THE EFFECTS OF HIGH AMBIENT TEMPERATURE ON ENERGY EXPENDITURE, UTILISATION AND PARTITION IN THE DOMESTIC FOWL

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ABSTRACT

A project was designed to study the effects of high temperature on food utilisation and growth rate in broiler chickens and to explore methods which might be used to improve performance when animals are kept at high temperature. The effects of high temperature were investigated through measurements and analysis of food and energy intake, energy metabolisability and energy expenditure. Male broilers were used throughout the study. 20 ° and 30 °C, respectively, were used as the moderate and high temperatures. The observations of the study are summarised below.

1- High temperature decreased food intake, growth rate, energy retention as protein and water retention but had no effect on energy retention as fat and little effect on total energy retention.

2- High temperature did not affect the proportion of apparent metabolisable energy retained as protein or the efficiency of energy retention from apparent metabolisable energy. However, it increased the proportion of apparent metabolisable energy retained as fat. The latter effect was attributable to the reduced energy requirement for thermoregulation.

3- Offering the birds a choice between a "high-protein" and a "high-energy" diet did not improve growth when the animals were exposed to high temperature (30 °C). Moreover, choice-feeding led to decreased food intake and, in turn, growth rate in birds kept at moderate temperature (20 °C) when compared with those given a complete compound diet.

4- Compared with birds kept at 20 °C and fed *ad libitum*, there was a lower concentration of plasma triiodothyronine in birds kept at 20 °C but pair-fed the same amount of food as birds eating *ad libitum* at 30 °C. Triiodothyronine concentration was shown to be affected directly by food intake as well as by ambient temperature.

5- High temperature reduced the quantity of digesta in the gut. It was suggested that this may be due to a reduced ability of the gut to process food.

6- Dietary modifications such as finely grinding and wetting the food led to increased food consumption and growth rate at high temperature.

7- Increasing the sodium chloride content of a finely ground and wetted diet improved metabolisability.

8- Increasing the protein content of a finely ground and wetted diet increased body weight gain but caused decreases in total energy retention, protein retention efficiency and metabolisability.

9- It is usually assumed that reduced food intake at high temperature results firstly from a decrease in energy requirements for thermoregulation and secondly from the need to minimise heat stress by reducing the heat increment of feeding. However, the results of this project suggest that the domestic fowl reduces its food intake at high temperature not to reduce or limit heat production, but because the gut is limited in the amount of food it can process. If the gut is "assisted" by providing wetted or finely ground food, food intake, growth rate and heat production all increase.

PUBLICATIONS ARISING FROM THIS THESIS

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DEDICATION

I dedicate this work to my father who passed away but is still living in my heart for his great personality, faithfulness and love; to my mother for her spiritual support, encouragement and tender prayers; and to sisters and brothers who have given much time to inspiring and supporting me throughout my academic life. I also dedicate it to my dear wife, who helped me in every possible way, for her suffering, loneliness, enduring patience, support, understanding and sacrifices. This work is also dedicated to my sons.

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Chapter One

Energy expenditure and utilisation: responses to high ambient temperature

1.1 Introduction

Poultry meat and egg production are important suppliers of protein of high biological value to humans throughout most of the world. Commercial production faces particular difficulties in tropical countries where the poultry industry is growing rapidly; these difficulties result from high ambient temperature. The adverse effects of thermal stress on poultry may also be seen during transit (Webster *et al.*, 1993).

High environmental temperature decreases food intake and growth rate (Adams *et al.*, 1962a; Adams *et al.*, 1962b; Cowan and Michie, 1977; Sinurat and Balnave, 1985; Geraert *et al.*,1993). Increasing food intake and, in turn, production by using artificial cooling systems is possible. However, building such systems is expensive.

The reduction in food intake by elevated ambient temperature has been attributed to the lower energy required for maintenance (Sykes, 1977). However, many authors (Fuller and Dale, 1979; Mitchell and Goddard, 1990; Kan, 1994) have suggested that the depression in growth rate in meat poultry when temperature increases is not entirely attributable to the reduction in food intake. These authors found that high temperature affects growth even when high-temperature birds eat the same amount of food as that consumed by birds kept at moderate temperature. They considered that the reduction in triiodothyronine hormone (T3) which occurs as a result of increasing temperature (May, 1978; Kühn and Nouwen, 1978; Klandorf *et al.*, 1981) might produce the effect directly. The role of T3 in food intake and growth has been explained by Guyton (1987) and Decuypere and Buyse (1988). At high temperature, the passage of the diet through the digestive tract is slow (Wilson *et al.*, 1980; Savory, 1986). Also Savory (1980, 1985) noted that meal initiation (hunger) was followed by partial gizzard emptying and shorter intervals between meals reflected the faster passage of food through the digestive tract.

The aims of this project were:

1- Studying the mechanisms of high ambient temperature effects on growth rate in meat poultry by measuring energy intake, metabolisability, expenditure and measuring the utilisation of this energy in growth processes.

2- Investigating the mechanisms which might be responsible for the reduction in food intake and to explore methods of improving growth at high ambient temperature.

1.2 Literature review:

1.2.1 High temperature and food utilisation

It is well known that high ambient temperature decreases food intake in birds (Adams *et al.*, 1962a; Adams *et al.*, 1962b; March and Biely, 1972; Farrell and Swain, 1977a; Sinurat and Balnave, 1985; Geraert *et al.*, 1993). As a result of the reduction in food intake, growth rate is depressed (Adams *et al.*, 1962a; Adams *et al.*, 1962b; Lei and Slinger, 1970; Swain and Farrell, 1975; Cowan and Michie, 1977, 1978).

On the other hand, the effect of elevated temperature on food conversion efficiency has been variously reported to increase (March and Biely, 1972; Hurwitz *et al.*, 1980; El Husseiny and Creger, 1980) to decrease (Lei and Slinger, 1970) or to have no effect (Adams *et al.*, 1962a; Wilson *et al.*, 1980; Savory, 1986). El Husseiny and Creger (1980) attributed the improvement in food conversion efficiency when temperature increased from 22 to 32 °C to the reduction in energy required to maintain body temperature, and these birds were able to store this energy in their bodies. However, Lei and Slinger (1970) explained that the reduction in food conversion efficiency by elevated temperature was because the slower growing birds used a greater proportion of their total food intake for maintenance rather than growth.

Water intake, in general, is correlated with food intake. However, although food intake by birds decreases as ambient temperature increases, their water consumption is still similar to that of birds which are kept at moderate temperature. Also, this consumption can be markedly increased when the temperature rises above a critical level (Duke, 1986a). Farrell and Swain (1977a) noted that water consumption between 9, 16, 22 and 30 °C was variable, especially above 16 °C, and no significant differences were noted. However, at 35 °C there was a significant increase. Similar results were found by Savory (1986), who reported that water intake was nearly twice as much per day at 32 as at 8 or 20 °C and water consumption did not increase markedly until ambient temperature exceeded 30 °C, since fowls which were kept at 30 °C did not drink more water than those at 20 °C. However, Waibel and MacLeod (1995) found that water intake was greater when turkeys were kept at 29 than at 16 °C. They attributed that to the need for more water for respiratory evaporative cooling processes.

The effect of temperature on evaporative water loss was discussed by Barott and Pringle (1941). They noted with hens between 10 and 13 months of age and kept at temperatures ranging from 10 to 35 °C (with relative humidity between 50 and 60%), that between 18 and 24 °C water elimination to keep body temperature at its normal level was a nearly constant 0.7 mg of water per hour per g live weight. At temperatures below 18 °C the rate of water elimination decreased at first slowly and then more rapidly, with conservation of heat becoming necessary at lower temperatures. However, when temperature increased to more than 24 °C, the rate of elimination began to increase and above 27 °C it increased very quickly since it reached respectively 1.6 and 2.5 mg of water per hour per g live weight at temperatures of 30 and 35 °C. The effect of elevated ambient temperature on water evaporation in birds was also reported in the review of Sykes (1977). He mentioned that evaporation increased from about 50 to about 110 g per 1.5 kg per day when temperature increased from 20 to 30 °C.

1.2.2 High temperature and metabolisable energy

The reported effect of increasing ambient temperature on metabolisable energy values varies between workers. Swain and Farrell (1975) found with cockerels at four weeks of age that metabolisability values (%) increased with increasing temperature from 5 to 34 °C. They suggested that the reason might be the effect of temperature on gut absorption capacity. Geraert *et al.* (1992) also reported increases in metabolisability values with male chickens at 8 weeks old maintained at temperatures of 22 and 32 °C. They attributed this to the decrease in food passage rate which occurs under the effect of elevated temperature (Wilson *et al.*, 1980) and that this may have increased the time for enzyme action.

However, Farrell and Swain (1977a) reported decreasing rather than increasing metabolisability values with increasing temperature in contrast to the findings of Swain and Farrell (1975) (mentioned above). They accounted for this reduction by the influence of endogenous energy losses on metabolisable energy values. Sibbald (1975) noted with adult roosters that metabolisability values were affected by the level of energy intake, being high when there was greater energy intake. He attributed this to the effect of endogenous energy losses (**EEL**), because it is suggested that under standardised conditions the excretion of metabolic faecal energy (**FEm**) and endogenous urinary energy (**UEe**) is constant. At low temperature the intake increases and at high temperature it decreases, while daily excretion of EEL is reasonably constant.

It has also been found that elevated ambient temperature had no effect on metabolisability values (Lei and Slinger, 1970; Olson *et al.*, 1972; El Husseiny and Creger, 1980; Yamazaki and Zhang, 1982; Zuprizal *et al.*, 1993).

