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DIURNAL-NOCTURNAL CHANGES IN FOOD INTAKE, GUT STORAGE OF INGESTA, FOOD TRANSIT TIME AND METABOLISM IN GROWING BROILER CHICKENS: A MODEL FOR TEMPORAL CONTROL OF ENERGY BALANCE

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Abstract 1. Diurnal-nocturnal changes in food intake, gut storage of ingesta, food transit time and heat production were studied in male broiler chickens reared under a 14L:10D lighting schedule (lights on from 06:00 to 20:00 h).

2. Food consumption during the scotophase was negligible. Peak food consumption during the photoperiod occurred at the beginning of the photoperiod and in the late afternoon.

3. During the photoperiod, the crop and proventriculus/gizzard contained only small quantities of ingesta. However, at the beginning of the scotoperiod, dried ingesta content of crop and proventriculus/gizzard increased by 10.5- and 2.76-fold respectively. This increase was followed by a gradual decrease towards the end of the scotoperiod.

4. Food transit time during the scotoperiod was significantly longer than that during the photoperiod.

5. The daily pattern of heat production closely followed the 14L:10D lighting schedule. Total heat production during darkness averaged 53% of total heat production during the photoperiod.

6. It was estimated that the storage of energy (as ingesta) in the crop and proventriculus/gizzard, followed by its gradual release and the increased food transit time during the night, contributed 75.5% of nocturnal energy needs. It must be recognised that these mechanisms play a major role in the energy balance of the growing chicken during periods without food intake.

INTRODUCTION

In adult laying hens on a conventional photoperiod, food consumption is almost entirely restricted to the period of light, with a peak in food consumption at the beginning or at the end of the photoperiod, or both (Savory, 1980). In juvenile meat-type chickens not on continuous lighting, feeding is again restricted to the

photoperiod with little or no feeding during the scotoperiod (Weaver and Siegel, 1968; Savory, 1976; Squibb and Collier, 1979; Buyse, 1991). Growing broilers reared on a day-night lighting schedule show peak food consumption in the morning (Savory, 1976, 1980; Buyse, 1991). However, immature broilers can be stimulated to increase their food intake towards the end of the photoperiod by providing a 'cue' (for example, simulating dusk; Savory, 1976) for the imminent onset of darkness. Ingesta from the late-afternoon increase in consumption are stored in both the crop and proventriculus/gizzard and are released gradually during the nocturnal fast. Indeed, from the ingesta content of the crop together with that of the proventriculus/gizzard, it was calculated that more than half of the nocturnal energy needs of laying hens were met by mechanical storage of energy in the upper gastrointestinal tract (Scanes *et al.*, 1987).

The present studies examined in growing male meat-type chickens the same questions. To what extent do the crop and perhaps also the proventriculus/gizzard mechanically store ingesta and thus provide energy for nocturnal needs? Is there an increase in food consumption late in the day which is available for storage? Does the rate of food transit change with time? Does metabolism differ between day and night?

MATERIALS AND METHODS

Studies 1 and 2 employed male broiler chickens (Hubbard) obtained from Avian Services (Frenchtown, New Jersey, USA). The chickens were maintained on a 14L:10D lighting schedule (lights on 06:00 to 20:00 h) with food (Agway Broiler Maker, Bordertown, New Jersey, USA) containing 13.12 MJ metabolisable energy and 220 g crude protein per kg and water freely available. Studies 3 and 4 employed male broiler chickens (Hybro) obtained from a local hatchery (Euribrid, Aarschot, Belgium). Chicks were reared in a floor pen and wood shavings were used as litter. Temperature was set at 30°C during the first week and reduced by 2°C per week until 20°C was reached. The chickens were maintained under 14L:10D (lights on 06:00 to 20:00 h) and a commercial broiler mash containing 13.4 MJ metabolisable energy and 220 g crude protein per kg and water were provided *ad libitum*.

