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The effect of dietary energy and protein levels on production in breeding female ostriches

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Abstract 1. In a study spanning two breeding seasons, we assessed the effect of different dietary energy and protein levels on body mass, body condition, and egg production of female ostriches.

2. During the first breeding season, groups were given diets with energy concentrations of 8·5, 9·5 and 10·5 MJ/kg dry mass (DM) metabolisable energy (ME) and protein concentrations of 135, 150 and 165 g/kg. In the second breeding season, groups were given diets with ME of 7·5, 8·5 and 9·5 MJ/kg and protein contents of 105, 120 and 135 g/kg.

3. Body mass of birds on diets of 7·5 and 8·5 MJ/kg ME decreased significantly in the course of the breeding season compared with birds fed on diets with higher energy contents and body measurements decreased, suggesting a loss of body condition.

4. Females fed on diets containing only 7·5 MJ/kg ME produced significantly fewer eggs at significantly longer intervals, resulting in fewer chicks hatched.

5. There was no significant difference in egg mass, initial chick mass, chick survival to one month of age and body mass of chicks at one month.

6. Dietary protein concentrations had no effect on egg production, egg mass, hatchability, initial chick mass, chick survival or chick mass at one month old.

7. The female ostriches regained their original body mass during the 4-month rest period between breeding seasons, but significant differences in some parameters during the second breeding season suggest that they may not have fully recovered their body condition.

8. A dietary energy content of 7·5 MJ/kg proved to have an adverse effect on egg production by breeding female ostriches, and it may be concluded from this study that a diet containing 8·5 MJ ME/kg DM and 105 g/kg protein should be regarded as the minimum that can be used for breeding female ostriches without compromising egg production.

INTRODUCTION

Adequate and appropriate nutrition is essential for the production of high quality commercially farmed animal species. South Africa has had a thriving ostrich industry for over a century. Despite this, our knowledge of the nutritional needs of ostriches is limited. The industry has consequently relied heavily on data derived from poultry, a practice that has recently been criticised (Cilliers and Angel, 1999). Egg production in breeding female birds is costly, in terms of both energy and specific nutrients, but whether egg production is limited by energy, protein, or specific nutrients seems to differ in different birds (see, for example, Bolton *et al.*, 1992; Williams, 1996; Nager *et al.*, 1997; Ramsay and Houston, 1997). A scarcity of nutritional data specific to breeding ostriches has sometimes been suggested to be the main reason for poor egg production during the breeding season. The specification for ostrich feeds in the Farm Feeds Act of 1947 is a minimum of 12% protein for *ad libitum* feeding and 13% for restricted feeding. The current trend, however, is to feed breeding ostriches on high energy and protein diets in an attempt to increase productivity. This practice does not necessarily always have beneficial effects on egg production. Rosebrough *et al.* (1983) found that energy and protein utilisation for egg production in large white turkeys was better in birds fed lower protein and energy diets and Scott *et al.* (1999) found that feeding laying hens diets containing protein levels between 16 and 19% had no significant effect on egg production. Similarly, Goerzen *et al.* (1996) reported no difference in egg production between hens fed *ad libitum* and those on a restricted diet. Malden

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et al. (1979) indicated that if broiler breeders were allowed to get too fat, egg production would be depressed during the laying period possibly because, as suggested by Badley (1997), excess fat deposits can prevent eggs from being deposited in the oviduct. The use of energy values derived from poultry when formulating diets for breeding ostriches has led to obesity in breeding birds (Cilliers and Angel, 1999), which may similarly affect breeding performance (Angel, 1993).

Energy and protein are the most expensive constituents of commercial animal feeds and the above information indicates that high levels of these in ostrich feeds may not be necessary and may even be detrimental. Studies by Salih *et al.* (1998) and Brand *et al.* (2000*b*), for example, indicate that feeding young ostriches lower energy diets had no effect on their growth rate. Lower energy diets consequently can be used when growing/finishing ostriches to slaughter age with no adverse effects on production, but with obvious financial implications (Brand *et al.*, 2000*a*). Ostriches have an enhanced digestive capacity compared with poultry and some other domestic stock (Cilliers, 1994; Brand, 2000) and Skadhauge *et al.* (1984) reported that ostriches could feed on lower quality fibrous plants because of the well-developed caecum and colon. The hindgut of ostriches is also adapted for hemicellulose and cellulose fermentation, and the production of volatile fatty acids in the hindgut can provide between 12 and 76% of the daily intake of metabolisable energy in growing ostriches (Swart, 1988) and presumably also in adults. High levels of dietary protein also appear unnecessary for ostriches. The growth rate and food consumption of growing ostriches (60 to 110 kg) fed on a 14% protein diet was better than that of birds fed higher protein level diets (Swart and Kemm, 1985).

