Influence of live mass, rate of passage and site of digestion on energy metabolism and fibre digestion in the ostrich (*Struthio camelus* var. *domesticus*)[1]

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Energy metabolism and digestion of dietary fibre in growing ostrich chicks were studied at different live masses (5–50 kg) by means of a total excreta collection method and a radioactive indicator method. Passage rate of digesta particles through the digestive tract and site of digestion were also investigated. Passage rate within live mass groups varied considerably (from 21 to 76 h). Overall mean passage rate was 40.1 h and it was independent of live mass. Digestibility coefficients for cell walls (NDF), hemicellulose and cellulose were 47%, 66% and 38% respectively, and were not influenced by live mass. The hindgut provided a suitable nutritional environment for fermentative microflora, especially in the enlarged haustrated colon of the ostrich. Of the total metabolizable energy in the diet, 12% disappeared in the hindgut.

Energiemetabolisme en veselvertering is met behulp van totale ekskretakolleksie sowel as 'n radioaktiewe merker by groeiende volstruiskuikens vanaf 5 tot 50 kg lewende massa bestudeer. Deurvloeitempo van digestapartikels en plek van vertering in die spysverteringskanaal is ook ondersoek. Deurvloeitempo het aansienlik tussen massagroepe gevarieer (21 tot 76 h), met 'n algehele gemiddeld van 40.1 h en was onafhanklik van lewende massa. Die koëffisiënte van verteerbaarheid van selwande, hemisellulose en sellulose was onderskeidelik 47%, 66% en 38% en is nie deur lewende massa beïnvloed nie. Die relatiewe groot agterderm, en meer spesifiek die kolon, het 'n geskikte mikrohabitat vir mikrobefermentasie verskaf. Van die totale metaboliseerbare dieetenergie is 12% uit die agterderm geabsorbeer.

Keywords: Cellulose, hemicellulose, NDF.

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Introduction

Ostriches are primitive, flightless birds belonging to the subclass Ratitae (Family: Struthionidae) and are related to the rheas of South America, the emu and cassowaries of Australia and the kiwi of New Zealand (Cooper *et al.*, 1992). In the wild, ostriches are herbivorous and digesters of fibrous plant material (Robinson & Seely, 1975; McLachlan & Liversidge, 1978). The ostrich also ingests hard objects such as pebbles or coarse sand, which assist in grinding and crushing its food in the gizzard. Ostriches have modifications in the hindgut such as well developed sacculated caeca and a capacious, haustrated colon (Cho *et al.*, 1984; Bezuidenhout, 1986), which indicate possible use of fermentative digestion of plant fibre (McLelland, 1979; Skadhauge *et al.*, 1984; Swart *et al.*, 1987a).

Domestication of the African ostrich (*Struthio camelus*) for commercial farming purposes dated from 1875–1864 (Smit, 1963; 1984). Today ostrich farming is a well established and important industry in the Little Karoo of South Africa. The intensive production of ostriches to produce meat, skins and feathers on complete dry-meal diets, based on poultry and pig nutritional standards, under feedlot conditions is a new development which has exceptional possibilities for the industry (Swart & Kemm, 1985).

Results from research with poultry suggest that plant fibre, although birds could digest it, was of little nutritional value (Thornburn & Willox, 1965). Fibre digestion is significant in some birds, notably in the family Tetraonidae (grouse and ptarmigan), as these birds utilize enlarged caeca as fermentation chambers. Even in these birds the contribution of fibre digestion to the total energy expenditure appears to be low, with less than 20% of basal energy metabolism derived from this source (Gasaway, 1976a; 1976b). No controlled study has, however, been conducted and therefore this experiment was designed to study the digestive strategies and capabilities of growing ostriches as influenced by live mass, rate of passage and site of digestion. These factors were examined in the ostrich together with the digestibility of various fibre constituents such as cell walls, hemicellulose and cellulose. In addition, methods to determine the apparent metabolizable energy (ME) of feedstuffs for ostriches were evaluated.