Study 1

Hourly changes in food intake throughout day and nights were measured in 52-d-old male broilers (2730 ± 89 g; $n = 9$). Before and during experimentation, birds were housed in individual cages ($59 \times 51 \times 34$ cm). At hourly intervals starting at 06:00 h, fresh food (250 g) was supplied. Food consumption was determined by difference.

Study 2

In this study, diurnal and nocturnal changes in gastrointestinal tract contents were examined in 32-d-old male broiler chickens (1306 ± 83 g, $n = 9$). Forty nine broilers were housed in groups of 7 in cages measuring $76 \times 117 \times 30$ cm and had free access to food and water. At several time intervals (17:30 to 18:00 h, 20:30 to 21:00

h, 01:00 to 01:30 h, 05:30 to 06:00 h and 13:00 to 13:30 h), 7 broilers were taken at random, stunned and killed in order to determine contents of ingesta within the gastrointestinal tract. Contents of the crop, proventriculus/gizzard, small intestine (duodenum, jejunum, ileum) and large intestine (including caeca and cloaca) were determined by difference (filled organ less emptied, washed and blotted organ). Ingesta from the crop and proventriculus/gizzard were dried to constant weights at 100°C. The dry ingesta contents of both organs were then calculated.

Study 3

In view of the possible changes in gut function, day:night differences in food transit time were also examined. At 21 d of age, 8 chickens were separated from the floor-reared flock and placed in individual cages (50 × 50 × 40 cm) equipped with individual feeding bowls and waterers. At 28 d of age, an estimate of food transit time was made by using food supplemented with either ferric oxide (red colour in food and faeces) or chromic oxide (green colour in food and faeces). At 12:30 h, all chickens were given the ferric oxide-labelled food *ad libitum*. At 19:30 h (0.5 h before the onset of darkness), feeding bowls were replaced by bowls containing chromic oxide-labelled food. At the end of the scotophase (05:30 h), the ferric oxide-labelled food was again provided. The time when the birds began to eat from each labelled food as well as the time of the first appearance of the respective marker in the droppings was recorded. Food transit time was considered to be the time interval between the first meal and the first appearance of the corresponding labelled droppings. This method of determining food transit time has been widely employed (Cherry and Siegel, 1978; Mateos *et al.*, 1982; Teeter *et al.*, 1985; Washburn, 1991) and is an estimate of the minimum passage time: that is, the time for ingesta passing most rapidly through the gastrointestinal tract. The body weight of the chickens averaged 1132 ± 22 g ($n = 8$).

Study 4

At 21 d of age, 10 chickens were equally divided between two open-circuit respiration chambers, with free access to food and water. The respiration chambers are described elsewhere (Michels *et al.*, 1974). After 7 d of acclimatisation, O₂ consumption and CO₂ output were measured for 0.5 h per chamber alternately for 48 h. Heat production was calculated from oxygen uptake and carbon dioxide output according to the formula of Romijn and Lokhorst (1961). At 35 d of age, the same experimental protocol was repeated except that the number of chickens was reduced to three per chamber in order to provide sufficient space for each. Heat production was expressed on a metabolic body weight basis (body weight in kg to the power 0.75). Body weights at 28 d and at 35 d averaged respectively 1145 ± 20 g ($n = 10$) and 1462 ± 30 g ($n = 6$).

Statistical analysis

Statistical analysis was performed by analysis of variance (ANOVA) or by ANOVA for repeated measures (study 1). Means were separated by LSD (study 1).

RESULTS

Study 1

Total food intake over 24 h averaged 180 g per chicken (Table 1). A negligible amount of food was consumed during the scotoperiod, less than 1% of that during the photoperiod. Marked differences in hourly food consumption occurred during the day. Peak consumption occurred at the beginning of the photoperiod (06.00 to 08.00 h) and in the middle of the afternoon (16.00 to 18.00 h) with a smaller peak towards the end of the morning (10.00 to 12.00 h).

