the low content of energy, total lipids, cholesterol and saturated fat, and the high content of protein and iron relative to that of beef, veal, pork, lamb, poultry, rabbit and horse meat (de Jong 1994; Fasone and Adamo 2001). However, the development of the industry is hampered by inadequate knowledge of nutritional requirements of this species, particularly those pertaining to the early-life stage. This may be partly responsible for the high mortality rate observed in the neonatal ostrich. Although the adult ostrich is capable of utilizing large amounts of fibre, the ostrich chick may lack the microbial population needed to digest fibre and be unable to grow optimally or to cope with environmental conditions (Schivavone *et al.* 1999) when fed high fibre diets.

Knowledge of ostrich nutrition and digestive physiology could assist ostrich nutritionists to ensure profitable production by formulating diets that are scientifically and economically appropriate for each stage of growth and production. Feedlot production of ostriches for meat, skin and feathers using complete dry-meal diets based on poultry and pig nutritional

Digestive anatomy and morphology

The ostrich is an avian herbivore that effectively digests plant fibre, specifically hemicellulose and cellulose, which can make a substantial contribution to the apparent metabolizable energy (ME) content of the diet (Swart *et al.* 1993b). Vertebrates are unable to synthesize the enzymes necessary to digest plant fibre, but many herbivores and some birds have overcome this by hosting a symbiotic relationship with microorganisms in the gut (Fuller 1984). The digestive tract of the ostrich includes the oral cavity and associated organs (beak, tongue, and salivary glands), oesophagus, proventriculus, small intestine, large intestine, rectum, cloaca and associated organs (liver and exocrine pancreas). In contrast to the digestive tract of chickens and turkeys, ostriches have no crop in which to store ingested food. However, ostriches have a relatively large true stomach (proventriculus) and gizzard, which enable them to store large quantities of feed. The ventriculus (gizzard) is a large bivalved structure located immediately caudal to the keel bone. Ostriches are hindgut fermenters and rely on microflora similar to that present in the rumens of other grazing animals for digestion of fibrous diets. The colon comprises 60% of the length of the intestinal tract in the ostrich but only 6% in the domestic chicken (Table 1).

Compared to the domestic fowl (Table 1), the ostrich has extremely well developed sacculated caeca (Miao *et al.* 2003) and, unlike other ratites, has an unusually long colon with a wide haustrated proximal part (Herd and Dawson 1984).

Development of intestinal structure and digestive enzyme function

Most reports on the development of digestive function in the ostrich are related to the gross morphology of the gastrointestinal tract (GIT) (Swart *et al.* 1993c; Cooper and Mahroze, 2004). The African ostrich has a longer colon than most other species within the genus (Table 2) (Swart *et al.* 1993c). This ensures greater utilization of fibrous diets than is the case with poultry or pigs.

There are no research reports on the mucosal structure of the GIT. A recent study (Iji *et al.* 2003) examined the development of digestive function from 3–72 days of age. The procedure involved extraction of the brush-border membrane using an adaptation of a method used in studies on broiler chickens (Iji *et al.* 2001). Unlike broiler chickens, the mucosa at the duodenum is relatively smooth, suggesting the presence

of shorter villi in this region of the ostrich's GIT. However, the protein content of the duodenal mucosa was greater than that of the jejunum or ileum at three days of age but not at subsequent periods of assessment (Figure 1). The protein content of the brush-border membrane of the duodenum was less than that of the jejunum or ileum at all ages, but it is unknown if this is related to the length of the microvilli. Development of the jejunum and ileum was similar at most ages.

In the study of Iji *et al.* (2003), the weight of the pancreas increased with age, from 8 g/kg body weight to 16 g/kg body weight (Table 3). Trypsin was not detected in the newly hatched ostrich but the enzyme was active from 27 days of age. The specific activities of chymotrypsin and lipase declined with age but there

Table 2 Intestinal lengths of ostriches and chickens.

	Ostrich ¹		Chicken ²	
	(cm)	(%)	(cm)	(%)
Small intestine	512	36	61	90
Caecum	94	7	5	7
Large intestine	800	57	2	3

Sources: ¹Fowler (1991), ²Calboun (1954)

Table 1 Body weight (kg) of ostriches and emus at various ages.