Methods

Animals

Fifteen ostrich chicks, hatched in an ostrich egg incubator maintaining an incubation temperature of 36 °C and relative humidity of 33–40% (Swart *et al.*, 1987b; Swart & Rahn, 1988) were reared indoors from day-old, and housed individually in sheep metabolism cages fitted with expanded metal floors, height-adjustable feeders and drinking troughs. The chicks were exposed to microbes under natural transmitting conditions similar to that of feedlot conditions, i.e. transmittal via handling of food, water, shovels, etc. by labourers. Overhead radiant heaters prevented minimum temperatures from dropping below 23 °C. The chicks were sacrificed at three live mass weights, viz. 5 ± 0.8, 15 ± 0.6 and 46 ± 2.0 kg, between 42 and 210 days of age.

Diet

An experimental diet (Table 1) was formulated to contain 17% crude protein and 11 MJ ME/kg according to poultry values tabulated by Du Preez *et al.* (1986). Neutral detergent fibre (NDF) content was 23%. The diet was fed *ad libitum* to all birds from day-old until they were sacrificed between 42 and 210 days of age.

Prior to mixing, all dietary components were ground to pass a 3-mm sieve, with the exception of the 45 kg live mass group in which case a 6-mm sieve was used. In addition, small amounts of insoluble pebbles were supplied separately.

Table 1 Composition of the experimental diet (air-dry basis) fed to ostrich chicks of different live masses (5–50 kg)

Component (g/kg)	
Maize meal	530
Lucerne meal (21% crude protein)	340
Fish-meal	84
Limestone powder	10
Monocalcium phosphate	26
Salt	10
Minerals + vitamins[1]	+
Composition	
Metabolizable energy (calculated) (MJ/kg)	
Poultry values[2]	10.8
Pig values[3]	10.9
Ruminant values[4]	9.9
Protein (6.25 × N) (%)	17.2
Fibre constituents (determined) (%)	
NDF (cell walls)	23.0
Hemicellulose	10.7
ADF	12.3
Cellulose	9.8
Lignin	2.5
Crude fibre	11.6
Calcium (%)	1.7
Phosphorus (%)	10.0

[1] Mineral-vitamin premix (Truka: Germiston, South Africa) added per kg mixed diet: 10 000 IU Vit. A; 2 000 IU Vit. D; 15 IU Vit. E; 2 mg Vit. K; 2 mg Thiamin; 8 mg Riboflavin; 4 mg Pyridoxine; 0.02 mg Vit. B12; 1.5 mg Folic acid; 0.05 mg Biotin; 10 mg Pantothenic acid; 30 mg Niacin; 250 mg Manganese; 66 mg Zinc; 1 mg Iodine; 30 mg Iron; 11 mg Zinc Bacitracin.

[2] Du Preez *et al.* (1986).

[3] Kemm & Ras (1981), IAFMM (1985), Siebrits (personal communication).

[4] NRC (1985).

Rate of passage experiments using ^{51}Cr-mordanted feed particles

A minute quantity of ^{51}Cr-labelled $Na_2Cr_2O_7$ (4 mg/100 g diet) with a high specific activity (10 mCi/200 mg $Na_2Cr_2O_7$: Energy Corporation of South Africa Ltd, Pretoria, South Africa) was used to mordant the complete diet according to the technique of Uden *et al.* (1980). Since the flow of dietary fibre alone is not representative of the flow of the complete mixed diet, samples of the complete diet were mordanted. Furthermore, it has been shown that large amounts of Cr can alter the specific gravity and thus modify the digestibility and flow characteristics of the diet (Ehle *et al*, 1984).

When a designated group attained its target average live mass, a pulse dose of ^{51}Cr-mordanted diet equal to 2% of the daily feed intake was administered orally. Quantitative collections of excreta were made at 2–6-h intervals during the day for 3–6 days following the dose of mordanted diet. No collections were made during the night, except for the group with 15 kg live mass, where collections continued during the night. Ostriches normally squat during the night and only void large quantities of excreta after first feeding in the morning.

Special excreta collection bags were constructed from plastic bags to fit snugly over the entire tail of the ostriches. The bag was then taped to a 60–100 mm wide stomach girdle which in turn consisted of waterproof adhesive plaster taped around the abdomen of the ostrich (Figure 1). The open end of the excreta bag was folded back and sealed with tape and could be opened for each collection.