Endogenous energy losses have been reported to be affected by temperature. Swain and Farrell (1975) and Farrell and Swain (1977b) found with 4-week-old cockerels and with broiler chickens at 7 weeks old, respectively, that endogenous nitrogen excretion decreased when temperature ranged from 5 to 34 °C and from 2 to 35 °C, respectively. This reduction was attributed to the greater amount of energy required for maintenance at lower temperatures. Similar results were obtained by Geraert *et al.* (1992), who reported a reduction in endogenous energy losses when ambient temperature was increased from 22 to 32 °C. However, it has been noted that endogenous energy losses did not differ in 12-month-old cockerels when the temperature decreased from 25-35 °C to the control 22 °C, but it increased at the cooler temperature 5-15 °C (Yamazaki and Zhang, 1982).

The influence of temperature on true metabolisable energy values was discussed by Yamazaki and Zhang (1982), who noted higher values of true metabolisability at cool temperatures (5 to 15 °C) than those found at control (22 °C) and hot (25 to 35 °C) temperatures. However, Geraert *et al.* (1992) reported increasing values with increasing temperature from 22 to 32 °C.

1.2.3 High temperature and energy expenditure

Energy expenditure is equal to the heat which leaves the body as heat loss. However, this heat production is affected by factors which require energy, such as maintenance (the energy required for sustaining the basic processes which occur inside the body). Other factors affecting energy expenditure are thermoregulation (the energy required for keeping animal at normal body temperature), activity and food intake. Researchers have studied all these factors in detail.

Greater heat production (kJ/d) with decreasing temperature from 35 to 2 °C was found in starving birds by Farrell and Swain (1977b). Similar results were reported when ambient temperature ranged between 5 and 34 °C and heat production was corrected to the same body weight (Swain and Farrell, 1975; Klandorf *et al.*, 1981; MacLeod, 1990, 1992). This increase in heat production was as a result of the increase in energy demand and the rate of energy transformation. However, the effect of elevated temperature on heat production when animals are fed was also studied. In earlier studies, Kleiber and Dougherty (1934) found with chicks from 5 to 15 days old that heat production Cal/kg$^{0.75}$ was depressed when temperature increased from 21 to 40 °C. A reduction in heat production (kJ/d) with increasing temperature was reported by Farrell and Swain (1977a) and Hoffmann (1991) and when corrected to the same body weight by Klandorf *et al.* (1981) and MacLeod (1990, 1992).

As mentioned above, heat production is affected by activity. When an animal moves that means that more energy should be available to the muscles and will then leave the body as heat. This was confirmed by Benedict *et al.* (1932) who found with Rhode Island Reds cocks fasted for 27 hours and kept at temperatures ranging between 21 and 28 °C that heat production during day was greater than night. They attributed this to physical activity, which was greater during day time. Also, Deighton and Hutchison (1940) reported with fasted Light Sussex breed birds that heat production was primarily associated with the activity of the bird such as standing, neck stretching or crowing. So, any change in locomotor activity or muscle tone was reflected by changes in heat production.

Food intake is known to change heat production. Heat production kJ/kg$^{0.75}$ was greater when birds were fed than when they were fasted. These results were confirmed by Klandorf *et al.* (1981) and MacLeod (1990, 1992). However, heat production was not only affected by fasting or feeding. The level of food intake was found to affect heat production also. MacLeod *et al.* (1979) reported with hens and cockerels at 20 weeks of age that restricting food intake to 80% of *ad libitum* led to reductions in heat production of respectively 34% and 28% per bird per day when compared with controls. Similar results were recorded by MacLeod and Hocking (1993) who mentioned 23% reduction in heat production per bird per day of hens between 44 and 48 weeks old when their food intake was restricted. This reduction in heat production was largely due to the reduction in body weight. However, heat production did not differ when it was corrected to same body weight (MacLeod and Shannon, 1978). The reduction in heat production as a result of the reduction in food intake was confirmed recently by (Zhou and Yamamoto, 1997). The role of feeding activity on heat production was also investigated. There was 30% less heat increment per unit weight of food with cockerels at 40 weeks when they were fed by tube compared with the control self-feeding (MacLeod, 1991b).

1.2.4 High temperature and energy retention

Energy retention is largely composed of the protein and fat which are retained in the body. In this section the effect of increasing temperature on protein retention will be discussed first, then its effect on fat retention and finally its effect on total energy retention.

As a result of greater food intake when birds are grown under moderate temperature compared with birds kept at high temperature, more protein will be eaten. Also because elevated ambient temperature had no affect on protein retention efficiency (MacLeod, 1990, 1992) a greater amount of protein will be retained in the bodies of those birds which are kept at moderate temperature. Swain and Farrell (1975) reported an increase in protein retention efficiency with increasing temperature from 5 to 34 °C. They attributed this increase to the reduction in nitrogen excretion (which was measured during starvation) as temperature increases. However, the same authors (Farrell and Swain, 1977a) reported a decrease in protein efficiency when temperature increased from 16 and 22 to 30 and 35 °C. They related this decrease in efficiency at high temperature to the reduction in food intake.

However, greater protein retention in birds which are kept at moderate temperature does not automatically imply an increase in the proportion (%) of carcass protein. Many studies have been carried out to examine the effect of temperature on the proportion of carcass protein. El Husseiny and Creger (1980) found with broiler chickens at 6 weeks old that increasing temperature from 22 to 32 °C led to a 1.94% higher value for the ratio of carcass protein. A reduction in the proportion of carcass protein by elevated ambient temperature was reported by Kleiber and Dougherty (1934), Olson *et al.* (1972) and Kubena *et al.* (1972).

However, no affect of increasing temperature on this ratio was reported by Swain and Farrell (1975) and Chwalibog and Eggum (1989). Howlider and Rose (1987) mentioned in their review that they used seventeen published papers and one unpublished report which represented data from a total of 71 experiments. The results obtained showed that there was no relationship between protein content of carcass (% of live weight) and rearing temperature.

The influence of high temperature on energy retention as fat has also been investigated by many workers. Elevating temperature from 18 to 33 °C increased the proportion of fat (Olson *et al.*, 1972; Kubena *et al.*, 1972; Howlider and Rose, 1987; El Husseiny and Creger, 1980), while Mickelberry *et al.* (1966) noted no effect of increasing temperature from 21 to 29 °C on the ratio of fat in broilers at 5 weeks old. Also, Sinurat and Balnave (1985) found that high temperature (25-35 °C) had no significant effect on abdominal fat content when birds were compared with those reared at temperature (18-26 °C), although slightly more was noted in the birds which were kept at high temperature.

However, because an increase in the proportion of fat content does not necessarily mean an increase in the total amount of carcass fat, the effect of elevated temperature on the total fat content is also discussed in this section. Kleiber and Dougherty (1934) found with chicks between 6 and 15 days old that elevating temperature from 21 to 32 °C increased the amount of fat in the carcass. A reduction in the concentration of carcass fat in broilers at 4 weeks old when ambient temperature increased from about 20 to 35 °C was reported by Farrell and Swain (1977a) when expressed as kJ/5 days and by MacLeod (1990, 1992) when estimated as kJ/kgW$^{0.75}$.

Total energy retention (protein and fat) kJ/5 days or kJ/kgW$^{0.75}$ was found to be less at high temperature than at moderate temperature (Farrell and Swain, 1977a; MacLeod, 1990, 1992). This was attributed to the reduction in food intake.

Conversely, Kleiber and Dougherty (1934) reported greater energy retention kJ/day at 32 °C than at 21 °C. They attributed this to the additional energy required to maintain body temperature at lower environment temperature.

The role of temperature on the efficiency of energy retention has also been studied by previous authors (Kleiber and Dougherty, 1934; Olson *et al.*, 1972; El Husseiny and Creger, 1980). They confirmed the positive effect of temperature on energy retention efficiency, and attributed this to the decreased requirements of energy for thermoregulation. However, Farrell and Swain (1977a) noted greater efficiency with the broilers which were kept at 22 °C than those kept at 30 °C.

1.2.5 High temperature and water retention

Water retention is affected by increasing temperature. Many workers have found a greater proportion of carcass water as temperature decreases (Kleiber and Dougherty, 1934; Kubena *et al.*, 1972; Olson *et al.*, 1972; Swain and Farrell, 1975). Mickelberry *et al.* (1966) found that increasing temperature from 21 to 29 °C had no affect on the moisture content of the carcass. However, as was mentioned above (Section 1.2.4), protein retention increases with decreasing temperature as a result of the greater food intake, water retention can be expected to be higher at moderate temperature because of the association between protein retention and water retention as reported by Adams *et al.* (1962a) and MacLeod (1991a). The effect of heat stress on water evaporation (discussed in Section 1.2.1) is also worth considering.

Chapter Two

General materials and methods

2.1 The calorimetry system

This system (Figures 2.1.a, 2.1.b) has been described in detail by Lundy *et al.* (1978), MacLeod (1980) and MacLeod *et al.* (1985). Briefly, it consists of three main parts.

1- Ten bird chambers.

2- The analysis system.

3- A computer-based control and data-acquisition system.

1- The chamber (Figure 2.2) is designed to hold a bird or group of birds of total weight up to 4 kg. The chamber is an airtight, thermally insulated, climatically controlled Perspex box, of internal dimensions 600 mm × 600 mm × 450 mm high, fitted with a Perspex door which is sealed by a rubber gasket and release nuts. A partition from floor to ceiling, separate by about 50 mm from the front and rear walls, divides the chamber into a test section (a) and an air-conditioning system (b). A 13-W fluorescent light put over the midline of the test section provides illumination. Bird or birds are housed in the test section. It is floored by a shallow tray that supports a heavy plastic-covered wire mesh. The tray is used for the quantitative collection of droppings. A calibrated drinker is provided in the test section. It is designed to minimise evaporative water losses. The test section also has a holder for a feeding trough to prevent the feeder from being turned over. The air conditioning system occupies about one-third of the chamber's volume, and it

Figure 2.1.a Gas and information flow in the multi-calorimeter system

Key

ST1 and ST2	computer-controlled motorised rotary switch valves 1 and 2 of the turkey system
SC1 and SC2	computer-controlled motorised rotary switch valves 1 and 2 of the fowl system
SIT and SIC	calibration gas injection switch valves
T and C	turkey and fowl systems
a	analogue inputs from analysis system transducers
b	analogue inputs from calorimeter transducers
c	analogue inputs from calibration system
d	analogue input / output lines to gas selector switch valves
e	digital input / output lines to calibration system

broken and intact lines indicate alternative switch positions

For a more detailed illustration of the Analysis Systems T and C refer to Figure 2.1.b.