While there appears to be some evidence that growing ostriches can be given low-energy and low-protein diets without adversely affecting their growth, it is not known what effects such diets may have on breeding birds. Because commercially farmed ostriches have an extended breeding season during which individual females may lay up to 50 or more eggs, the demands for energy, protein and specific nutrients for egg formation may be especially high and nutrition may play a particularly important role in egg production. Inadequate provision of energy and protein in their diets may lead to fewer small, poor quality eggs and, consequently, poor quality hatchlings with reduced fitness (Williams, 1994; Deeming *et al.*, 1996). At the same time, in the present economic climate, it is necessary to find cost-effective diets for breeding birds without compromising egg production and hatchability. In this study, we assessed the effects of dietary energy and protein levels on the body condition and productivity of breeding female ostriches.

MATERIALS AND METHODS

Experimental birds used in the study were African black ostriches from the commercial breeding flock at the Little Karoo Agricultural Development Centre near Oudtshoorn, South Africa. The management of the breeding flock was described by Van Schalkwyk *et al.* (1996), and the collection, subsequent treatment, and incubation of the eggs by Van Schalkwyk (1998).

The trial ran over two breeding seasons (1998/1999 and 1999/2000). Ninety pairs of adult breeding ostriches were divided randomly into 9 groups of 10 pairs/group during each experimental year. Groups therefore comprised different breeding pairs during each successive breeding season. Each breeding pair was kept in its own separate breeding pen throughout the breeding season. During the first breeding season, groups were given diets with energy concentrations of 8·5, 9·5 and 10·5 MJ/kg dry mass (DM) metabolisable energy (ME) and protein concentrations of 135, 150 and 165 g/kg. Corresponding lysine levels were 6·5, 7·5 and 8·5 g/kg. The 90 pairs of breeders were again randomly divided for the second season and the groups were given diets with energy contents of 7·5, 8·5 and 9·5 MJ/kg ME and protein contents of 105, 120 and 135 g/kg. Corresponding lysine levels were 4·9, 5·9 and 6·9 g/kg. Diets (Tables 1 and 2) were formulated according to requirements and composition values presented in the Elsenburg Ostrich Feed Database (Brand, 2000). During both the first and second seasons, the diets were analysed according to AOAC methods (AOAC, 1984) to determine protein and lysine concentrations. The diets for the second season were analysed further to determine the fat, calcium and phosphorus contents. The feed was milled to pass through a 3-mm sieve and pelleted. The breeding birds were fed three times a week and each bird was given 2·5 kg DM/d throughout the breeding season (June to January). Ostriches deposit fat in a sub-peritoneal and subcutaneous layer over the sternum and ribs (Deeming *et al.*, 1996), and measurements of thoracic and abdominal girth, in conjunction with body mass, can thus provide an indication of body condition. We consequently measured the body mass, thoracic girth, abdominal girth and tail circumference of the female ostriches at the beginning and end of the breeding season. Laying interval, egg production, egg mass and fate of eggs set in the incubator were recorded throughout the

Table 1. *Composition of the 9 experimental diets (kg/tonne) fed to breeding birds during the first breeding season (1998/1999). Asterisks indicate components that were analysed*