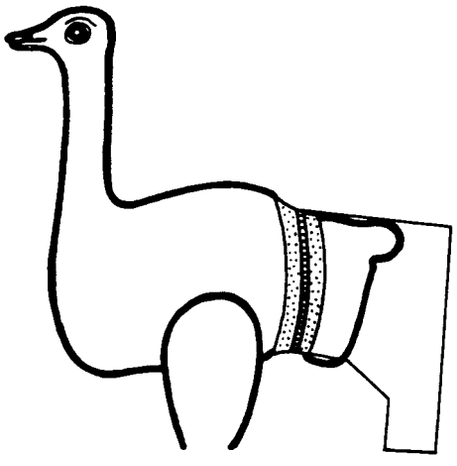

Figure 1 Illustration of ostrich chick with stomach girdle and excreta collection bag.

Radioactivity in excreta was determined using a Gamma counter (LKB Wallac Gamma counter 1282: Denmark) and expressed as cpm ^{51}Cr per g DM. The mean retention time (R_t) of mordanted particles was calculated from the time the marker first appeared in the excreta as proposed by Pienaar &

Roux (1984), using the equation proposed by Graham & Williams (1962), viz.:

$$R_t = \frac{1}{N} \Sigma [n.½(t^1 + t)] \quad (1)$$

where n is the ^{51}Cr counts excreted between times t and t^1, Σ represents the sum of these counts for successive intervals until n becomes zero, and N is the total ^{51}Cr counts excreted.

Digestibility trials – Total collection and inert indicator methods

Clean excreta collection bags were attached to each of the 15 ostriches. Prior to this, their tail feathers were clipped and brushed to prevent contamination of excreta with scales. Subsequently 2% of the experimental diet was replaced by ^{51}Cr-mordanted diet and mixed homogeneously on a daily basis. This was fed *ad libitum* throughout the experimental period. To ensure input-output equilibrium of ^{51}Cr, a 7-day adaptation period was allowed which, in retrospect, was at least three times the R_t of the diet. This was followed by a 5-day collection period during which individual daily feed intake and total excreta voided (faeces + urine) were measured. Excreta were collected quantitatively three times daily at 8:00, 12:00 and 18:00, except for the middle group where excreta collection was continued into the night – artificial light being supplied. Daily collections were weighed, pooled and kept refrigerated (2 °C) in air-tight plastic containers untill required for further analyses. In addition, daily excreta collections of the 15 kg live mass group were stored separately to study day-to-day variation in digestibility of DM and energy.

At the end of the collection period the pooled excreta for each bird was thoroughly blended. Approximately 2 g of each blend was then accurately weighed into porcelain crucibles in triplicate for dry matter (DM) determination. A representative sample was then freeze-dried, ground to pass a 1-mm sieve and stored for further chemical analyses.

Fibre analysis was performed on *ca.* 5 g freeze-dried samples which had been allowed to equilibrate with air moisture. Cell wall content or NDF was determined using a Tecator Fibretec hot extraction apparatus after removal of starch with α-amylase (Robertson & Van Soest, 1981). Acid detergent fibre (ADF) and acid detergent lignin (ADL) were analysed according to the method of Goering & Van Soest (1970). For ADF, protein was hydrolysed by acid pepsin treatment (Robertson & Van Soest, 1981). Hemicellulose was then calculated as the difference between NDF and ADF. Differences between ADF and ADL provided values for cellulose.

Gross energy (GE) values were determined by combustion of dry matter samples in an adiabatic bomb calorimeter (DDS 400; Digital Date Systems, Randburg, South Africa). The same analyses were performed on representative feed samples for each group.

Apparent ME of the diet was calculated using the following equation:

$$ME\ (MJ/kg\ diet) = [GE - (FE + UE)]/\ FI \quad (2)$$

where GE is gross or ingested energy, (FE + UE) is energy in faeces plus urine voided as total excreta (Fraps *et al.*, 1940) and FI is feed intake.