Months of age	Ostrich		Emu	
	Average ¹	Potential ²	Average ¹	Potential ²
0	0.9	0.9	0.4	0.4
1	4.1	4.3	2.5	2.6
3	26.4	28.2	8.0	8.5
5	52.3	56.4	16.0	17.0
7	86.4	100.0	22.0	23.3
9	109.1	127.3	27.5	28.9
11	122.7	141.0	32.5	33.8
13	129.5	147.7	36.5	38.0
15	134.1	150.0	40.0	41.2

¹Assuming good management, average genetic potential and moderate ambient temperature

²Assuming excellent management, greater than average genetic potential and moderate ambient temperature

Source: Scheideler and Sell (1997)

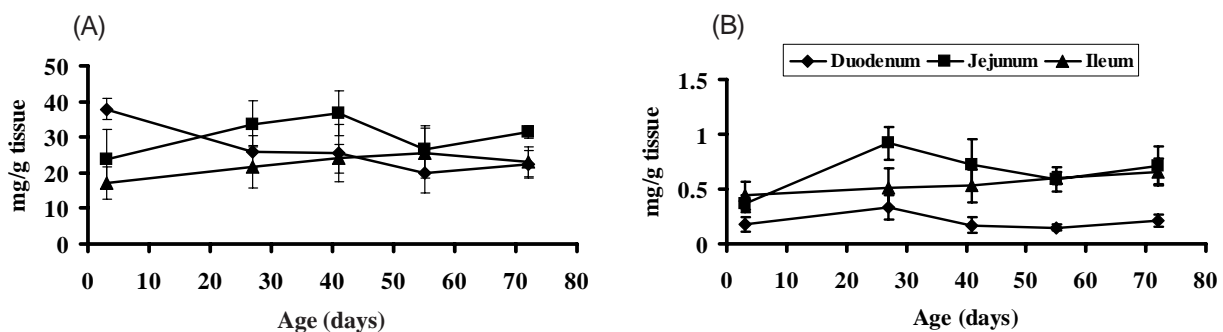


Figure 1 Protein content (mg/g tissue) of the intestinal mucosa (A) and brush-border membrane (B) at different sites in the gut of the ostrich. Source: Iji *et al.* (2003).

was very little change in the activity of amylase with age. The duodenum was the major site of sucrase activity (Table 4), and its activity was higher than that of maltase, unlike the case in broiler chickens (Iji *et al.* 2001). There was also a general reduction in specific activities of digestive enzymes, as is the case with poultry, but there are no reports on total enzyme activities in the ostrich. In broiler chickens, the total activity of membrane-bound enzymes usually increases with age as the villi grow longer (Iji *et al.* 2001).

Fermentative digestion

The utilization of high-fibre diets by ostriches in captivity or in the wild is well documented (Swart *et al.* 1993a,c; Cilliers 1998). Because there were no reports on the development of fermentative capability with age, the amount of fibre that should be fed to various age groups was largely a matter of conjecture. Iji and Boomker *et al.* (unpublished) investigated fermentative capability by measuring gas production from digesta obtained

Table 3 Weight of the pancreas (g/kg body weight), protein content (mg/g tissue) and activities of digestive enzymes at various growth stages of the ostrich.

Age (days)	Weight	Protein	Amylase ¹	Trypsin ²	Chymotrypsin ²	Lipase ³
3	8 ^b	48.6	0.04	Not detected	180.6 ^a	30.9 ^a
27	20 ^a	50.0	0.05	45.4 ^a	165.8 ^a	27.8 ^a
41	20 ^a	48.9	0.04	21.1 ^{ab}	85.9 ^b	9.2 ^b
55	17 ^a	50.8	0.04	6.5 ^b	84.0 ^b	9.5 ^b
72	16 ^a	51.3	0.04	8.3 ^b	77.4 ^b	6.0 ^b
SEM	0.21 ^{***}	5.52	0.005	11.84 ^{**}	37.71 ^{***}	5.60 ^{***}

^{a,b,c,d} Means within columns with different superscript are significantly different (** $P < 0.01$, *** $P < 0.001$)

¹ nmoles glucose/mg protein/minute; ² nmoles p-nitroaniline/mg protein/minute; ³ µmoles tributyrin digested/mg protein/minute

Source: Iji *et al.* (2003)

Table 4 Protein content (mg/g tissue) and activities of digestive enzymes in the brush-border membrane of the duodenum, jejunum and ileum at various ages in the ostrich.