TABLE 1

Hourly changes in food consumption of 52-d-old male broilers on a 14L:10D lighting schedule (lights on from 06.00 to 20.00 h) (study 1)

Time of day (h)	Food intake (g/h)
0600-0700	20.1 ± 1.9 ^f
0700-0800	17.2 ± 1.7 ^{ef}
0800-0900	4.9 ± 1.5 ^b
0900-1000	10.6 ± 1.5 ^{cd}
1000-1100	15.1 ± 0.75 ^{de}
1100-1200	14.3 ± 1.5 ^{de}
1200-1300	7.2 ± 1.0 ^{bc}
1300-1400	14.2 ± 2.5 ^{de}
1400-1500	9.9 ± 2.0 ^c
1500-1600	11.1 ± 1.3 ^{cd}
1600-1700	20.3 ± 1.9 ^f
1700-1800	16.1 ± 2.3 ^{ef}
1800-1900	8.7 ± 1.9 ^{bc}
1900-2000	10.1 ± 0.85 ^{cd}
2000-0600	0.12 ± 0.03 ^a

Values are means ± standard error ($n = 7$).

Means not having a superscript in common differ significantly ($P < 0.05$).

TABLE 2

Diurnal-nocturnal variations in wet weight of ingesta (g per chicken) in the gastrointestinal tract of 32-d-old male broilers on a 14L:10D lighting schedule (lights on 06.00 to 20.00 h) (study 2)

Organ	Time of day (h)				
	1730-1800	2030-2100	0100-0130	0530-0600	1300-1330
Crop	2.5 ± 1.6 ^{ab}	28.4 ± 6.9 ^c	11.6 ± 3.5 ^b	0.17 ± 0.08 ^a	2.0 ± 1.9 ^{ab}
Proventriculus/gizzard	10.3 ± 1.0 ^{ab}	22.2 ± 3.0 ^c	11.0 ± 1.9 ^{ab}	7.4 ± 1.5 ^a	15.1 ± 2.0 ^b
Small intestine	22.7 ± 2.3 ^{ab}	23.0 ± 2.2 ^b	29.3 ± 3.3 ^b	13.9 ± 1.7 ^a	26.8 ± 2.3 ^b
Large intestine	17.4 ± 2.5 ^b	28.2 ± 2.7 ^c	17.9 ± 1.3 ^b	9.8 ± 2.5 ^a	16.5 ± 3.2 ^{ab}

Values are means (g) ± standard error ($n = 7$).

Means not having a superscript in common differ significantly ($P < 0.05$).

Study 2

Daily changes in the contents of wet ingesta in the gastrointestinal tract, subdivided into 4 regions, are summarised in Table 2. During the photophase, the

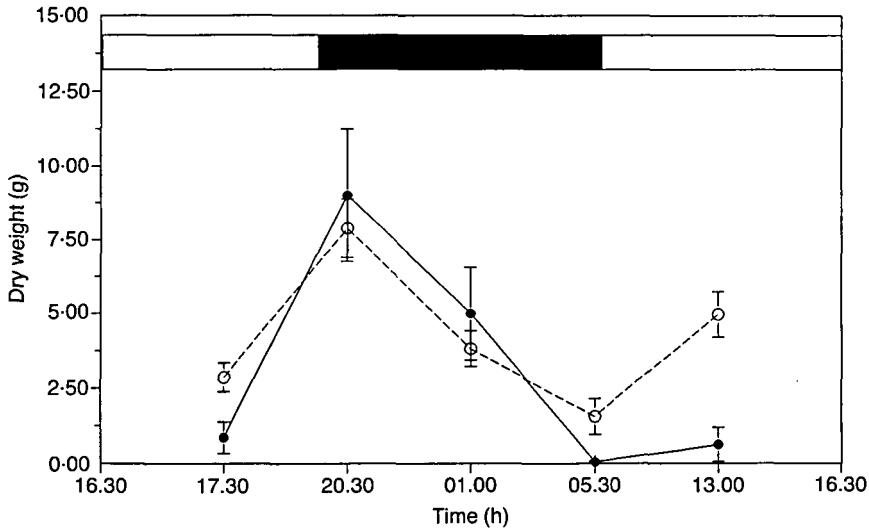


FIG. 1.—Diurnal-nocturnal variation in dried ingesta contents of crop (●) and proventriculus/gizzard (○) in 32-d-old male broilers on a 14L:10D lighting schedule (Study 2).