In addition, the method of Hill & Anderson (1958) was used to calculate ME by means of an inert radioactive indicator (^{51}Cr), according to the following equation:

$$ME/g\ diet = GE/g\ diet - \frac{indicator/g\ diet}{indicator/g\ excreta} . GE/g\ excreta \quad (3)$$

It should be noted that the use of radioactive counts (cpm ^{51}Cr/g DM) in the present calculation of ME instead of actual indicator quantity (mg Cr/g DM) could invalidate the gravimetric concept and requires some verification. The ratio of diet:excreta indicator indicates the relative proportion of excreta originating from 1 g of diet ingested. In contrast to the gravimetric method, the use of radioactive counts is highly specific, sensitive and repeatable, provided a constant count volume is maintained and samples have the same density. Since diet and excreta have different densities, standards of known specific activity had to be prepared for diet and excreta. Standards were prepared by mixing 100 g of untreated diet with 1.5 g ^{51}Cr-mordanted diet and excreta. The count ratio (198/525 = 0.377) was then compared to the gravimetric ratio, 1.5/4 = 0.375, i.e. 1 – 0.375 = 62.5% DM digestibility. The difference between count and gravimetric ratio was not significant ($P > 0.05$) and therefore the use of radioactive counts in the present study was valid. Thus, in order to determine ME using ^{51}Cr counts, tubes for gamma counting were weighed, filled to a constant volume with dried, ground samples of the experimental diet or excreta of each bird respectively, and weighed again. The triplicate tubes were then counted for ^{51}Cr activity and the counts thus obtained, divided by the mass of the sample in the tube to give a corrected value (Pienaar *et al.*, 1983). ME was then calculated by substituting these values into eqn. (3).

Relative contribution of fore- and hindgut to energy digestion

On completion of the 5-day collection period, the ostriches were sacrificed while still in ^{51}Cr equilibrium. NDF, GE and cpm ^{51}Cr/g DM were determined for representative freeze-dried digesta samples, taken separately from each gut segment of each ostrich. To study the relative disappearance of dietary energy from the fore- and hindgut, the corresponding values were accordingly substituted into eqn. (3).

Statistical analyses

The t test for groups of unequal sizes (Snedecor & Cochran, 1969) was applied to indicate differences ($P < 0.05$) between groups.

Results and Discussion

Rate of passage

The mean retention times (R_t) of diet particles in the gastro-intestinal tract are shown in Table 2 for ostriches of different live masses. R_t varied considerably within groups of similar live mass, ranging from 21 to 76 h for all groups, the coefficient of variation being 34.8%. However, differences between groups were not significant ($P > 0.05$) and the overall mean R_t was 40.1 ± 3.9 h. This was in agreement with data presented by different authors for pigs (39 h; Clemens *et al.*, 1975a), hay-fed sheep (38 h; Thewis *et al.*, 1976), goats (38 h; Castle, 1956), horses (38 h; Van der Noot *et al.*, 1967),

Table 2 Ingesta retention times (R_t) and dry matter contents of the gastro-intestinal tract for ostriches of different live masses

Measurement	Livemass range (kg)		
	5–10	15–18	42–50
R_t (h)			
Range	25.5–50.9	20.9–43.5	34.7–75.7
Mean	39.0	31.8	47.9
Digesta contents (g DM)			
Proventriculus + gizzard	121.5	162.2	321.2
Small intestine	19.2	28.3	25.2
Caecum + colon	157.8	240.2	721.2

kangaroos (41 h; McIntosh, 1966) and the rock hyrax (43 h; Clemens, 1977), but much longer than for several avian species like chickens (7 h; Sklan *et al.*, 1975), geese (6 h; Clemens *et al.*, 1975b), turkeys (10 h, Björnhag & Sperber, 1977) and ptarmigan (3 h; Gasaway, *et al.*, 1975) as reviewed and calculated by Warner (1981).

Prolonged retention times of the digesta are associated with increased absorption of water from the gut (Warner, 1981). The absorption of Na and volatile fatty acids (VFA) would account for most of the water removed during the passage of digesta through the large intestine (Argenzio & Stevens, 1984; Skadhauge *et al.*, 1984) which, together with microbial fermentation, provides an important adaptation to arid zone herbivory. Probably the most important aspect is the existence of conditions suitable for microbial fermentation and efficient fibre digestion – a well documented digestive strategy in ruminants. The observed rate of passage for ostriches corresponded to the rates of other herbivores with either foregut or hindgut fermentation and efficient fibre digestion. In contrast, rate of passage in the Australian emu (*Dromaius novaehollandiae*), a large ratite bird with significant fibre digestion (35–45% of NDF), was found to be only 5.5 h (Herd & Dawson, 1984).