Age (days)	Region	Protein	Maltase ¹	Sucrase ¹	AP ²
3	Duodenum	0.18 ^d	30.2 ^a	293.3 ^a	2.41 ^a
	Jejunum	0.37 ^{cd}	29.0 ^a	233.7 ^a	2.54 ^a
	Ileum	0.44 ^{bc}	24.8 ^a	114.4 ^b	1.15 ^{ab}
27	Duodenum	0.33 ^{cd}	8.5 ^{bc}	68.8 ^{cd}	1.09 ^c
	Jejunum	0.92 ^a	11.0 ^{bc}	24.4 ^{de}	1.02 ^c
	Ileum	0.51 ^{bc}	13.0 ^b	52.5 ^{cd}	1.33 ^{bc}
41	Duodenum	0.17 ^d	13.6 ^b	90.2 ^{bc}	1.81 ^{ab}
	Jejunum	0.72 ^{ab}	9.0 ^{bc}	15.7 ^{de}	0.62 ^c
	Ileum	0.53 ^{bc}	9.3 ^{bc}	23.1 ^{de}	0.98 ^c
55	Duodenum	0.15 ^d	8.8 ^{bc}	54.8 ^{cd}	2.38 ^a
	Jejunum	0.59 ^b	7.6 ^{bc}	13.2 ^{de}	0.80 ^c
	Ileum	0.60 ^{bc}	9.1 ^{bc}	18.5 ^{de}	1.05 ^c
72	Duodenum	0.21 ^d	5.4 ^c	29.6 ^{de}	1.06 ^c
	Jejunum	0.72 ^{ab}	6.7 ^c	9.0 ^e	0.60 ^c
	Ileum	0.67 ^b	5.7 ^c	7.5 ^e	0.57 ^c
	SEM	0.08	8.11	47.00	0.84

Source of variation

Age	**	***	***	***
Region	***	NS	***	***
Age x Region	*	**	***	***

^{a,b,c,d} Means within columns with different superscript are significantly different (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

¹ nmoles glucose/mg protein/minute; ² µmoles p-nitrophenol/mg protein/minute

Source: Iji *et al.* (2003).

from the colons and caeca of ostriches aged 55 and 72 days of age. Gas production was rapid at 55 days and increased with age. The activities of some microbial enzymes were also investigated (Table 5). At 55 days of age, the specific activities of microbial β -D-glucosidase and β -D-galactosidase were higher ($P < 0.01$ and $P < 0.001$, respectively) in the caeca and colon than in the ileum. The activities of these enzymes were similar at 72 days of age but that of microbial protease differed between regions of the gut. Although there was a reduction in the specific activities of the main fibre-targeting enzymes (β -glucosidase and β -galactosidase) with age, there was an increase in the activities of protease and alkaline phosphatase.

Cilliers (1998) showed that ostriches can digest up to 60% of dietary plant cell wall material (neutral detergent fibre). Other studies showed that the hindgut of the ostrich has a large capacity, neutral pH, high concentration of volatile fatty acids (VFA), low lactic acid concentration and high ammonia nitrogen ($\text{NH}_3\text{-N}$) concentration (Deeming 1999; Lambiase *et al.* 1999; Colombo *et al.* 2000; Jamroz 2000; Fasone and Adamo 2001). These reports demonstrate that the ostrich is a unique avian herbivore whose large hindgut chambers are specialized for fermentative digestion. The long retention time of fibrous feed in the GIT ensures exposure of feed particles to microbial digestion for extended periods. This is evidenced by high digestibility of cell walls (47%), hemicellulose (66%) and cellulose (38%), and a high net production of VFA, mainly acetate (Swart *et al.* 1993a). Slow rates of digesta passage are associated with increased digestion, fermentative microbial activity, water absorption (Warner 1981) and electrolyte absorption (Skadhauge 1998). The long retention time and neutral pH provide a suitable environment for fermentative microflora in the enlarged hindgut of the ostrich (Swart *et al.* 1993b). Furthermore, gastric grinding and digestion in the acidic environment

(pH 1.2–2.1) of the proventriculus and gizzard may play an important role in facilitating microbial fermentation in the lower intestinal tract by exposing plant fibre (Skadhauge 1998). Even though many farmers offer chicks roughage, few studies have been conducted on the ability of the neonatal ostrich to utilise fibre. Schiavone *et al.* (1999) reported that consumption of fibre by ostriches younger than three months had a negative effect.