Ingredients	Diet 1	Diet 2	Diet 3	Diet 4	Diet 5	Diet 6	Diet 7	Diet 8	Diet 9
Lucerne meal	605·5	605·5	605·5	605·5	605·5	605·5	605·5	605·5	605·5
Oat bran	255·0	239·0	239·0	127·5	119·5	111·5	0·0	0·0	0·0
Maize meal	0·0	0·0	0·0	100·0	100·0	100·0	200·0	200·0	200·0
Soybean oilcake	11·2	64·6	64·6	5·6	57·9	110·2	0·0	51·2	102·3
Barley	78·2	39·1	39·1	111·2	66·2	21·3	144·1	93·3	42·5
Dicalcium phosphate	20·0	20·0	20·0	20·0	20·0	20·0	20·0	20·0	20·0
Limestone	7·5	5·8	5·8	8·6	7·8	7·0	9·8	9·8	9·8
Monocalcium phosphate	13·9	17·0	17·0	13·3	14·5	15·7	12·6	12·0	11·3
Salt	5·0	5·0	5·0	5·0	5·0	5·0	5·0	5·0	5·0
Min. and vit. premix	2·0	2·0	2·0	2·0	2·0	2·0	2·0	2·0	2·0
Synthetic lysine	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
Synthetic methionine	1·7	2·0	2·0	1·4	1·7	2·0	1·0	1·3	1·6
TOTAL	1000·0	1000·0	1000·0	1000·0	1000·0	1000·0	1000·0	1000·0	1000·0
Composition (calculated)									
ME, MJ/kg	8·5	8·5	8·5	9·5	9·5	9·5	10·5	10·5	10·5
Protein, g/kg*	135	150	165	135	150	165	135	150	165
Lysine, g/kg	6·5	7·5	8·5	6·5	7·5	8·5	6·5	7·5	8·5
Met-cys, g/kg	4·5	5·3	6·1	4·5	5·3	6·1	4·5	5·3	6·1
Tryptophan, g/kg	2·5	2·9	3·2	2·6	2·9	3·3	2·6	3·0	3·3
Threonine, g/kg	4·8	5·7	6·5	5·1	5·9	6·7	5·3	6·1	6·8
Crude fibre, g/kg	256·0	250·7	245·3	225·5	223·3	221·2	195·0	196·0	197·0
Fat, g/kg	14·0	13·5	13·0	17·1	16·5	15·9	20·2	19·5	18·7
Calcium, g/kg	20	20	20	20	20	20	20	20	20
Phosphorus, g/kg	8·0	8·8	9·6	8·0	8·4	8·8	8·0	8·0	8·0

Table 2. *Composition of the 9 experimental diets (kg/tonne) fed to breeding birds during the second breeding season (1999/2000). Asterisks indicate components that were analysed*

Ingredients	Diet 1	Diet 2	Diet 3	Diet 4	Diet 5	Diet 6	Diet 7	Diet 8	Diet 9
Lucerne meal	138·6	69·3	0·0	280·5	216·7	152·9	422·3	364·0	305·7
Oat bran	700·0	701·7	703·3	486·6	502·7	518·8	273·2	303·8	334·3
Maize meal	14·0	7·0	0·0	130·8	108·5	86·2	247·6	210·0	172·4
Soybean oilcake	81·5	91·7	102·0	40·8	78·0	115·2	0·0	64·2	128·4
Cottonseed oilcake	0·0	59·6	119·2	0·0	29·8	59·6	0·0	0·0	0·0
Dicalcium phosphate	39·9	37·4	34·8	39·6	37·6	35·7	39·3	37·9	36·5
Limestone	13·9	20·8	27·7	10·3	15·1	19·9	6·6	9·3	12·0
Salt	5·0	5·0	5·0	5·0	5·0	5·0	5·0	5·0	5·0
Min. and vit. premix	4·0	4·0	4·0	4·0	4·0	4·0	4·0	4·0	4·0
Synthetic lysine	1·3	1·6	1·8	1·2	1·1	0·9	1·1	0·6	0·0
Synthetic methionine	1·8	2·0	2·2	1·3	1·6	2·0	0·9	1·3	1·7
TOTAL	1000·0	1000·0	1000·0	1000·0	1000·0	1000·0	1000·0	1000·0	1000·0
Composition (calculated)									
ME, MJ/kg	7·5	7·5	7·5	8·5	8·5	8·5	9·5	9·5	9·5
Protein, g/kg*	105	120	135	105	120	135	105	120	135
Lysine, g/kg*	5·4	5·7	6·1	5·4	5·4	6·1	5·4	5·7	6·1
Met-cys, g/kg	3·7	4·6	5·4	3·7	4·5	5·4	3·7	4·5	5·4
Tryptophan, g/kg	1·2	1·3	1·4	1·6	1·7	1·9	1·9	2·1	2·3
Threonine, g/kg*	3·3	3·5	3·8	3·3	3·5	4·8	3·3	3·5	3·8
Crude fibre, g/kg	235·5	222·6	209·6	220·4	211·0	201·7	205·3	199·5	193·7
Fat, g/kg*	16·6	19·2	18·4	16·6	17·3	18·4	21·4	21·2	18·4
Calcium, g/kg*	15·5	15·1	19·5	18·6	18·3	19·9	17·9	18·8	17·2
Phosphorus, g/kg*	9·3	8·7	11·3	9·8	10·4	10·6	10·3	10·5	10·2

breeding season, as was the mass of successfully hatched chicks at 4 weeks of age. Data were analysed according to a 3 energy × 3 protein factorial design with energy and protein levels as main factors (Statgraphics, 1991).

As is common practice on South African farms, females were separated from males after the breeding season for a 4-month rest period. During this period (February to May), the birds were fed on a maintenance diet (Table 3). In the first rest period, the body mass of females was determined monthly to monitor changes, but body mass was determined only at the beginning and end of the second rest period.