A typical cumulative excretion curve for ^{51}Cr-marked diet particles and dry matter is presented in Figure 2 for an ostrich of 40.5 kg live mass.

The ostriches did not exhibit an even pattern of excretion, as they tended to void more faeces in the morning than at other times of the day. Ostriches, like emus, tend to squat, apparently asleep throughout the night. The first faeces are usually voided in large quantities after they have risen in the morning, especially after first feeding. This, and the striking differences in digesta and water content in different segments of the gastro-intestinal tract (Figure 3), suggest that digesta might be retained in the hindgut overnight, providing an environment suitable for anaerobic microbial fermentation and the absorption of water together with VFA (Skadhauge *et al.*, 1984). Diet particles tend to be retained for further communition in the stomachs of the ostrich before being presented to the lower intestinal tract. This is common amongst foregut fermenters. Communition of food particles in the ostrich takes place in the gizzard by means of a mechanical gastric grinding process similar to the process in several other avian species (Clemens *et al.*, 1975b; Sklan *et al.*, 1975; Herd & Dawson,

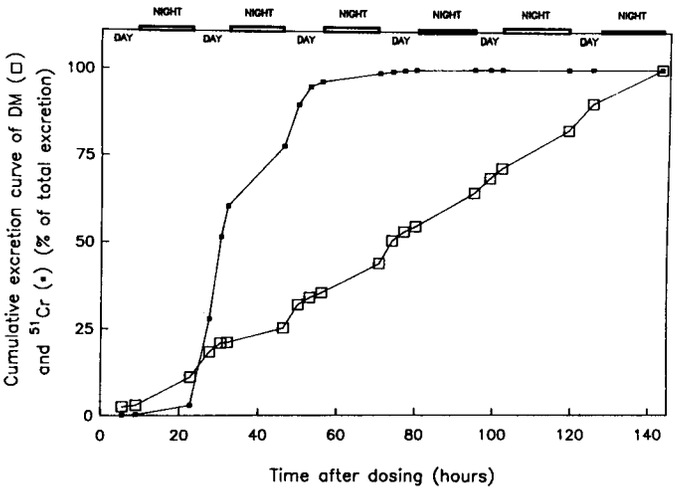

Figure 2 Typical cumulative excretion curve of dry matter (DM) and counts of ^{51}Cr attached to feed particles obtained for an ostrich of 40.5 kg live mass. Mean retention time (R_t) of the diet was 34.7 h.

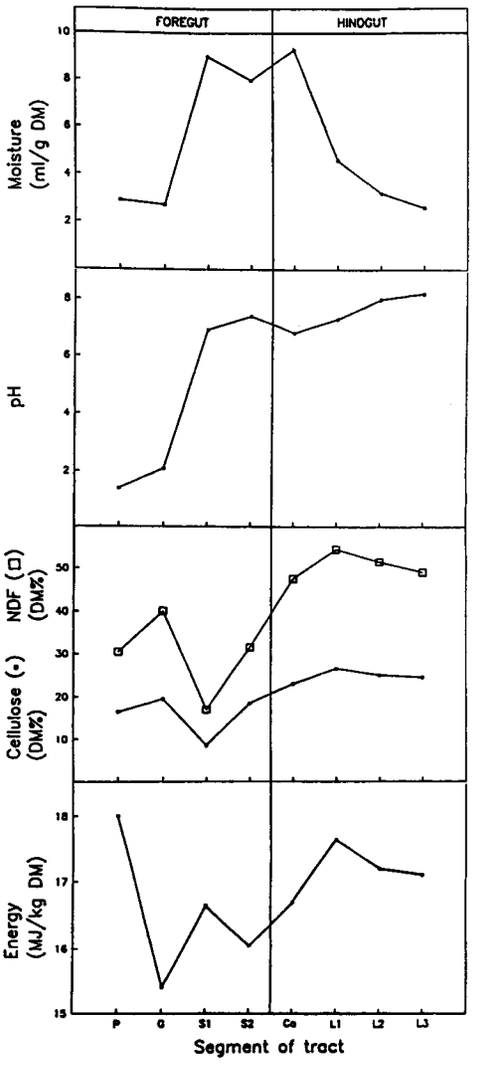

Figure 3 Mean moisture contents, pH, NDF and cellulose, and energy contents in different segments of the gastro-intestinal tract of ostriches (P = proventriculus; G = gizzard; S1 = proximal small intestine; S2 = distal small intestine, Ca = caeca; L1 = proximal colon; L2 = mid-colon; L3 = distal colon).