crop contained only small quantities of ingesta. However, at the first sampling period in the scotophase, the wet ingesta content of the crop had increased 11.4-fold ($P < 0.0001$). There were then progressive decreases ($P < 0.05$) in crop ingesta contents at the second and third nocturnal sampling points. A qualitatively similar pattern was observed with the contents of the proventriculus/gizzard. A 2.16-fold increase ($P < 0.01$) in ingesta contents was observed between the 17.30 to 18.00 h sampling time and the beginning of the scotophase (20.30 to 21.00 h). Subsequently, contents had decreased ($P < 0.05$) by the 01.00 to 01.30 h and 05.30 to 06.00 h sampling times. To preclude the possibility that these changes were attributable to gastric secretion and water consumption, crop and proventriculus/gizzard contents were dried. Water consumption was negligible at night (1.2% of daily consumption) and was hence unlikely to contribute to the apparent weight of ingesta. Changes in dried ingesta contents of these organs are shown in Fig. 1. A similar pattern was observed to that with total ingesta. Dried contents of the crop and proventriculus/gizzard increased ($P < 0.001$) 10.5-fold and 2.76-fold, respectively between the last photophase sampling point (17.30 to 18.00 h) and the beginning of the night (20.30 to 21.00 h). There was a progressive reduction ($P < 0.05$) in ingesta contents at the two successive scotophase sampling points. Changes in the contents of the small and large intestine were also monitored (Table 2). The lowest content of wet ingesta in the small intestine was observed at 05.30 to 06.00 h and the highest (almost double) at 01.00 to 01.30 h. The contents for the time periods between 13.00 to 13.30 h and 01.00 to 01.30 h did not differ significantly from one another. The maximum and minimum contents of wet ingesta of the large intestine and caeca were observed at the beginning and at the end of the scotophase respectively.

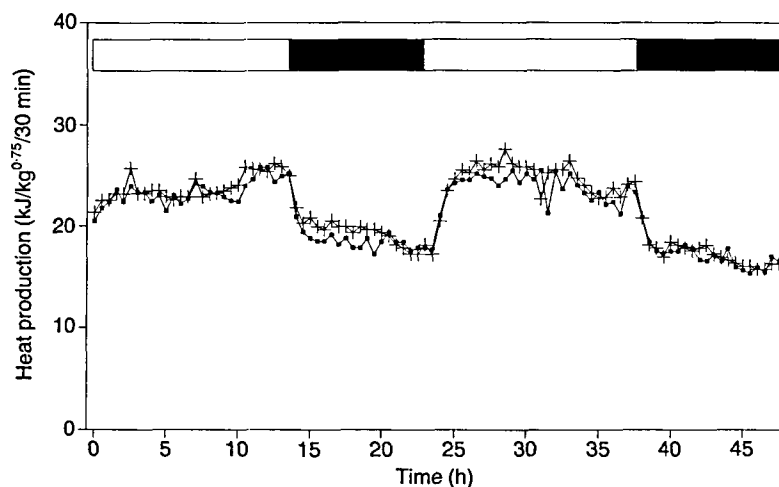


FIG. 2.—Daily variation in heat production ($\text{kJ/kg}^{0.75}/30 \text{ min}$) of 28-d-old male broilers on a 14L:10D lighting schedule (Study 4). Respiration chamber 1 (■), respiration chamber 2 (+).

Study 3

Food transit time was greatest at the end of the photoperiod and the beginning of the scotophase (Table 3). Food transit time at 'morning' and at 'noon' averaged respectively 187 min and 173 min while at the beginning of the scotophase, food transit time increased to 215 min ($P < 0.05$).