(MacLeod, Lundy and Jewitt, 1985)

Figure 2.1.b. The controlled pressure and flow analysis system.

Key

F	float-and-cone flowmeter
NV	needle-valve
TBB	test-bench barometer

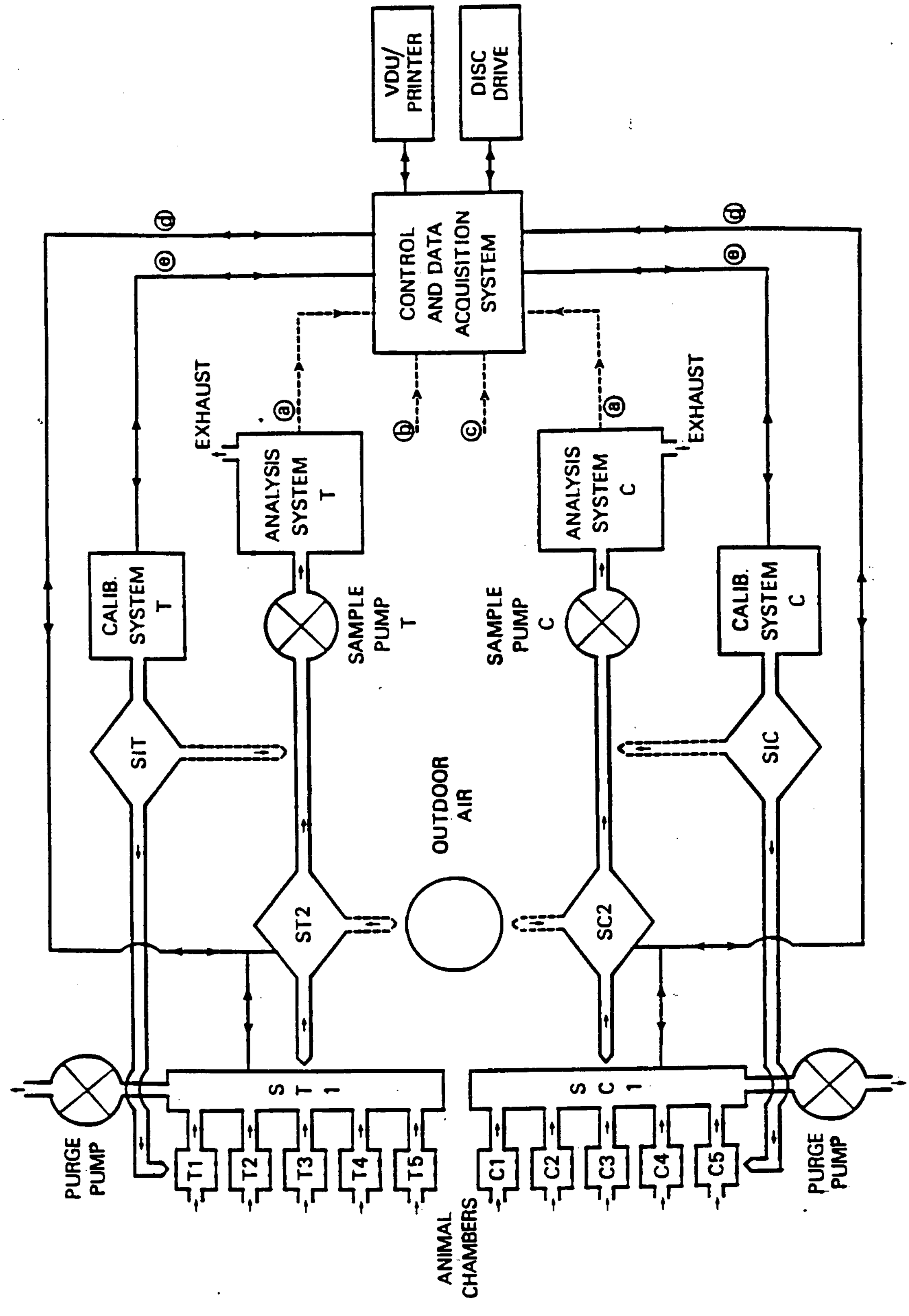


Figure 2.1.a. Gas and information flow in the multi-calorimeter system.

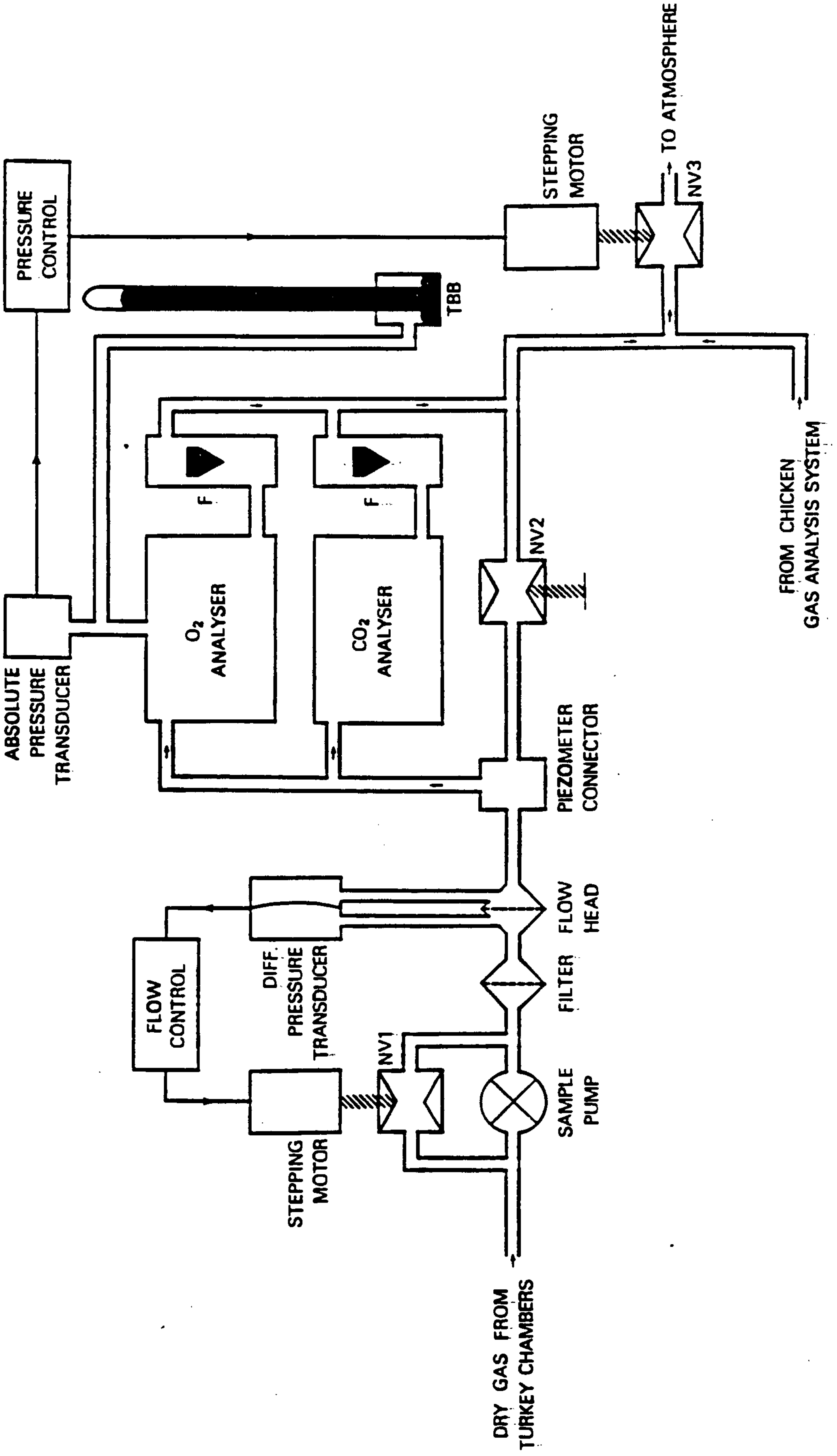


Figure 2.1.b. The controlled pressure and flow analysis system.