Table 3. *Composition of the diet (kg/tonne) fed to females during the rest period*

Ingredients	Diet
Lucerne	580·6
Oat bran	138·1
Barley	249·0
Limestone	25·0
Salt	5·0
Min. and vit. premix	2·0
Synthetic methionine	0·4
TOTAL	1000·0
Composition (calculated)	
ME, MJ/kg	9·1
Protein, g/kg	133
Lysine, g/kg	6·3
Met-cys, g/kg	3·5
Threonine, g/kg	5·0
Tryptophan, g/kg	3·0

RESULTS

No interactions were observed between energy and protein levels ($P > 0{\cdot}70$). The main effects of the different energy and protein levels in the diet are consequently presented separately.

Dietary energy levels

Mean body mass of female ostriches assigned to the different dietary energy levels at the beginning of the first breeding season averaged between 111 and 115 kg and did not differ between the different experimental groups (Table 4). At the end of the breeding season, however, females fed on the diet containing 8·5 MJ/kg ME had lost 8·5 kg body mass, those fed on the 9·5 MJ/kg ME diet had not changed mass and those fed on the 10·5 MJ/kg ME diet had gained 5 kg body mass. The body mass of birds given the low-energy diet was less than that of females given the higher energy diets (Table 4).

At the beginning of the first breeding season there was no difference in the mean thoracic girth of females fed the different diets (Table 4). At the end of the season the thoracic girth of birds on the 8·5 MJ/kg ME diet had decreased and was significantly less than that of birds given the higher energy diets ($P = 0{\cdot}001$), in which the thoracic girth had increased by 2·8 and 3·1 cm, respectively. Abdominal girth and tail circumference also did not differ for the various groups at the beginning of the season ($P > 0{\cdot}05$) and both measurements decreased in all birds, with the largest decrease being shown by birds given the 8·5 MJ/kg ME diet. By the end of the breeding season these measured significantly less than in birds given the higher energy diets (Table 4). Although the body mass of females fed on the 8·5 MJ/kg ME diet was significantly less at the end of the breeding season than that of females fed on higher energy diets, their body mass increased on the maintenance diet during the rest period and by the third month of the rest period their mean mass was indistinguishable from that of the other females (Table 4).

Mean body mass of females at the onset of the second breeding season averaged between 116 and 119 kg and did not differ significantly (Table 4). The body mass of all females decreased over the course of the second breeding season, with those birds fed on the diet containing 7·5 MJ/kg ME losing 24·5 kg and those fed on diets with 8·5 and 9·5 MJ/kg losing an average of 12 kg. The body mass of birds on the lowest energy diet was significantly lower at the end of the breeding season than that of the females fed diets of 8·5 and 9·5 MJ/kg (Table 4). There were no differences ($P > 0{\cdot}05$) in the thoracic girth of birds on the different diets at the beginning of the second season. Thoracic girth of birds in all groups decreased over the course of the season, with the biggest decrease (8·8 cm) being measured in the birds fed on the lowest energy diet and the smallest decrease (5·3 cm) in birds fed on the highest energy diet. The difference in thoracic girth at the end of the season was significantly lower in birds fed on the 7·5 compared to those fed on the 9·5 MJ/kg ME diet ($P < 0{\cdot}02$). In contrast to thoracic girth, abdominal girth and tail circumference differed significantly in experimental groups at the onset of the second breeding season, with abdominal girth and tail circumference of the group assigned to the low-energy diet being significantly less than in the group assigned to the 9·5 MJ/kg diet and to both groups assigned to the higher energy diets (Table 4). Abdominal girth decreased in all experimental groups by between 8 and 15 cm. The decrease was significantly lower in the group given 8·5 MJ/kg than in the 7·5 and 9·5 MJ/kg groups. Tail circumference changed little in the birds but at the end of the season also measured significantly less in birds fed the lowest energy diet compared with the other two groups. As with the first breeding season, the body mass of all birds increased during the rest period, and by the end of the 4-month period it was statistically indistinguishable between diets.

The number of eggs produced by females during the first breeding season averaged between 44 and 54 and there was no difference between diet groups (Table 4). Similarly, there were no significant differences in the mass of eggs laid by the various groups, the laying interval, the number of chicks hatched, the number of chicks surviving to one month old or the body mass of chicks at one month (Table 4).