TABLE 3

Ingesta transit times of male broiler chickens (28 d of age) reared under 14L:10D lighting schedule (lights on 06:00 h to 20:00 h)

Time	Ingesta transit time (min)
1230	173 ± 14^a
1930	215 ± 13^b
0530	187 ± 28^a

Values are means \pm standard error ($n = 8$).

Different superscripts indicate significant differences ($P < 0.05$).

Study 4

Daily patterns of heat production per kg metabolic body weight are illustrated in Figs 2 and 3. At both ages and respiration chambers, the daily pattern of heat production closely followed the light:dark pattern. At the onset of the photoperiod, heat production increased sharply and then fluctuated throughout the light period. When lights are turned off, heat production decreased steadily. There was a tendency for a continued decrease in heat production throughout the scotoperiod. Total heat

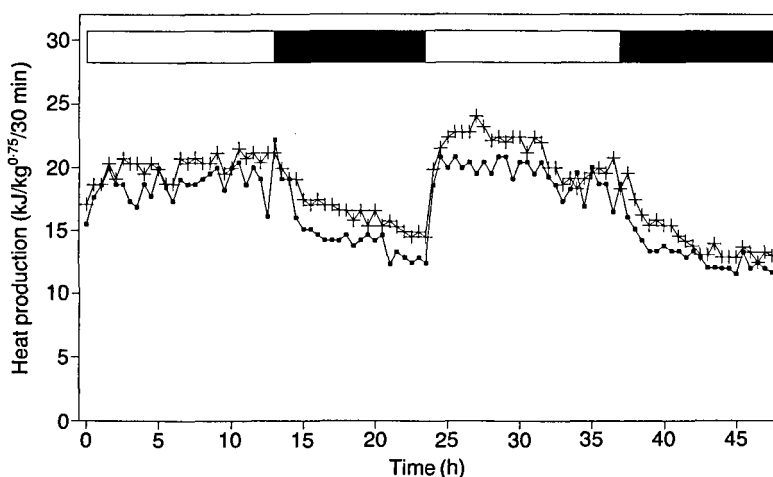


FIG. 3.—Daily variation in heat production ($\text{kJ/kg}^{0.75}/30 \text{ min}$) of 35-d-old male broilers on a 14L:10D lighting schedule (Study 4). Respiration chamber 1 (■), respiration chamber 2 (+).

production during darkness averaged 53% of total heat production during the photoperiod (Table 4).

TABLE 4

Total heat production ($\text{kJ/kg}^{0.75}$) divided over 14L and 10D periods during two consecutive days and at two ages (study 4)

	0-24 h		24-28 h	
	14L	10D	14L	10D
Age 28 d				
Chamber 1	652.4	368.2	664.1	341.7
D:L ratio	0.564		0.514	
Chamber 2	665.5	348.7	692.2	343.5
D:L ratio	0.578		0.496	
Age 35 d				
Chamber 1	523.9	284.8	540.0	256.0
D:L ratio	0.544		0.474	
Chamber 2	560.7	326.7	589.0	282.6
D:L ratio	0.583		0.480	

DISCUSSION

Food consumption was very low at night and there were peaks in consumption immediately following the nocturnal fast and in the late afternoon. This was similar to previous reports (Weaver and Siegel, 1968; Squibb and Collier, 1979; Buyse, 1991). The increased food intake in the late afternoon is first diverted to the crop and then accumulates in the proventriculus/gizzard for utilisation during the nocturnal fast. The large increases in ingesta contents in crop and proventriculus/gizzard at the

TABLE 5

Summary of the diurnal-nocturnal changes in food intake and metabolism

	$\text{kJ/kg}^{0.75}$	$\text{kJ/kg}^{0.75} \text{ h}$
Food intake ¹		
During 14 L	1105	78.9
During 10 D	7.4	0.74
Nocturnal energy loss ²		
From crop and proventriculus/gizzard	251	25.1
Corrected for nocturnal feed intake	244	24.4
Heat production ³		
During 14 L	610	43.6
During 10 D	323	32.2
(ratio L:D)	(52.9)	(73.8)
Nocturnal energy needs ⁴	323	32.3
Energy release from crop and proventriculus/gizzard as % of nocturnal energy needs	(75.5)	(75.5)