1984). This process exposes a larger surface area for enzymic attack and when combined with the low pH in the proventriculus and gizzard of the ostrich, may enhance enzymic degradation of the hemicellulose backbone. In ruminants, increased surface area for attack is provided by rumination and breakdown of food particles by microbial digestion (Hungate, 1966).

Nutrient and energy digestion

Total collection method

Table 3 shows the fibre digestion and metabolizable energy values obtained by means of the total collection method for ostriches of different live masses.

Table 3 Nutrient digestibility of the experimental diet fed to ostriches of different live masses. Values are means ± *SE*

	Livemass range (kg)		
Measurement	5–10 (n = 6)	15–18 (n = 5)	42–50 (n = 4)
Feed intake			
DM (g/day)	556.1[a] ± 21.3	745.2[b] ± 31.8	947.7[c] ± 148.0
ME (MJ/day)	7.15	9.15	11.22
Digestibility (%)			
DM	74.9 ± 1.7	71.7 ± 0.5	67.2 ± 1.8
NDF (cell walls)	52.4[a] ± 2.2	43.7[b] ± 0.6	45.6[a,b] ± 3.2
Hemicellulose	69.3[a] ± 1.0	62.7[b] ± 0.4	66.2[a] ± 3.8
ADF	35.8 ± 3.4	26.4 ± 0.8	39.3 ± 3.2
Cellulose	42.1[a] ± 2.7	38.2[b] ± 0.6	35.1[a,b] ± 2.6
Lignin	11.9 ± 5.7	4.3 ± 5.5	8.1 ± 5.8
Energy digestion			
ME (MJ/k)	12.85[a] ± 0.2	12.28[b] ± 0.1	11.84[a,b] ± 0.6
ME (% of GE)	78.9 ± 1.3	75.4 ± 0.5	72.7 ± 2.1

[a–c] Denote significance of differences in rows ($P < 0.05$).

Only a small difference ($P < 0.05$) existed between ostriches of 6 and 15 kg live mass (but not between 6 and 45 kg live mass) for ME values and digestibility of certain fibre fractions (NDF, hemicellulose, cellulose). It should be noted, however, that the middle group had a shorter retention time and hence faster rate of passage (Table 2), which most likely was a response to continuous excreta collection during nocturnal cycles for that particular group and not to live mass as such, resulting in lower digestive efficiency.

The overall mean ME value of the diet on an air-dry basis was 12.33 ± 0.31 MJ/kg and was somewhat underestimated using poultry, pig or ruminant values (see Table 1). Sibbald (1982) reported zero values for metabolizability of cellulose and sawdust in studies with poultry. This provides a probable explanation for the underestimation of ME content of the diet of the ostrich chicks (Table 1) when applying poultry standards. It is generally agreed that chickens (*Gallus gallus domesticus*) do not digest plant fibre, and more specifically cellulose, to any significant extent, most probably because of short retention times. In fact, crude fibre is regarded as a reliable indigestible marker when used to predict feed intake from excreta production in poultry (Almquist & Holloran, 1971; Sibbald, 1982).