Table 4. *The effect of different dietary energy level on live body mass, body measurements and production of female ostriches over two breeding seasons (mean ± SE)*

Production parameters	Energy level (MJ/kg) first season (1998)			Significance level (P)	Energy level (MJ/kg) second season (1999)			Significance level (P)
	8·5	9·5	10·5		7·5	8·5	9·5	
Number of breeding pairs, *n*	30	30	30		30	30	30	
Starting mass, kg	111·3 ± 2·9	114·7 ± 2·9	112·8 ± 2·9	0·705	118·9 ± 2·8	116·1 ± 2·7	116·7 ± 2·7	0·659
End mass, kg	102·7 ± 2·5[a]	114·6 ± 2·5[b]	117·9 ± 2·5[b]	0·001	94·5 ± 2·5[a]	103·6 ± 2·4[b]	104·8 ± 2·4[b]	0·007
Mass change, kg	−8·5 ± 2·8[a]	−0·1 ± 2·8[b]	5·1 ± 2·8[b]	0·003	−24·5 ± 2·0[a]	−12·4 ± 2·0[b]	−11·9 ± 2·0[b]	0·001
Thoracic girth, cm								
Start of breeding season	118·6 ± 0·8	118·8 ± 0·8	121·1 ± 0·8	0·064	123·0 ± 1·1	124·2 ± 1·1	123·7 ± 1·1	0·735
End of breeding season	117·3 ± 1·1[a]	121·6 ± 1·1[b]	124·2 ± 1·1[b]	0·001	114·2 ± 1·1[a]	117·0 ± 1·0[ab]	118·4 ± 1·0[b]	0·021
Abdominal girth, cm								
Start of breeding season	145·3 ± 1·6	145·8 ± 1·6	147·5 ± 1·6	0·619	141·4 ± 1·3[a]	142·9 ± 1·3[ab]	145·6 ± 1·3[b]	0·080
End of breeding season	137·4 ± 1·6[a]	143·9 ± 1·6[b]	143·5 ± 1·6[b]	0·007	133·7 ± 1·5[b]	128·3 ± 1·5[a]	135·6 ± 1·5[b]	0·002
Tail circumference, cm								
Start of breeding season	105·5 ± 1·3	106·4 ± 1·3	106·2 ± 1·3	0·897	95·2 ± 1·6[a]	100·9 ± 1·6[b]	101·5 ± 1·6[b]	0·009
End of breeding season	100·3 ± 1·1[a]	103·3 ± 1·1[ab]	104·4 ± 1·1[b]	0·042	95·9 ± 1·4[a]	99·4 ± 1·3[ab]	101·3 ± 1·3[b]	0·023
Rest period								
Rest period starting mass, kg	102·7 ± 2·5[a]	114·6 ± 2·5[b]	117·9 ± 2·5[b]	0·001	93·9 ± 2·6[a]	102·2 ± 2·5[b]	105·0 ± 2·5[b]	0·007
Rest period, first month, kg	106·7 ± 2·8[a]	110·9 ± 2·8[ab]	117·9 ± 2·8[b]	0·019	–	–	–	–
Rest period, second month, kg	118·1 ± 2·8[a]	126·4 ± 2·9[b]	127·4 ± 2·8[b]	0·044	–	–	–	–
Rest period, third month, kg	119·4 ± 2·8	125·7 ± 2·9	127·6 ± 2·8	0·106	–	–	–	–
Rest period, fourth month, kg	112·8 ± 2·7	117·5 ± 2·9	120·9 ± 2·8	0·108	113·1 ± 2·9	117·6 ± 3·9	113·6 ± 3·2	0·650
Production								
Egg production, *n*	50·3 ± 4·2	53·9 ± 4·2	43·7 ± 4·1	0·215	36·0 ± 4·0[a]	51·1 ± 3·9[b]	54·0 ± 3·8[b]	0·037
Laying interval, d	5·9 ± 0·7	5·1 ± 0·7	6·7 ± 0·7	0·303	11·5 ± 1·4[a]	6·9 ± 1·4[b]	7·4 ± 1·4[b]	0·042
Live chicks hatched, %	62·9 ± 4·6	59·5 ± 4·7	66·9 ± 4·4	0·507	54·9 ± 4·5	45·3 ± 4·3	57·2 ± 4·3	0·124
Hatchling mass, g	881 ± 15·2	891 ± 16·2	897 ± 15·2	0·753	872 ± 15·8	831 ± 15·3	865 ± 15·3	0·150
Number of chicks per hen at one month, *n*	12·7 ± 2·0	13·5 ± 2·0	13·1 ± 2·0	0·956	8·4 ± 1·6	10·3 ± 1·5	12·6 ± 1·5	0·167
One-month-old mass, kg	3·3 ± 0·1	3·2 ± 0·1	3·4 ± 0·1	0·684	2·0 ± 0·1	2·0 ± 0·1	1·9 ± 0·1	0·748
Egg mass								
Initial mass, g	1473·2 ± 20·1	1475·5 ± 20·6	1477·6 ± 20·2	0·982	1429·6 ± 19·8	1409·3 ± 19·3	1459·4 ± 19·1	0·186

[a, b]Denote significant ($P \leq 0{\cdot}05$) difference within rows.