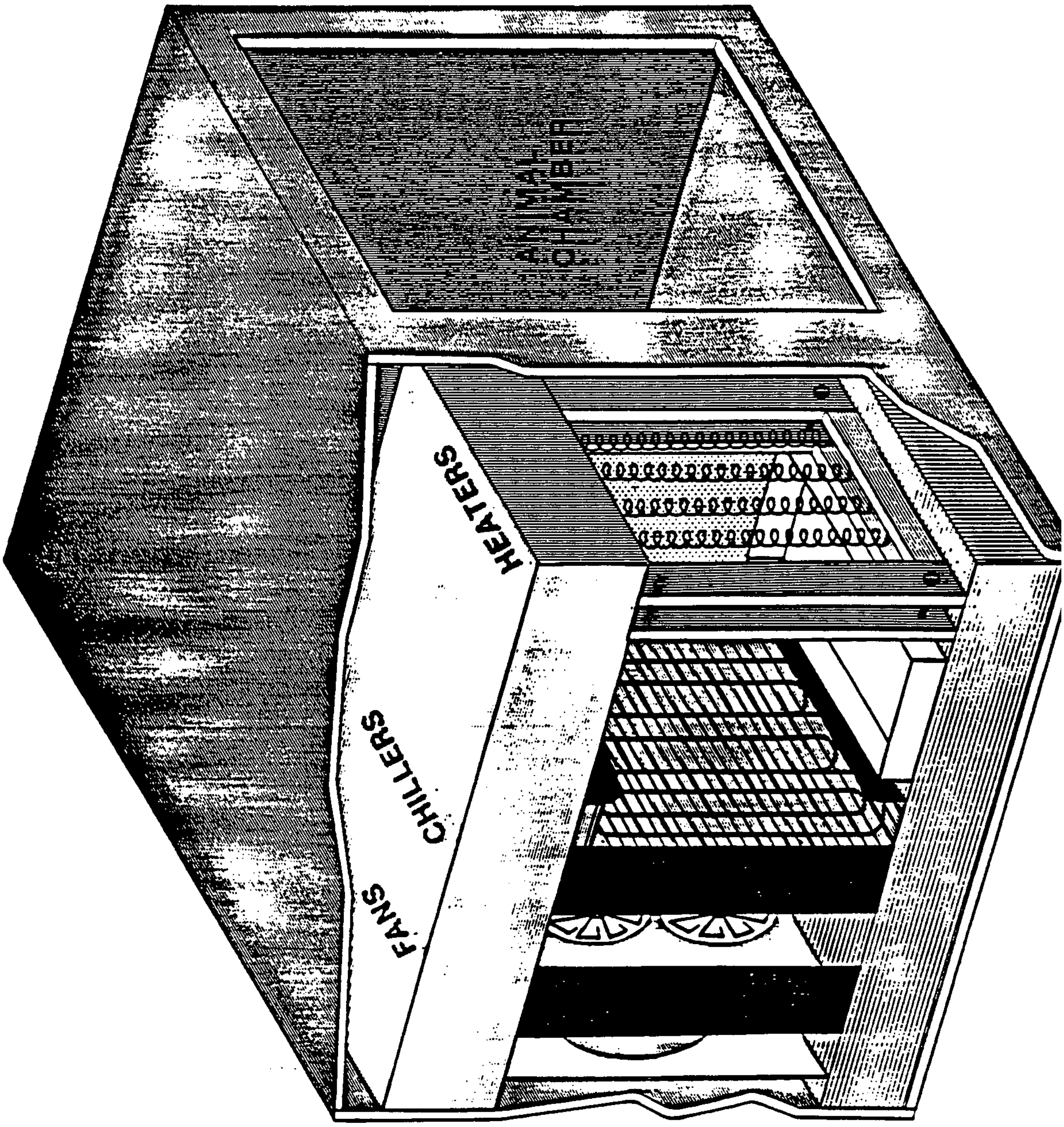


Figure 2.2. Block diagram of calorimeter chamber.

contains on orifice plate (1), recirculating fans (2), two heat exchangers (3) and two heaters (4).

2- The analysis system is situated in a controlled-temperature room kept at 20 °C. It consists of three principal parts: a gas volume flowmeter, a paramagnetic oxygen analyser and an infra-red carbon dioxide analyser. Flow rate is determined by measuring the pressure drop across a sintered bronze disc. Partial pressure of oxygen is measured by a Servomex OA184 paramagnetic oxygen analyser. Partial pressure of carbon dioxide is measured by a Servomex 1490 infra-red gas analyser. Analysis system pressure and flow are servo-controlled.

3- The computer control and acquisition system. This system controls the selection of different samples (fresh air, gas sample) and sends the chosen sample to the analysers (O_2 and CO_2 analysers). Also, this system acquires data from the measuring transducers and calculates oxygen consumption, carbon dioxide production and finally heat production.

2.1.1 The operation of the calorimetry system

1- Oxygen and carbon dioxide calculations:

Fresh air is drawn from the room (in which the calorimeter chambers are kept) into the chambers. This flow of air occurs because all chambers are under negative pressure which is created by a diaphragm pump. Fresh air enters the chambers through a tube fixed in the test section and leaves chambers through another tube sited in the air-conditioning system section. Gas samples which leave the chambers are dried by a refrigerated condensation drier. The dry air then passes to the gas selector valve. Also fresh air is drawn from the room for 1 minute before each calorimeter is sampled but this air goes directly to the drier without entering chambers, and then to the gas selector valve. The function of this valve is to arrange the connection between the different gas samples and fresh air with the oxygen and carbon dioxide analysers. For instance, when chamber 1 is chosen the valve connects this chamber with the analysis system while the other chambers are purged. These analysers measure the ratios of O_2 and CO_2 in the sample chosen, whether chamber samples or fresh air. Finally by knowing the proportions of O_2 and CO_2 in the air entering and leaving chambers and by knowing the flow rate of the air, oxygen consumption and carbon dioxide production can be calculated in the conventional manner from the difference between the volumes of these gases which enter and leave the calorimeter during the period of observation (10 minutes).

2- Heat production calculations:

Heat production (H, kJ) is computed by the formula of Romijn and Lokhorst (1961), which is converted to SI units, from O_2 consumption and CO_2 production (dm^3 STP): $H = 16.20\ O_2 + 5.00\ CO_2$. No correction is made for nitrogen excretion since Romijn and Lokhorst (1961, 1966) reported that the error resulting from this omission is about 0.2% and no more than 1.5% even at a high rate of protein catabolism.

2.2 Apparatus used for energy and protein measurements

Energy (kJ/g) and nitrogen (g/kg) in the diets and samples were measured, respectively, by adiabatic bomb calorimetry and by a LECO FP328 nitrogen analyser, which measures nitrogen in the gaseous phase after combustion of the sample.

2.3 Energy and protein calculations

Metabolisable energy and protein retention values were calculated by conventional methods (Sibbald, 1976; Whittow, 1986).

$$\mathrm{IAME} = \mathrm{EI} - ((\text{faecal} + \text{urinary})\ \text{energy})$$

where IAME is apparent metabolisable energy, and EI is gross energy intake.

$$\mathrm{Amet} = \mathrm{IAME} / \mathrm{EI}$$

$$\mathrm{Amet} = \mathrm{IAME} / \mathrm{FI}$$

where Amet is apparent metabolisability, and FI is total food intake in g.

$$\mathrm{ITME} = \mathrm{IAME} + (\text{endogenous}\ (\text{faecal} + \text{urinary})\ \text{energy})$$

where ITME is true metabolisable energy.

$$\mathrm{Tmet} = \mathrm{ITME} / \mathrm{EI}$$

$$\mathrm{Tmet} = \mathrm{ITME} / \mathrm{FI}$$

where Tmet is true metabolisability.

$$\mathrm{RE} = \mathrm{IAME} - \mathrm{HP}$$

where RE is total energy retention in the body, and HP is heat production from the animal.

$$\mathrm{ERE} = \mathrm{RE} / \mathrm{IAME}$$

where ERE is energy retention efficiency from apparent metabolisable energy. Also, proportions of apparent metabolisable energy retained as protein and fat were calculated by

$$\mathrm{PARP} = \mathrm{REP} / \mathrm{IAME}$$

where PARP is proportion of apparent metabolisable energy retained as protein, and REP is energy retention as protein.

$$\mathrm{PARF} = \mathrm{REF} / \mathrm{IAME}$$

where PARF is proportion of apparent metabolisable energy retained as fat, and REF is energy retention as fat.

energy retention as protein was calculated as follows:

$$\mathrm{RN} = \mathrm{NI} - \mathrm{NE}$$

where RN is nitrogen (g) retained in the body, NI is nitrogen consumed in the diet and NE is nitrogen lost in the excreta. Then protein retention in grams can be calculated by multiplying nitrogen retention in grams by 6.25. Energy retention as protein (REP) was estimated as (22.6 × RP), where each gram of protein contains 22.6 kJ. Energy retention as fat (REF) was obtained by subtracting energy retention as protein from total energy retention. To estimate growth rate as dry matter in grams (GRDM), fat retention in grams was calculated as (REF / 38.9), where each gram of fat contains 38.9 kJ. The values of 22.6 and 38.9 kJ per g of protein and fat, respectively, were used (Whittow, 1986). Finally water retention of carcass (WRC) in grams was then estimated by subtracting growth rate as dry matter from total growth rate.

Protein retention efficiency was calculated by dividing total protein retention by total protein intake as follows:

$$\mathrm{PRE} = \mathrm{RP} / \mathrm{PI}$$

where PRE is protein retention efficiency, RP is protein retention (g) and PI is protein intake.

The proportions of protein (PRC%), fat (FRC%), water (WRC%) and dry matter (GRDM%) in total weight gain were estimated.

2.4 Thyroid hormones assays

Both triiodothyronine (T3) and thyroxine (T4) concentrations were measured using commercial coated-tube kits (Pantex thyroid hormone assays kit [CT] - Biogenesis, UK).

2.4.1 Assay principles

Assay principles for T3 and T4 were as follows: the set of standards (Tables 2.1 and 2.2) and fixed amounts of radiolabelled tracers compete for a fixed number of antibody binding sites on coated tubes. Ligands (triiodothyronine and thyroxine) in samples or standards reduce tracer-antibody binding on tubes. The basis of the radioimmunoassay was the quantitative relationship between ligand concentration and proportion of antibody-bound tracer. Tracer bound to the walls is counted after supernatant removal. Standard binding values were plotted against concentrations. The line of best fit is drawn between points. Sample binding values interpolated on the line give triiodothyronine and thyroxine concentrations.

2.4.2 Assay procedure for T3 and T4

1- 100 or 25 μL of the standards or samples of T3 and T4, respectively, were pipetted into the coated tubes (Tables 2.1 and 2.2).

2- 1000 μL of the tracer was also pipetted into the coated tubes (Tables 2.1 and 2.2).

3- The mixture was vortexed, incubated for 2 or 1 hour with T3 and T4 respectively, at a temperature of 37 °C. The liquid phase was then aspirated and discarded.

4- Bindings of standards and samples were measured using radioimmunoasssay (RIA) Gamma-Master.