Nutritional requirements

Although commercial diets are available, there is little specific information on nutritional requirements of ratites (Cilliers 1998). Most ratite diets are modified from poultry formulations by changing protein levels and increasing vitamin and trace mineral levels. Most ratite growers feed diets that contain 17–24% crude protein (CP) during brooding and growing, and 22–23% CP during laying. In comparative trials on ostriches of up to eight weeks of age, the highest mean body weight was obtained with a 20% CP diet, although an 18% CP diet favoured feed conversion efficiency (FCE) (Gandini *et al.* 1986). Some growers allow their birds access to forage, while others provide only prepared feed. Alfalfa is suitable for growing and breeding ostriches but is not suitable for neonates because of their relatively undeveloped microbial population. The consensus is that ratites require more fibre in the diet than chickens require, but the optimum levels are unknown. Swart *et al.* (1993a) reported a reduction in ME with an increase in the fibre content of diets fed to ostriches. Most studies on nutrient requirements of this species have been conducted using older birds. Studies on neonates such as that currently underway at the University of Stellenbosch, South Africa (T. Brand, personal communication) have only recently have been initiated.

Table 5 Activities of microbial enzymes in the digesta of the ileum, caeca and colon of ostriches at various ages.

Age (days)	Region	Protease ¹	β -D-glucosidase ²	β -D-galactosidase ²	Alkaline phosphatase ²
55	Ileum	17.8 ^c	0.90 ^b	1.64 ^b	77.6 ^b
	Caeca	41.0 ^c	6.32 ^a	32.20 ^a	153.6 ^b
	Colon	24.9 ^c	6.24 ^a	37.61 ^a	72.4 ^b
72	Ileum	63.6 ^{bc}	0.24 ^b	0.45 ^b	135.8 ^a
	Caeca	181.9 ^a	1.87 ^{ab}	3.00 ^b	217.1 ^a
	Colon	117.6 ^{ab}	1.89 ^b	5.25 ^b	240.8 ^a
	SEM	34.47	2.31	9.95	56.10

Source of variation

Age	***	**	***	**
Region	*	**	***	NS
Age x region	NS	NS	**	NS

Means within columns with different superscript are significantly different (* $P < 0.05$, ** $P < 0.01$; *** $P < 0.001$)

¹ng azocasein/mg protein/minute; ²nmoles p-nitrophenol/mg protein/minute

Source: Iji (unpublished)

Commercial diets for ostriches are formulated by extrapolation from poultry formulations. Current practice is to feed diets containing 21–23% CP from hatching to three months of age and to reduce the protein level after three months of age. When an ostrich is 3–6 weeks old, the microflora of the caecum and large intestine is similar to that of the rumen. Therefore, the ostrich may have the ability to digest fibre from a young age (Janssens *et al.* 1996). However, *ad libitum* feeding of lucerne from seven days of age resulted in decreased growth rate and lower body weight at 28 days of age compared to birds fed pelleted diets (Schivavone *et al.* 1999). This persisted up to three months of age.

Implications for dietary formulations

It is generally agreed that ostriches can utilize a considerable amount of dietary fibre. Indeed, commercial practice is to offer a source of fibre *ad libitum* to facilitate continuous feeding activity. Ostriches tend to be more negatively affected by single meals over short periods than domestic poultry (Sambraus, 1995). However, the dietary fibre content should be lowered for chicks and increased as they grow older.

The inability of the digestive tract of the ostrich chick to secrete trypsin immediately after hatching constitutes a major difference between this species and broiler chickens. This suggests that utilization of dietary protein during early life will be less efficient in the ostrich than in poultry. Commercial diets for ostriches are still based on poultry formulations, but it is unlikely that the high levels of dietary protein used in broiler chicken diets will be efficiently utilized by the neonatal ostrich. The activity of amylase is low and remains relatively unchanged from hatch until 72 days of age. Inadequate utilization of dietary protein and starch during early life in ostriches may partly account for their high neonatal mortality rates, which can exceed 50%. Ostriches would benefit from the inclusion of composite microbial enzymes in the diet to stimulate proteolytic and amylolytic activity in early life. The implications of lower maltase activity relative to that of sucrase are unclear. Both enzymes exist as a complex in the ostrich (Oosthuizen *et al.* 1998) and in chickens (Biviano *et al.*, 1993), so it is unlikely that terminal starch (disaccharide) digestion will be adversely affected.

Conclusion

There is a dearth of information on the protein requirements of the ostrich. Although ostriches may be able to subsist on low protein diets because of their ability to utilise fibrous diets, there is a need to define protein requirements. If it is established that the ostrich is unable to utilize large amounts of protein in early life, commercial diets should be adjusted accordingly. However, it may be more important to increase the ability to utilize protein and starch in early life to reduce

neonatal mortality. In later life, high dietary fibre content would reduce the costs of production. The current practice of rearing ostriches on diets formulated for other species may limit productivity and can have an adverse effect on the health of these birds.

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