Of more importance were the surprisingly high digestibilities obtained for NDF (47%), and particularly for hemicellulose (66%) and cellulose (38%). The significant digestibility of hemicellulose, almost twice as high as cellulose digestibility, is apparently due to microbial digestion in the well developed hindgut of ostriches (Skadhauge *et al.*, 1984; Bezuidenhout, 1986; Swart *et al.*, 1987; 1993). Van Gylswyk & Schwartz (1984) showed that hemicellulose digestion in the hindgut of several vertebrates is usually greater than that of cellulose. This has also been observed in the hindgut of the ruminant (Ulyatt *et al.*, 1975) whereas in the rumen, cellulose is generally digested more efficiently (Beever *et al.*, 1972; Thomson *et al.*, 1972). Keys & De Barthe (1974) reported hemicellulose digestibility of 43% in pigs consuming diets that contained 50% lucerne (ostriches in present study - 66%). Significant digestion of hemicellulose, but not of cellulose, has been observed in the gastro-intestinal tract anterior of the caecum in the pig (Kass *et al.*, 1980; Keys & De Barthe, 1974 as cited by Van Gylswyk & Schwartz, 1984), and it has been suggested that exposure of hemicellulose to acid in the stomach may modify its structure to make it more degradable (Dierenfeld *et al.*, 1982).

The small decrease ($P < 0.05$) in NDF, hemicellulose and cellulose digestion between 6 and 15 kg live mass (Table 3) was related to a corresponding decrease in retention time (Table 2) and not live mass as such, and is most probably indicative of microbial degradation of fibre fractions in the hindgut of ostriches. Decreased retention time would imply a faster passage rate and thus decreased time for fibre (NDF) digestion. The high concentration of volatile fatty acids reported by Skadhauge *et al.* (1984) and Swart *et al.* (1987) in the large caeca and the wide haustrated proximal part of the colon of ostriches confirmed active fermentation of carbohydrates in the hindgut.

A recent investigation into the dietary energy requirements of the Australian emu showed that they digested 35–45% of the NDF and 7–9% of the cellulose in their diets containing 26–36% NDF. This was ascribed to microbial fermentation (Herd & Dawson, 1984) even though mean retention time was short. In the present ostrich study NDF was analysed after treatment with α-amilase (Robertson & Van Soest 1981). NDF was initially analysed according to the original method of Goering & Van Soest (1970) which overestimated NDF digestibility by 42% ($P < 0.01$). Furthermore, changes in ME (MJ/kg) followed changes in cellulose digestibility (Table 3), which suggest that the ability of ostriches to digest cellulose could contribute to the ME of the diet.

The day-to-day variations of ME (13.59 ± 0.3 MJ/kg DM; CV = 2.3%) and dry matter digestibility (71.3 = 2.1%; CV = 3.0%) were particularly small. In addition, the between-animal variation was 4.5% for ME and 5.5% for DM digestibility.

Indicator method

The ME and digestibility values obtained by application of eqn. (3) (Table 4) were in agreement with corresponding values obtained from total collection (Table 3). ME values were practically the same, while NDF digestibility differed by only 4%.

Table 4 NDF digestibility and ME as determined by ^{51}Cr-indicator

Live mass (kg)	Sample	γ-counts (cpm ^{51}Cr/g DM)	GE (MJ/g DM)	NDF[1] (g/g DM)	ME[1] (MJ/kg DM)	NDF digest. (%)
5 ± 0.8	diet	302	0.01809	0.2524	14.30 ± 0.28	49.0 ± 1.6
(*n* = 3)	excreta	1129	0.01520	0.4810		
15 ± 0.6	diet	431	0.01809	0.2592	13.57 ± 0.25	42.2 ± 1.4
(*n* = 3)	excreta	1503	0.01567	0.5214		
46 ± 2.0	diet	661	0.01809	0.2533	13.15 ± 0.34	44.6 ± 3.9
(*n* = 3)	excreta	2038	0.01485	0.4327		
Mean					13.67	45.3

[1] Multiply by 0.90 to convert to air-dry basis.

The indicator procedure gave somewhat lower but less variable values than did total collection, as also reported by Pryor & Connor (1966) and Coates *et al.* (1977) in studies with poultry. Sibbald *et al.* (1960) found that the indicator method yielded more precise, but not necessarily more accurate, data. According to Blaxter *et al.* (1956) the act of defecation may not leave the gut or its lower part, in a standard, repeatable state of fill so that end-period errors may be considerable.