Table 2.1. Summary of triiodothyronine radioimmunossay protocol.

ng/mL	standard or sample µL	tracer µL
0	100	1000
0.25	100	1000
0.50	100	1000
1.00	100	1000
2.00	100	1000
4.00	100	1000
8.00	100	1000
sample 1	100	1000

Table 2.2. Summary of thyroxine radioimmunossay protocol.

ng/mL	standard or sample µL	tracer µ L
0	25	1000
5	25	1000
10	25	1000
20	25	1000
40	25	1000
80	25	1000
160	25	1000
sample 1	25	1000

5- Finally the results were worked out by Assay Zap^{TM} software to calculate the concentrations. The bindings ratios of standards and samples were calculated relative to 0 standard as follows:

%B/B0= (counts of standard or sample / count of 0 standard) × 100

Chapter Three

Free-choice feeding and energy metabolism of growing broilers at moderate (20°C) and high (30°C) ambient temperatures

3.1 Introduction

It was mentioned in Sections (1.1, 1.2.1) that high ambient temperature decreased food intake and also growth rate (Adams *et al.*, 1962a; Adams *et al.*, 1962b; Lei and Slinger, 1970; March and Biely, 1972; Swain and Farrell, 1975; Farrell and Swain, 1977a; Cowan and Michie, 1977, 1978). Poultry scientists have tried to alleviate this effect of temperature on growth by different methods. One of these methods is the increase in nutrient concentrations (especially protein or amino acids) in the diet to prevent the reduction in nutrient intake, and this will be discussed below.

3.1.1 High temperature and protein level

In early study, Mills (1944) found with rats kept at 33 °C that growth rate was improved and was the same as at 20 °C when dietary protein concentration was increased from 6 to 36%. This improvement in growth resulted partly from the increase in food intake with elevated protein level. However, the optimal food intake with the rats kept at 20 °C occurred when protein concentration was 18% and did not increase after that level.

March and Biely (1972) reported similar results with cockerels at 16-d-old. They conducted two experiments, the first being designed to test the effect of temperatures of 20 °C and 31.1 °C on the response of chickens to different levels of lysine, 0.15, 0.30 and 0.60%. Results from this experiment showed that, when the diet was supplemented with 0.60% lysine, growth rate was similar at 20 °C and 31.1 °C. However, as the lysine level of the diet was decreased, the birds kept at higher temperature ate less and grew more slowly than did those kept at lower temperature. In the second experiment, they studied the effect of temperatures of 18.3, 22.2 and 29.4 °C and the effect of 2 energy levels (3030 and 3870 cal/g; 12.7 and 16.2 kJ/g dry weight) each energy level being supplemented with lysine at levels of 0, 0.227, 0.474 and 0.681%. They noted that, at any level of lysine, food consumption and growth rate were depressed when the environmental temperature or energy level in the diet increased. Also, they noted that growth rate at any temperature was improved by increasing lysine level. They concluded that, at high temperature or high level of energy, food intake decreases and that may induce an imbalance between the effective protein level of the diet and total caloric input and consequently growth rate decreases.

However, studies by other researchers have suggested no response to increasing protein level when birds are exposed to high temperature. Heywang *et al.* (1953) noted with New Hampshire chicks fed diets containing different concentrations of protein (20.3, 21.6, 24.8, 26.9, 29.1%) and kept at either at 17 °C or 27 °C that, the best growth occurred when protein concentration was between 24 and 25% regardless of the ambient temperature. Also, gains of the birds kept at 17 °C and fed lowest protein concentration (20.3%) were better than those on the highest protein concentration (29.1%) and kept at 27 °C. Similar results were found by Adams *et al.* (1962a, 1962b) who reported that protein requirement for maximal growth in 4-week-old chicks did not appear to be influenced by ambient temperature, and a level of 17% protein seemed adequate in both environments (21 and 29 °C). Also, the poor growth obtained at 29 °C environment could not be attributed to a reduction in protein intake, since protein intake per day with higher protein level

23% at 29 °C was greater than that of the lower protein level 14% at 21 °C, yet growth rate was considerably reduced at high temperature.

Cowan and Michie (1978) confirmed similar results. They investigated the effect of diets with different levels of protein (178, 210, 243, 275 and 308 g/kg) on broilers between 22 and 57 d old and kept at temperatures of 16, 21, 26, and 31 °C. Their results showed that increasing protein concentrations apparently did not reduce growth depression with the birds reared at 26 or 31 °C. The reason was the reduction in food intake which occurred with increasing temperature. More recently, increasing protein level from 19 to 23% did not alleviate the depression in growth which occurred at 32 °C in male chickens (Geraert *et al.*, 1993).

3.1.2 High temperature and choice-feeding

Some scientists have examined the use of choice-feeding for alleviating the effect of high temperature on growth. In this method of feeding, birds are offered two diets, one of which provides energy and the other of which is high in its content of protein. The bird can in principle, therefore, adjust its intake of energy and protein according to its requirement. For instance, the bird might increase its intake of protein even if its total intake is reduced by elevated temperature.

Mastika and Cumming (1987) conducted a series of experiments on broilers to test a choice-feeding system given to birds exposed to cyclical temperatures between 20 and 33 °C. They offered a free choice between whole sorghum (10% CP, 13.16 MJ ME/kg) and protein concentrate (41.6% CP, 9.74 MJ ME/kg), while the control birds were given a complete finisher diet (19.1% CP, 12.32 MJ ME/kg). Their results indicated the importance of giving birds a training period to let them learn how to use this system. They noted that, although food intake and body weight gains were not affected by feeding treatments (complete diet, choice-feeding experienced and choice-feeding inexperienced birds), the inexperienced broilers consumed less sorghum and twice as much protein concentrate as the experienced birds when choice fed. Thus, the inexperienced group was significantly less efficient in utilising protein than the experienced ones. These authors also noted that, when complete diet or choice-diet was offered at either a constant 20 °C or cyclical 20 and 33 °C, on 16 hours light, a 3% depression in body weight was recorded with the birds on complete diet and kept at cyclical temperature. However, body weight of the choice-fed birds was not depressed by cyclical temperature. Also, they found that choice-fed birds housed at cyclical temperature consumed significantly less energy but maintained their protein intake when compared with those fed either with the complete diet or by choice-feeding and kept at 20 °C.

Shariatmadari and Forbes (1993) reported with broilers and laying hens that chickens can match their protein intake closely to their requirements when they are given diets which allow this. They noted that, although choice-fed birds selected significantly less protein intake (19% CP), their live weight gain and carcass protein content were similar to those of birds which were fed on a high-protein diet (28% CP). Of course, the similar deposition of protein with different intakes gave a greater efficiency of protein utilisation with the birds on the choice diet. Factors which may affect the use of choice-feeding systems efficiently have been reviewed by Rose and Kyriazakis (1991) and by Forbes and Kyriazakis (1995).

However, it has been noted that using this system does not give better utilisation either with broilers (Cumming, 1983; Rose, 1985; Sinurat and Balnave, 1986) or with laying hens (Leeson and Summers, 1978), since all these authors noted similar production in the birds which were given complete diet and those offered choice-feeding. Rose (1995) reported in his review that there was no evidence that choice feeding systems gave any improvements in the productive performance or the efficiency of protein utilisation when compared with complete diet system for growing pigs, growing broiler chickens or laying hens.

Using the conventional complete diet system rather than a choice-feeding system was recommended for better production by Cowan and Michie (1977). They offered a complete diet and a choice between whole wheat and a higher-protein compound diet containing either 252 or 516 g/kg crude protein to broilers from 22 to 57 d old and kept at environmental temperatures of 16, 21, 26 or 31 °C. They found that food and protein intakes and growth rate were reduced by increasing temperature. Without respect to temperature, choice-fed birds ate less food but maintained their intake of protein to equal that consumed on the complete diet. So, the birds given choice diet and kept at high temperatures did not select protein to keep their intake of it the same as those kept at lower temperatures. Growth rate was greater in birds fed on the complete diet than in those given the choice diet. Lower production with choice-feeding when compared with complete diet was reported by Summers and Leeson (1978) in broilers and by Desmayati *et al.* (1983) in laying hens.

The aims of the current experiment were:

1- To serve the first objective of this thesis (mentioned in the introduction to the thesis) which was to study the effect of high ambient temperature on growth rate by measuring energy intake, metabolisability, expenditure and measuring the utilisation of this energy for growth.

2- To provide more information on the optimum management for better growth: giving a complete diet with high protein content or offering choice-feeding when the birds are exposed to heat stress, in view of the conflicting opinions about using these systems.

3.2 Materials and methods

3.2.1 Experimental design

A 4 × 4 Latin square was employed, combining four replicate runs and four treatments: complete diet, moderate temperature 20 °C (**CM**); complete diet, high temperature 30 °C (**CH**); free choice, moderate temperature 20 °C (**FM**) and free choice, high temperature 30 °C (**FH**). Relative humidity ranged between 50% and 70%. Treatments were randomly assigned. A second 4 × 4 Latin square was run in the same way, with the treatments re-randomised. The second Latin square was conducted to increase the number of replicates. Data were treated by analysis of variance and least significant difference (**LSD**) between means was calculated (Snedecor and Cochran, 1971). To avoid rejecting results which may be of interest a $p<0.10$ level was considered significant.

3.2.2 Experimental work

Twenty-four 1-d-old broiler males (Ross Breeder Ltd, Newbridge, Midlothian) were kept in two climate chambers of internal dimensions 1.21 m high × 0.9 m × 0.9 m (MacLeod *et al.*, 1985). There were 12 birds per group, one receiving a complete diet, the other a choice feeding diet (whole wheat and high protein diet). The diet compositions are summarised in Table 3.1. Two feeders were offered to each group whether they were on complete diet or the choice feeding treatment. However, the two feeders of complete diet treatment contained the same diet, while choice feeding treatment had whole wheat in one feeder and the high protein diet in the other feeder. Temperature was reduced from 35, to 20 °C at 5 °C intervals every 5 d until 20-d old and thereafter held constant until the end of the experiment at 60 d of age.

Table 3.1. The composition of complete diet which was given to the birds on complete diet treatments and the composition of the two feeds offered to choice-feeding treatments. The complete diet was an old Institute (Poultry Research Centre) standard diet, which had slightly lower than optimal methionine and cystine contents (methionine 3.45 and cystine 3.68 g/kg).