Egg production in the second season ranged from 36 to 54 eggs/female. Birds on the 7·5 MJ/kg ME diet had a lower egg production than females on 8·5 and 9·5 MJ/kg ME ($P<0·05$) because of a significantly longer laying interval ($P<0·05$). There was, however, no difference in the mean mass of eggs ($P>0·10$). The percentage of chicks hatched was not affected by diet ($P>0·10$) and there was no significant difference in the body mass of chicks hatched, their survival to one month old or their body mass at one month old. The body mass of chicks at one month old was substantially lower than that of chicks hatched in the first breeding season. It is unlikely that the poor growth of chicks is related to female nutrition in the second breeding season because hatchling masses were similar to the previous year. The relatively low mass at one month old is more likely to reflect generally poor growth of chicks in this particular year because chicks other than those from experimental birds were similarly affected.

Dietary protein levels

The body mass of females given diets with different protein concentrations averaged between 111 and 117 kg at the beginning of the first breeding season and their mean body mass did not differ (Table 5). By the end of the breeding season, females on 135 and 150 g/kg protein had lost about 2 kg and those on 165 g/kg protein had gained 1·0 kg, but the mean mass of the groups did not differ (Table 5). Experimental groups also did not differ in mean thoracic girth, abdominal girth or tail circumference at the beginning of the season. Thoracic girth of birds on all dietary protein contents increased slightly, whereas abdominal girth and tail circumference decreased. There were, however, no significant differences in any measurements between groups at the end of the season (Table 5).

The body mass of all birds increased during the rest period and they began the second breeding period heavier than they had been at the start of the previous season but the mean body mass of groups assigned to different dietary protein contents did not differ (Table 5). Thoracic girth, abdominal girth and tail circumference also did not differ significantly in the various groups. During the second breeding season, the body mass of all groups of birds decreased. Loss of body mass averaged between 14·5 and 18 kg, but there was no trend between the extent of such loss and dietary protein, and mean body mass did not differ significantly between the various groups at the end of the breeding season. Similarly, no significant differences in measurements were found in mean body mass, thoracic girth, abdominal girth or tail circumference at the end of the second breeding season due to protein levels, although measurements of thoracic girth and abdominal girth decreased substantially in all groups (Table 5). Again, the body mass of all birds increased during the post-breeding rest period.

Females given diets with different protein contents produced a mean of between 48 and 52 eggs/female over the first breeding season and between 41 and 50 eggs/female for the second season, but egg production did not differ in birds on different dietary protein contents (Table 5) nor was there any difference in the mean initial mass of eggs laid. The first breeding season was 221 d, which gives a mean laying interval ranging from 5·1 to 6·7 d. The second breeding season was 280 d and the laying interval ranged from 7·9 to 9·7 d. There was no significant difference between the various treatments. No difference was evident in the percentage of chicks hatched from eggs produced by birds on different dietary protein (Table 5). There were no differences in the hatching mass of chicks, their survival to one month old or their body mass at one month old.

DISCUSSION

Egg production in birds is costly in terms of energy and nutrients. The required energy and nutrients for egg formation may be derived from daily food intake or from stored reserves. Daily food intake is probably a more important source of nutrients for small birds than stored reserves, but is also likely to be important in birds that lay many eggs or in birds that continue to lay replacement eggs if eggs are removed (Carey, 1996). This applies particularly to commercial species like poultry and ostriches, where the principal objective is to maximise egg or chick production. Provision of adequate and appropriate nutrition is therefore especially important in such species. If energy or nutrients are limiting, birds can compensate by reducing egg size or the number of eggs laid, or by increasing the laying interval and spreading the cost of egg formation over a longer period. Young breeder fowls given diets containing different amounts of protein, for example, laid similar sized eggs but those given low-protein diets laid significantly fewer eggs (Lilburn *et al.*, 1987). In ostriches, egg production was not affected in birds fed on diets containing between 8·5 and 10·5 MJ/kg ME, but birds fed on diets with only 7·5 MJ/kg ME laid significantly fewer eggs at a laying interval almost twice that of birds fed higher energy diets. This resulted in fewer chicks hatched. Furthermore,