¹ Calculated from Table 1 (study 1).² Calculated from Table 2 (study 2).³ Calculated from Table 4 (study 4).⁴ Assumed to be equal to nocturnal heat production.

beginning of the night support the view that both organs have a storage function. In the case of the crop this is in agreement with the conclusion of many others, including Farmer *et al.* (1983); Savory and Hodgkiss (1984); Savory (1985); Scanes *et al.* (1987) and Boa-Amponsem *et al.* (1991).

The changes in food transit time are consistent with the concept of diversion of ingesta from late afternoon and early evening for temporary storage in the crop and also perhaps in the proventriculus/gizzard. In the present study, food transit time was estimated by the time difference between the first meal and the first appearance of marker in faeces. The estimated food transit time was very similar to previous observations (Savory and Hodgkiss, 1984; Teeter *et al.*, 1985; Washburn, 1991; Buyse, 1991). In the present study, the food transit time increased at the beginning of the scotophase. A change in ingesta transit time was perhaps unexpected in view of the absence of changes in transit time following restricted feeding (Washburn, 1991) or between continuous and intermittent lighting (Buyse, 1991). However, the longer food transit time at the beginning of the scotophase is entirely consistent with the observations of the marked increases in the ingesta contents of both the crop and proventriculus/gizzard and with reduced gastric motility during the scotophase (Duke and Evanson, 1976; Roche and Ruckebush, 1978; Shimada, 1986). Thus, both organs store ingesta during the night. Similar increases (more than 10-fold) in crop contents have been observed in birds on a 'skip-a-day' restricted feeding regimen, emphasising the storage role of the crop (Boa-Amponsem *et al.*, 1991). The changes in contents of wet ingesta in the lower gastrointestinal tract may reflect ingestion, gastric secretion and shifts in the time of defaecation.

Heat production (energy expenditure) was reduced during darkness; heat production in the scotophase averaged 53% of that during the photophase. This compared with studies in adult hens (67%, Tullett *et al.*, 1980; 60%, MacLeod *et al.*, 1980; 67%, MacLeod and Jewitt, 1984) and adult males of a dwarf line (60%, Herremans and Decuyper, 1986). Similarly, heat production is reduced by starvation (by 32% in