Ingredients	**Complete diet**	**Choice-diet**	
g/kg		**Balancer**	**Wheat**
Wheat meal	600	-	1000
Fish meal	23	58	-
Soyabean meal	300	750	-
Meat & bone meal	50	125	-
Limestone	20	50	-
Salt	2	4.5	-
Vitamin mix	2.5	6.25	-
Mineral mix	2.5	6.25	-
Crude protein	250	460	110
ME (kJ/g)	11.6	9.7	12.8

Two birds were taken from each group at 20, 30, 40 and 50 d of age and the 4 birds (similar weights) put in calorimetry chambers (see Section 2.1) individually for 8 d. It is worth noting that choosing 20 d old for starting the experiment was to make sure that the birds have reached an age at which the temperature 30 °C is considered a heat stress, and also to give birds the required time which they need to be trained to using choice-feeding system (Mastika and Cumming, 1987). The first 3 d were for acclimatisation. The second period of 3 d was the fed measurement period, when food and water intake, growth rate and heat production were recorded.

Diets were offered in the same way as mentioned above. Food was available during the first 6 d and water during the whole run (8 d). The lighting pattern was 23 hours light: 1 hour dark. Droppings were collected daily during the feeding measurement days. At the end of the last day of the fed measurement period, body temperature was measured by inserting a thermistor probe (1.5 cm) into the rectum. The day after the 3 d period of fed measurements, food was withdrawn to prepare birds for measurement of fasting heat production and for collecting excreta to estimate endogenous energy losses. The latter was used for calculating true metabolisable energy values on the last day of the run.

The samples of droppings were stored at -20 °C in sealed aluminium dishes until they were oven-dried at 40 °C for 5 d. Then they were equilibrated with atmospheric moisture for 24 h, weighed and ground for measurements of energy and protein. Each diet and droppings sample was measured in duplicate and the mean was calculated. The mean of the measurement period (3 d) was taken. Results were expressed per bird per d. The calculations of energy and protein contents and the apparatus used for measuring them in the diet or droppings samples are described in Sections 2.2 and 2.3.

3.3 Results

3.3.1 Food, protein and water intakes and growth rate

Table 3.2 shows the food intake (FI) results. Birds fed on the complete diet and kept at moderate temperature (20 °C) consumed 29% more by weight ($p<0.001$) than those kept at high temperature (30 °C) on the same diet. No significant difference was found between the total intakes of birds kept at moderate and high temperature when choice-fed. Birds receiving the complete diet and kept at moderate temperature ate 22% more food ($p<0.01$) than those given the choice diet and kept at the same temperature. No difference was detected between birds kept at high temperature on different feeding systems. When diet means were combined, birds kept at moderate temperature ate 19% more ($p<0.001$); across temperatures, 13% more food was consumed ($p<0.01$) when the complete diet was fed. A significant interaction ($p<0.05$) was noted between temperature and diet.

Protein intake (PI) was 27% ($p<0.01$) greater in birds fed on the complete diet and kept at moderate temperature than in those kept at high temperature and fed on the same diet (Table 3.2). The difference between birds fed by choice feeding was less (18%; $p<0.10$). Also, a significant difference ($p<0.001$) was found between the birds kept at moderate temperature on different feeding systems; protein intake was 46% greater in those fed on the complete diet. Birds kept at high temperature and fed on the complete diet ate 36% more protein ($p<0.01$) than those given the free-choice diet and kept at same temperature. Across feeding systems, birds kept at moderate temperature consumed 23% more protein ($p<0.001$) than those kept at high temperature. When temperature means were combined, birds fed on the complete diet ate 42% more protein ($p<0.001$) than those receiving choice feeding. The interaction between diet and temperature was barely significant ($p<0.10$).

Table 3.2. The effect of temperature and feeding system on food intake (**FI**), protein intake (**PI**), water intake ml. (**WI**) and growth rate (**GR**). Means are presented as g/bird. d

Diet	Temperature	FI	PI	WI	GR
Complete	20 °C	151a*	38a	260a	67a
	30 °C	117b	30b	255a	43b
Choice	20 °C	124b	26bc	202b	45b
	30 °C	115b	22c	236a	36b
SED		6.2	1.8	13.7	9.5
Temperature effect					
Moderate	20 °C	138a	32a	231a	56a
High	30 °C	116b	26b	246a	40b
Diet effect					
Complete diet		134a	34a	258a	55a
Choice diet		119b	24b	219b	41a
SED		4.4	1.2	9.7	6.7
Interaction: P		<0.05	<0.10	<0.05	NS

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

Water intake (**WI**) did not differ significantly between birds fed on the complete diet and kept at different temperatures (Table 3.2). A significant ($p<0.05$) difference was detected between the birds fed by choice feeding and kept at different temperatures; it was 17% greater with those kept at the higher temperature. Birds receiving the complete diet and kept at moderate temperature drank 28% more water ($p<0.01$) than those given the choice diet and kept at same temperature. No significant difference was found between birds kept at high temperature on different feeding systems. However, temperature had no effect on the amount of water intake when its effect was studied across feeding systems, but the effect of feeding system was significant ($p<0.01$). Water intake was 18% greater with birds on the complete diet than choice-fed birds. The interaction between temperature and diet was significant ($p<0.05$).

Growth rate (**GR**) was 56% greater ($p<0.05$) in birds at moderate temperature than in those at high temperature when the complete diet was offered (Table 3.2). No significant difference was noted between choice-fed birds, although growth rate was 25% greater at moderate temperature. Birds on the complete diet grew 49% more rapidly ($p<0.05$) than choice-fed birds when they were kept at moderate temperature and no significant difference in growth was found between birds giving different feeding systems and kept at high temperature, although it was 19% greater with birds on the complete diet. High temperature depressed growth by 29% ($p<0.05$) compared with moderate temperature. Feeding system also had an effect, with growth rate 34% ($p<0.10$) greater on complete diet than on choice diet. No significant interaction between diet and temperature was detected.

3.3.2 Metabolisable energy intakes

Table 3.3 shows the apparent metabolisable energy intake (**IAME**) results. It was 24% higher ($p<0.01$) in the birds kept at moderate temperature (20 °C) than at high temperature (30 °C) in the complete diet group. No temperature effect was

Table 3.3. The effect of temperature and feeding system on intake of apparen metabolisable energy (IAME), endogenous energy losses (EEL) and intake of tru metabolisable energy (ITME). Means are presented as kJ/bird. d.

Diet	Temperature	IAME	EEL	ITME
Complete	**20 °C**	1692*a	70a	1763a
	30 °C	1370b	45b	1416b
Choice	**20 °C**	1494b	72a	1567b
	30 °C	1402b	46b	1448b
SED		68.80	7.06	68.10
Temperature effect				
Moderate	**20 °C**	1593a	71a	1665a
High	**30 °C**	1386b	46b	1432b
Diet effect				
Complete diet		1531a	58a	1590a
Choice diet		1448a	59a	1508a
SED		48.70	4.99	48.10
Interaction: P		<0.05	NS	<0.05

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

found when the birds were choice-fed. Birds on the complete diet and kept at moderate temperature consumed 13% more metabolisable energy ($p<0.05$) than those kept at the same temperature but choice-fed. No difference was noted between birds kept at high temperature and given the different feeding systems. Birds kept at moderate temperature consumed 15% more energy ($p<0.01$) than those kept at high temperature and there was no overall effect of feeding system. A significant interaction was recorded ($p<0.05$) between diet and temperature.

Endogenous energy losses (**EEL**) were 55% ($p<0.01$) greater in birds kept at moderate temperatures than those kept at high temperatures whether they were on complete diet or choice diet (Table 3.3). High temperature reduced the values of endogenous energy losses ($p<0.001$) when compared with those obtained by birds kept at moderate temperature. Feeding system had no effect on these values. The interaction was not significant.

True metabolisable energy (ME corrected for endogenous energy losses, see Section 2.3) intake (**ITME**) values are shown in Table 3.3. Birds on the complete diet and kept at moderate temperature consumed 25% more ($p<0.001$) than those on the same diet but kept at high temperature. No significant difference was recorded between choice-fed birds. However, birds receiving the complete diet and kept at moderate temperature metabolised 13% more energy ($p<0.05$) than the birds given the choice diet and kept at same temperature and there was no difference between birds kept at high temperature on different feeding systems. Temperature had an effect; high temperature depressing these values by 14% compared with moderate temperature ($p<0.001$). No effect of feeding system was noted. The interaction between diet and temperature was significant ($p<0.05$).

3.3.3 Energy expenditure and body temperature

Heat production is shown in Table 3.4. It was calculated per bird per d and then per g body weight when the birds were fed or fasted to adjust for the effect of body size. However, greater fed heat production kJ per bird per d (**HP kJ/d**) was recorded with the birds kept at moderate temperature (20 °C) and receiving different feeding systems ($p<0.001$ and $p<0.01$) than with their counterparts which were kept at high temperatures (30 °C). Greater (12%; $p<0.05$) fed heat production was found at 20 °C with the birds on complete diet than those given the free-choice diet. No difference was detected between birds kept at high temperatures and receiving different feeding systems. Across diets, temperature had the effect of decreasing heat production 19% ($p<0.001$); across temperatures, birds on the complete diet produced 9% more ($p<0.05$) heat than those on the free-choice diet. No significant interaction between diet and temperature was noted.

When fed heat production was calculated (**HP kJ/g**) per g of body weight, birds kept at 20 °C and receiving different feeding systems had similar heat productions, which were significantly ($p<0.001$) greater (19%) than that obtained in the birds which were kept at high temperatures (Table 3.4). Also, similar heat production was recorded between the birds of both groups kept at high temperatures. Again, the effect of temperature alone showed a significant ($p<0.001$) difference and no overall affect of feeding system was noted. The interaction was not significant.