Table 5. *The effect of different dietary protein level on live body mass, body measurements and production of female ostriches over two breeding seasons (mean ± SE)*

Production parameters	Protein (%) first season (1998)			Significance level (*P*)	Protein (%) second season (1999)			Significance level (*P*)
	13·5	15·0	16·5		10·5	12·0	13·5	
Number of breeding pairs, *n*	30	30	30		30	30	30	
Starting mass, kg	116·6 ± 2·9	111·4 ± 2·9	110·8 ± 2·9	0·312	119·9 ± 2·8	112·9 ± 2·8	118·9 ± 2·7	0·530
End mass, kg	114·4 ± 2·5	109·1 ± 2·5	111·8 ± 2·5	0·320	103·5 ± 2·5	98·4 ± 2·5	101·0 ± 2·4	0·575
Mass change, kg	−2·2 ± 2·8	−2·3 ± 2·8	1·0 ± 2·8	0·632	−16·4 ± 2·0	−14·5 ± 2·0	−17·9 ± 2·0	0·471
Thoracic girth, cm								
Start of breeding season	120·6 ± 0·8	119·7 ± 0·8	118·2 ± 0·8	0·126	123·4 ± 1·1	123·0 ± 1·1	124·5 ± 1·1	0·607
End of breeding season	121·1 ± 1·1	121·1 ± 1·1	120·9 ± 1·1	0·993	117·1 ± 1·0	115·1 ± 1·0	117·4 ± 1·1	0·242
Abdominal girth, cm								
Start of breeding season	146·5 ± 1·6	147·0 ± 1·6	145·1 ± 1·6	0·677	143·7 ± 1·3	142·4 ± 1·3	143·8 ± 1·3	0·692
End of breeding season	142·3 ± 1·6	141·3 ± 1·6	141·3 ± 1·6	0·862	133·6 ± 1·5	132·1 ± 1·5	132·0 ± 1·5	0·698
Tail circumference, cm								
Start of breeding season	106·9 ± 1·3	105·2 ± 1·3	106·0 ± 1·3	0·657	100·7 ± 1·6	96·5 ± 1·6	100·5 ± 1·6	0·117
End of breeding season	104·1 ± 1·1	101·2 ± 1·1	102·7 ± 1·1	0·196	99·1 ± 1·4	97·8 ± 1·4	99·8 ± 1·3	0·561
Rest period								
Rest period starting mass, kg	114·4 ± 2·5	109·1 ± 2·5	111·8 ± 2·5	0·320	102·4 ± 2·6	98·6 ± 2·5	100·1 ± 2·4	0·575
Rest period, first month, kg	115·4 ± 2·8	110·7 ± 2·8	109·4 ± 2·8	0·279	–	–	–	–
Rest period, second month, kg	123·1 ± 2·8	124·6 ± 2·8	124·2 ± 2·9	0·924	–	–	–	–
Rest period, third month, kg	126·7 ± 2·8	123·8 ± 2·8	122·2 ± 2·9	0·511	–	–	–	–
Rest period, fourth month, kg	119·4 ± 2·8	116·0 ± 2·7	115·7 ± 2·8	0·586	114·4 ± 2·9	115·8 ± 3·9	114·0 ± 3·1	0·938
Production								
Egg production, *n*	48·8 ± 4·2	47·7 ± 4·1	51·5 ± 4·2	0·800	49·7 ± 3·8	41·4 ± 3·9	50·0 ± 4·0	0·218
Laying interval, d	6·1 ± 0·7	5·6 ± 0·7	6·1 ± 0·7	0·889	7·9 ± 1·4	9·7 ± 1·4	8·3 ± 1·4	0·604
Live chicks hatched, %	62·5 ± 4·7	69·3 ± 4·5	57·5 ± 4·5	0·183	53·2 ± 4·3	47·4 ± 4·5	56·8 ± 4·4	0·321
Hatchling mass, g	892 ± 16·2	888 ± 15·3	889 ± 15·2	0·988	870 ± 15·8	847 ± 15·5	851 ± 15·1	0·560
Number of chicks per hen at one month	12·2 ± 2·0	14·6 ± 2·0	12·6 ± 2·0	0·659	11·3 ± 1·6	7·8 ± 1·5	12·2 ± 1·5	0·108
One-month-old mass, kg	3·5 ± 0·1	3·3 ± 0·1	3·1 ± 0·1	0·113	2·1 ± 0·1	1·9 ± 0·1	2·0 ± 0·1	0·123
Egg mass								
Initial mass, g	1485·0 ± 20·6	1466·4 ± 20·2	1473·9 ± 20·2	0·811	1435·9 ± 19·8	1423·3 ± 19·4	1439·2 ± 19·0	0·830