The relative disappearance of digested nutrients between different sites of the gastro-intestinal tract of ostriches showed that about 88% of energy was digested in the foregut and 12% in the hindgut. Disappearance of ingested energy up to, and including the distal colon, presumably approximates digestible energy (DE) of the diet and was 0.95 times the ME value, a factor commonly used by pig nutritionists to convert DE to ME. However, the validity of DE values is based on the assumption that digesta in the rectum-colon is not contaminated with urine or uric acid. In contrast to most other birds observed (Skadhauge, 1981; 1982), no sign of retrograde flow of urine into the terminal colon was observed in the ostrich (Skadhauge *et al.*, 1984; also this study), such as threads of uric acid or 'urine-like' composition of the contents (Skadhauge, 1968). Just (1982a; 1982b) reported relative energy disappearance in the caecum-colon of pigs that increased from 17% to 26% as dietary fibre increased from 4% to 6% (protein content 23.5%) and dropped to 13% when diet protein was decreased by 7 percentage units. However, relative disappearance of digested crude fibre in the hindgut remained constant (95%) with increasing dietary fibre, but decreased by 40 percentage units when diet protein was decreased. Just (1982a; 1982b) stated that 'the proportion of digested energy disappearing in the hindgut increased with increasing content of crude fibre, because more nutrients were transferred to this region'. The results of Just *et al.* (1983) clearly illustrate the significance of the fermentation processes in the hindgut of pigs, as 54% to 97% of the digested fibre disappeared in that region.

MacRae & Armstrong (1969; cited by Van Gylswyk & Schwartz, 1984) showed that only 9% of the total digested cellulose was degraded in the hindgut of sheep when hay alone was fed. Inclusion of dietary concentrates (barley) increased relative cellulose digestibility in the hindgut to 29%. In the ostrich, NDF and cellulose content (Figure 3) were inversely related to energy contents (MJ) of the digesta in the foregut, and directly related to digesta energy in the hindgut. This is probably indicative of a rapid removal of the more readily available 'acid-soluble' carbohydrates and protein from the stomachs into the small intestine that could result in irregularities of solid digesta movement, relative to liquid digesta flow, that may change from fore- to hindgut (Warner, 1981). Sklan *et al.* (1975) reported similar preferential retention of the particulate phase in the stomachs of poultry.

Hemicellulose and cellulose digestibility in the ostrich was well within the values reported for other known hindgut and foregut fermenters by Van Gylswyk & Schwartz (1984). Finally, theoretical formulation of diets using poultry, pig or ruminant ME values clearly resulted in underestimation with respect to the ME values of the experimental diet for ostriches. Determination of ME standards for ostrich feedstuffs is consequently a prerequisite for correct diet formulation and also in order to study nutritional requirements of ostriches. According to the between- and within-animal variation as well as experience gained with the experimental procedures during this study, an experimental design utilizing five ostriches, 60–90 days old, and a total collection period of five days allowing an adaptation period of 14 days for different feedstuffs, is suggested.

Conclusions

The results of this study provide conclusive proof that ostriches effectively digest plant fibre, more specifically hemicellulose (66%) and cellulose (38%), which could make a positive contribution to the apparent metabolizable energy of the diet consumed and seems to be independent of live mass. Since low rates of digesta passage are generally associated with increased digestion, increased fermentative microbial activity and increased water absorption (Warner, 1981) together with electrolyte absorption (Skadhauge *et al.*, 1984), the long retention time in the gastro-intestinal tract together with advantageous pH values (see Figure 3), provide a suitable environment for fermentative microflora especially in the enlarged hindgut of ostriches (Swart *et al.*, 1993). Furthermore, the way ostriches subject diet particles to gastric grinding and digestion in a relatively strong acid environment (pH 1.2–2.1) in the proventriculus and gizzard, could play a major part in the exposure of fibre fractions to microbial fermentation in the lower intestinal tract as suggested by Skadhauge *et al.* (1984) and Swart *et al.* (1987a).

However, an important question remains as to whether energy digested and absorbed in the hindgut, presumably liberated by microbial fermentation, is utilized with the same efficiency compared to that generated and absorbed in the foregut. To answer this question, microbial fermentation in the gastro-intestinal tract of ostriches should be quantified. Furthermore, the efficiency of energy utilization from different feedstuffs at different fibre levels, needs to be quantified in order to evaluate ostrich ME values as a criterion for evaluating feedstuffs for ostrich production in future.

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