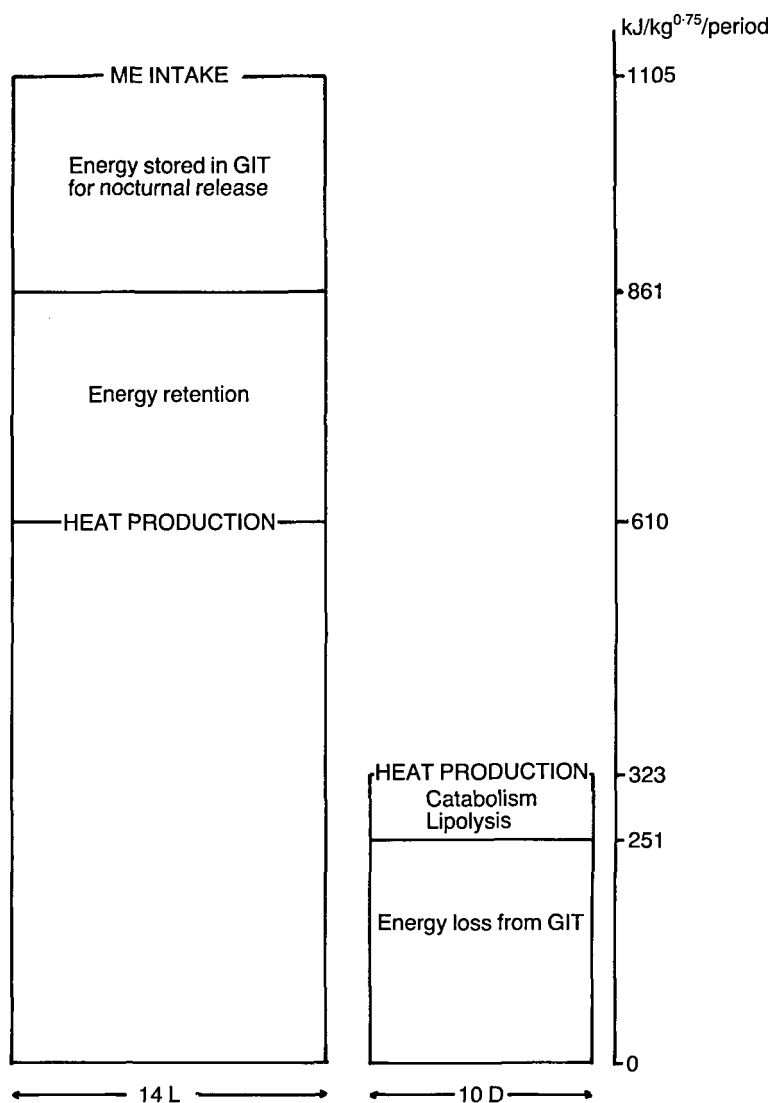


FIG. 4.—A model for the temporal control of energy balance in growing male broiler chickens. GIT: gastrointestinal tract.

adult male chickens and by 41% in adult hens, (MacLeod *et al.*, 1979) which is perhaps analogous to the nocturnal fast. In addition, Michels *et al.* (1985) observed that the variation in oxygen consumption between day and night decreased when ambient temperature was lowered. The nocturnal decline in heat production in young chickens is consistent with the observations of a reduction in heart rate (Klandorf *et al.*, 1978) and in body temperature (Decuyper and Kuhn, 1984).

The decrease in metabolism at night may be attributable to the low circulating

levels of 3,3',5-triiodothyronine (T_3), minimum concentrations of T_3 being observed at night (Klandorf *et al.*, 1978; Decuyper and Kuhn, 1984; Buyse *et al.*, 1987). In chickens, as in other species, thyroid hormones act to increase metabolic rate and heat production. Indirect evidence for this comes from the reports of reduced heat production and body temperature in thyroidectomised chicks (Mellen and Wentworth, 1962; Davison *et al.*, 1980). In addition, Muramatsu *et al.* (1989) demonstrated that intramuscular T_3 injections in young male White Leghorn chicks increased heat production. Alternatively, it may be argued that the lack of food intake at night acts to reduce plasma concentrations of T_3 . Indeed, starvation results both in reduced plasma T_3 in young chickens (May, 1978) and in the abolition of the nocturnal decline in plasma concentrations of T_3 (Decuyper and Kuhn, 1984).

The quantitative importance of the temporary storage of ingesta in the crop and proventriculus/gizzard can be estimated, assuming that nocturnal heat production reflects nocturnal energy needs, that is, zero energy balance, and that the dried weight of ingesta in crop and proventriculus/gizzard is an accurate measure of its energy content. The latter assumption is reasonable in view of the similarity between crop and gizzard carbohydrate content and that of food (Scanes *et al.*, 1987). On the basis of these assumptions, it can be calculated that the storage of energy (as ingesta) in crop and proventriculus/gizzard and its gradual release during the night, may contribute 75.5% of the nocturnal energy needs (Table 5 and Fig. 4). Scanes *et al.* (1987) estimated that, in the adult hen, the crop and proventriculus/gizzard provided 57% of the nocturnal energy needs. However, during the night there may be a shift away from anabolism and growth (for example, muscle protein synthesis) to catabolism and/or liver lipid and glycogen depletion (Wilson and McFarland, 1969) and/or increased lipolytic activity in adipose tissue (Scanes *et al.*, 1987). The mechanical storage of ingesta in the gastrointestinal tract, its gradual release and the longer food transit time during the night are important physiological mechanisms in regulating the energy balance of the growing chicken during periods without food intake.

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