the body mass of female ostriches fed on diets with a low-energy content (7·5 and 8·5 MJ/kg ME) generally decreased and was significantly lower by the end of the season than that of birds given a higher energy diet of 9·6 MJ/kg ME. They also showed decreases in thoracic and abdominal girth, suggesting a general loss of body condition. In contrast, different levels of dietary protein between 105 and 165 g/kg had little effect on egg production, laying interval, egg mass or hatchability and, although body mass of birds given diets with different protein content decreased and they lost body condition, body mass and measurements did not differ significantly at the end of the breeding season. These results indicate that, at this stage, energy rather than protein is the main constraint on egg production. This is consistent with results of Lopez and Leeson (1995*a*), who found no difference in egg production between breeding fowls fed on diets with protein levels between 10 and 16%, although birds given the 10% protein diet were significantly lighter than those fed the 16% protein diet, which indicates a loss of body condition. Similarly, Nager *et al.* (1997) found that supplementary feeding with two different levels of protein did not affect egg size or clutch size of great tits (*Parus major*).

These results are, however, contrary to several studies that indicate that protein is the main constraint on egg production in at least some species of birds. In lesser black-backed gulls (*Larus fuscus*), protein reserves, but not fat (energy) reserves, decline during egg formation and the level of protein reserves also determines the ability of birds to lay replacement eggs (Houston *et al.*, 1983). In years of low food availability, clutch size is depressed by protein limitation but not by energy (Bolton *et al.*, 1992). Similarly, captive mallards fed on protein-enriched diets laid more eggs at a faster rate than those given low-protein diets (Eldridge and Krapu, 1988). Food supplementation experiments also suggest a greater significance of protein, rather than energy, in zebra finches (*Taeniopygia guttata*) and blue tits (*Parus caeruleus*), which laid larger eggs when their diets were supplemented with protein than when supplemented with fat (energy) (Williams, 1996; Ramsay and Houston, 1997).

Female nutrition, through egg size and constituents, can also affect hatchling size and fitness (Williams, 1994; Carey, 1996). Zebra finches whose diets were supplemented with protein laid larger eggs with a greater proportion of yolk and albumen protein (Williams, 1996). Egg mass and yolk content of broiler breeders also increased as dietary energy and protein increased (Spratt and Leeson, 1987), and black-backed gulls whose diets were supplemented with fish (protein) not only showed an increase in clutch size, but also laid larger eggs that produced larger and heavier hatchlings (Bolton *et al.*, 1992). In contrast, Lopez and Leeson (1995*b*) and de Brum *et al.* (1996) found that different dietary levels of protein had no effect on offspring performance of broiler breeders when chick mass, growth rate and mortality were used as indicators of offspring performance. In ostriches, different levels of dietary energy and protein, as used in this experiments, had no significant effects on the mean mass of eggs laid, the mean mass of hatchlings, or their survival to one month old. Although there were substantial differences in the mass of chicks at one month old in the two seasons, this appears to be related to factors other than female nutrition.

Although there were no significant differences in egg mass, chick mass and survival between birds given diets with different energy and protein contents in the two successive breeding seasons, substantial differences were evident in the performance of breeding females for those seasons, even among birds given the same diets in both seasons. The laying intervals of birds given the 8·5 and 9·5 MJ/kg diets in the second season were longer ($P \leq 0{\cdot}05$) by 1·0 and 2·3 d, respectively, although there was no significant difference in egg mass, hatchling mass, month-old mass or chick survival. Although the mean mass of birds at the beginning of the second breeding season was slightly greater than at the beginning of the first season, thoracic girth, abdominal girth and tail circumference were generally slightly less, suggesting that the birds had possibly not accumulated adequate body reserves during the 4-month rest period.

These experiments lead to the conclusion that energy content of ostrich diets appears to be the main constraint on egg production during breeding. Birds fed on low-energy diets laid fewer eggs at longer intervals than birds given higher energy diets and lost more body condition over the course of the breeding season. Body mass of birds fed on diets containing 9·5 and 10·5 MJ/kg ME generally increased, or decreased less. In contrast, different concentrations of dietary protein had no significant effects on experimental groups. It may be concluded from this study that a diet containing at least 8·5 MJ ME/kg DM and 105 g/kg protein are sufficient for female breeding ostriches. Future studies are necessary to find the minimal protein and accompanying amino acid requirement for ostrich breeders. In our study, the female birds regained their original live body mass within 4 months during the rest period, but body measurements suggested that they might not have been capable of fully recovering body reserves.

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