Fasted heat production per bird per d (**FHP kJ/d**) behaved (Table 3.4) similarly to fed heat production (per g). Birds kept at 20 °C had similar heat production. Also no significant difference ($p>0.10$) was found between the birds housed at high temperature. However, heat production was significantly (25%; $p<0.01$) greater with the birds kept at moderate temperatures than those reared at high temperatures. The effect of high temperature across feeding systems gave a significant difference; it was 24% greater ($p<0.001$) with the birds kept at 20 °C.

Table 3.4. The effect of temperature and feeding system on fed heat production kJ/bird. d. **(HP kJ/d)**, fed heat production kJ per g body weight **(HP kJ/g)**, fasted heat production kJ/bird. d. **(FHP kJ/d)** and fasted heat production kJ per g body weight **(FHP kJ/g)**.

Diet	Temperature	HP kJ/d	HP kJ/g	FHP kJ/d	FHP kJ/g
Complete	**20 °C**	1162a*	0.85a	748a	0.53a
	30 °C	917c	0.70b	612b	0.43b
Choice	**20 °C**	1036b	0.83a	709a	0.54a
	30 °C	867c	0.71b	559b	0.44b
SED		41	0.020	35	0.013
Temperature effect					
Moderate	**20 °C**	1099a	0.84a	729a	0.54a
High	**30 °C**	892b	0.71b	586b	0.44b
Diet effect					
Complete diet		1040a	0.78a	680a	0.48a
Choice diet		952b	0.77a	634a	0.49a
SED		29	0.014	25	0.009
Interaction: P		NS	NS	NS	NS

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

Feeding system also had an effect; 7% greater heat production ($p<0.10$) was noted with birds fed on the complete diet. The interaction between diet and temperature was not significant.

Fasted heat production (**FHP kJ/g**) per g of live weight was not affected by feeding system when birds were kept either at 20 °C or at 30 °C (Table 3.4). However, temperature did have an effect. Birds which were kept at high temperatures had 19% less ($p<0.001$) heat production than those kept at moderate temperatures. Again, studying the effect of temperature alone gave a significant difference; FHP was 23% ($p<0.001$) higher with the birds reared at moderate temperature, and no overall effect of feeding system was noted. No significant interaction was detected between diet and temperature.

Heat increment of feeding (Table 3.5) was calculated by subtracting fasting heat production from fed heat production per bird per d (**HI kJ/d**). No significant ($p>0.10$) difference was found among three treatments (birds on complete diet and kept at high temperature or choice-fed and kept at both moderate and high temperatures). The only heat increment which was significantly different was that measured in the birds fed on the complete diet and kept at moderate temperature. It was 27% higher ($p<0.05$) than in the birds kept at same temperature but receiving the choice diet, and was 35% ($p<0.01$) greater than that of the birds housed at high temperatures. There was a significant temperature effect, higher heat increment (21%; $p<0.05$) being recorded in the birds reared at 20 °C. Feeding system also had an effect, 13% more heat ($p<0.10$) being produced by birds on the complete diet. The interaction between diet and temperature was significant ($p<0.10$).

When heat increment (**HI kJ/g**) was calculated per g of food intake (heat increment kJ per bird per day / food intake in g per bird per day), or as fraction of metabolisable energy intake (**HI kJ/kJ**) (heat increment kJ per bird per day / metabolisable energy intake per bird per day), no difference was noted either

Table 3.5. The effect of temperature and feeding system on heat increment kJ/bird. d. (HI kJ/d), heat increment kJ per g of food intake (HI kJ/g) or as fraction of apparent metabolisable energy intake (HI kJ/kJ) and fed body temperature (FBT °C).

Diet	Temperature	HI kJ/d	HI kJ/g	HI kJ/kJ	FBT °C
Complete	**20 °C**	414a*	2.8a	0.25a	41.2c
	30 °C	305b	2.6a	0.22a	42.0ab
Choice	**20 °C**	327b	2.6a	0.22a	41.4bc
	30 °C	308b	2.7a	0.22a	42.2a
SED		30	0.28	0.022	0.34
Temperature effect					
Moderate	**20 °C**	371a	2.7a	0.24a	41.3b
High	**30 °C**	307b	2.7a	0.22a	42.1a
Diet effect					
Complete diet		360a	2.7a	0.24a	41.6a
Choice diet		318a	2.7a	0.22a	41.8a
SED		21	0.20	0.016	0.24
Interaction: P		<0.10	NS	NS	NS

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

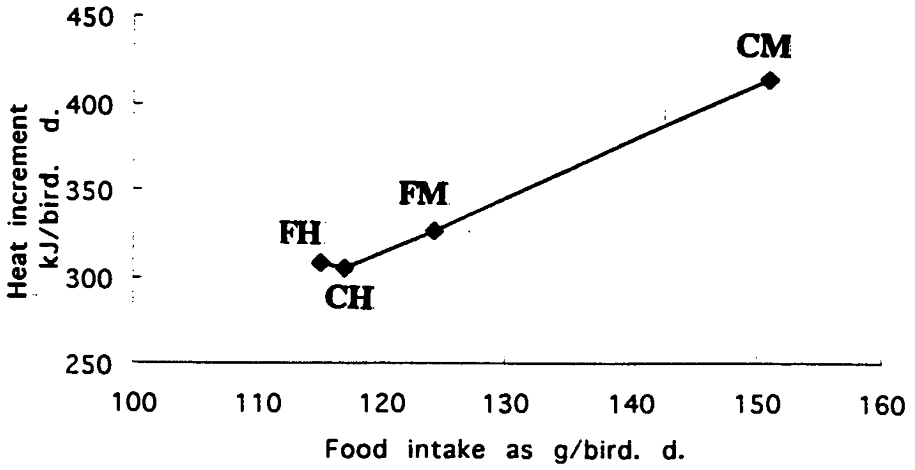


Figure 3.1.a. The relationship between food intake and heat increment associated with this food; it is clear how heat increment increased as food intake increased.

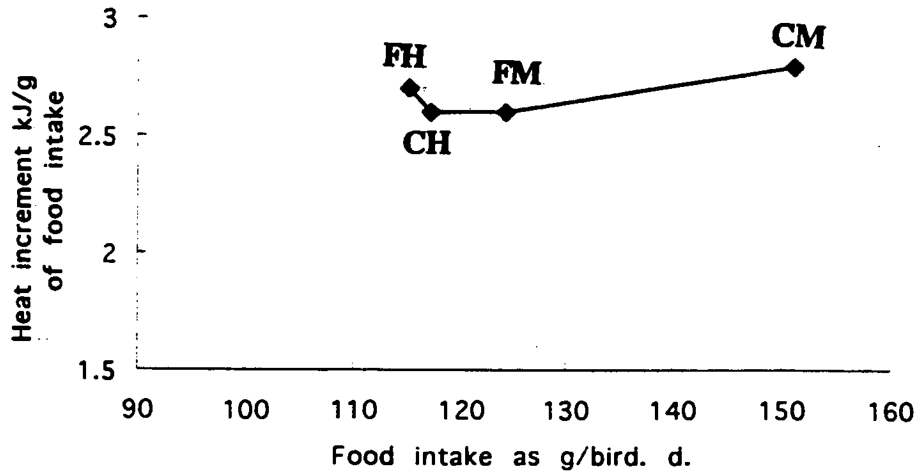


Figure 3.1.b. The relationship between food intake and heat increment associated with this food when calculated per g of the food intake; heat increment per g of food intake did not change as food intake increased from 115 or 117 g with the birds kept at 30 °C to 124 or 151 g with the birds kept at 20 °C. Free-choice diet, high temperature (FH); complete diet, high temperature (CH); free-choice diet, moderate temperature (FM) and complete diet, moderate temperature (CM).

between treatments or between temperatures or feeding systems (Table 3.5). The heat increment which was produced for each g of food intake was about 2.7 kJ, and it was about 0.23 kJ for each kJ metabolised. The interaction was not significant. The relationship between heat increment and food intake per d or per g intake is shown in Figure (3.1.a,b).

Fed body temperature (**FBT** °C) is shown in Table 3.5. No effect of feeding system was recorded when the birds were kept at the same ambient temperature. However, a significant effect ($p<0.05$) was found when ambient temperature increased, whether birds were on complete diet or choice-diet feeding. There was therefore a significant temperature effect ($p<0.01$) and no significant feeding system effect. The interaction was not significant.

3.3.4 Energy retention

Protein, fat and total energy retention are presented in Table 3.6 and Figure 3.2.a,b,c. Greater energy retention (27% more) as protein (**REP**) was found with the birds kept at 20 °C ($p<0.01$) than the birds at 30 °C when they were fed on the complete diet. Birds receiving the choice diet and kept at 20 °C had 12% more protein retention than those on same diet and kept at high temperature (30 °C) but this difference was not significant ($p>0.10$). More protein was retained (50%, 33%) by birds fed on the complete diet than those on the choice diet when kept at 20 °C and 30 °C, respectively ($p<0.001$, $p<0.01$). Again there was a significant temperature effect, with high temperature decreasing the amount of protein retained by 17% ($p<0.01$) below that recorded with birds at moderate temperature (20 °C). Also, feeding system had an affect. Birds on the complete diet had 42% greater protein retention ($p<0.001$). No significant interaction was recorded between diet and temperature.

Table 3.6. The effect of temperature and feeding system on energy retention as proteir (REP), energy retention as fat (REF) and total energy retention (RE) Means are presented as kJ/bird. d.

Diet	Temperature	REP	REF	RE
Complete	**20 °C**	412*a	119b	531a
	30 °C	325b	128b	453a
Choice	**20 °C**	274bc	184b	458a
	30 °C	244c	291a	535a
SED		24	39	54
Temperature effect				
Moderate	**20 °C**	343a	152a	495a
High	**30 °C**	285b	210a	494a
Diet effect				
Complete diet		369a	124b	492a
Choice diet		259b	238a	497a
SED		17	28	39
Interaction: P		NS	NS	<0.10

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

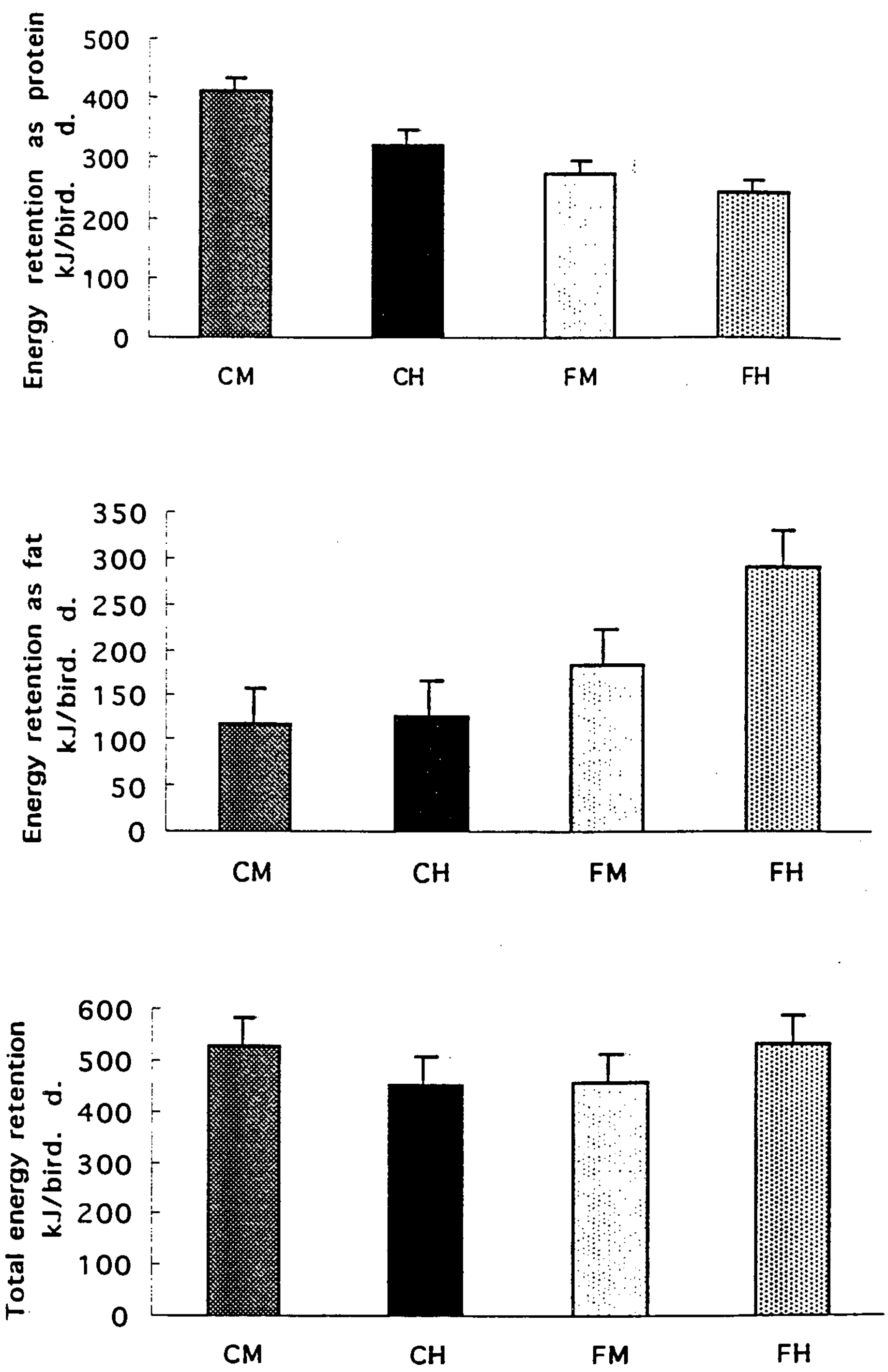


Figure 3.2.a,b,c. The effect of temperature and feeding system on protein, fat and total energy retention. Complete diet moderate temperature (CM), complete diet high temperature (CH), free-choice diet moderate temperature (FM) and free-choice diet high temperature(FH).

Energy retention as fat (**REF**) did not differ significantly between the different treatments, except with those birds which were receiving the choice-diet and kept at high temperature. This group had greater ($p<0.05$) energy as fat than other treatments. The temperature effect was less significant ($p<0.10$); energy retention as fat was 38% greater with the birds kept at high temperature. Feeding system had a stronger effect, with birds on the choice diet retaining 92% more fat ($p<0.01$). Diet and temperature had no significant interaction.

Total energy retention (**RE**) did not differ significantly ($p>0.10$) between the different treatments. Also, neither high temperature nor feeding system had any effect on this value. The diet and temperature interaction was significant ($p<0.10$).

3.3.5 Food conversion efficiency and energy metabolisability

The efficiencies of food and energy intake are displayed in Tables 3.7 and 3.8. Food conversion efficiency (**FCE**) was not affected by either high ambient temperature or by changing feeding system. No significant interaction was noted between diet and temperature.

Protein retention efficiency (**PRE**) behaved in a similar way to food conversion efficiency. No significant difference could be detected between different treatments. Also, no difference was attributable to the effect of temperature or to the effect of the feeding system when these were calculated separately. Interaction was not significant.

High temperature had no effect on apparent metabolisability, per g of food intake (**Amet kJ/g**) or as a fraction of total energy intake (**Amet kJ/kJ**), when the complete diet was offered. Similar results were noted with choice-fed birds. However, this metabolisability did differ with feeding system, but only with the birds which were kept at 20 °C; it was 8% ($p<0.05$) greater with the choice-fed birds than those on the complete diet. Feeding system, but not temperature, had a significant

Table 3.7. The effect of temperature and feeding system on food conversion efficiency (FCE) and protein retention efficiency (PRE).

Diet	Temperature	FCE	PRE
Complete	**20 °C**	0.44*a	0.48a
	30 °C	0.37a	0.48a
Choice	**20 °C**	0.35a	0.47a
	30 °C	0.32a	0.48a
SED		0.061	0.027
Temperature effect			
Moderate	**20 °C**	0.40a	0.48a
High	**30 °C**	0.35a	0.48a
Diet effect			
Complete diet		0.41a	0.48a
Choice diet		0.34a	0.48a
SED		0.043	0.019
Interaction: P		NS	NS

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

Table 3.8. The effect of temperature and feeding system on apparent metabolisability and true metabolisability per g of food intake (**Amet kJ/g**), (**Tmet kJ/g**) or as fraction from total energy intake (**Amet kJ/kJ**), (**Tmet kJ/kJ**).

Diet	Temperature	Amet kJ/g	Amet kJ/kJ	Tmet kJ/g	Tmet kJ/kJ
Complete	**20 °C**	11.21*b	0.70b	11.68b	0.72b
	30 °C	11.74ab	0.73ab	12.13ab	0.75ab
Choice	**20 °C**	12.12a	0.75a	12.74a	0.79a
	30 °C	12.26a	0.76a	12.66a	0.78a
SED		0.32	0.020	0.35	0.023
Temperature effect					
Moderate	**20 °C**	11.67a	0.73a	12.21a	0.76a
High	**30 °C**	12.00a	0.74a	12.40a	0.77a
Diet effect					
Complete diet		11.48b	0.72b	11.91b	0.74b
Choice diet		12.19a	0.75a	12.70a	0.79a
SED		0.22	0.013	0.25	0.016
Interaction: P		NS	NS	NS	NS

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

effect. Birds on choice diet had higher apparent metabolisability ($p<0.05$) than those given the complete diet. No significant interaction was noted.

True metabolisability (**Tmet kJ/g** or **Tmet kJ/kJ**) values followed the same pattern as those noted with apparent metabolisability values. It increased significantly (10%; $p<0.05$) when feeding system changed with the birds kept at 20 °C but no difference was recorded between birds kept at high temperatures (30 °C). Also, temperature had no overall effect on these values while feeding system had a significant effect ($p<0.05$), true metabolisability being 7% higher with the choice-fed birds. Interaction was not significant.

3.3.6 Energy retention proportions and efficiencies

The proportion of apparent metabolisable energy retained as protein (**PARP**) (Table 3.9, Figure 3.3) did not differ between birds on the same feeding system when the temperature increased. However, this proportion was affected significantly ($p<0.001$) by feeding system. It was about 33% greater in those on complete diet. This was also very clear when the effect of temperature or the effect of feeding system was studied separately, since no temperature effect and a significant ($p<0.001$) feeding system effect were found. Interaction was not significant.

No significant difference in the proportion of apparent metabolisable energy retained as fat (**PARF**) (Table 3.9, Figure 3.3) was noted between the birds on complete diet and kept at different temperatures, although it was 29% greater with those kept at high temperature. A significant difference ($p<0.01$) was found between the choice-fed birds, this proportion being 82% greater with those housed at high temperature. The proportion of apparent metabolisable energy retained as fat was significantly higher when feeding system changed. It was 57% ($p<0.10$) and 122% ($p<0.001$) higher with the birds receiving choice diet than those on complete diet when they were kept at 20 °C and 30 °C, respectively. This proportion was

Table 3.9. The effect of temperature and feeding system on the proportions of apparent metabolisable energy retained as protein (**PARP**), as fat (**PARF**) and on energy retention efficiency (**ERE**).

Diet	Temperature	PARP	PARF	ERE
Complete	**20 °C**	0.24*a	0.07b	0.31b
	30 °C	0.24a	0.09b	0.32ab
Choice	**20 °C**	0.18b	0.11b	0.29b
	30 °C	0.18b	0.20a	0.38a
SED		0.010	0.021	0.028
Temperature effect				
Moderate	**20 °C**	0.21a	0.09b	0.30b
High	**30 °C**	0.21a	0.15a	0.35a
Diet effect				
Complete diet		0.24a	0.08b	0.32a
Choice diet		0.18b	0.16a	0.34a
SED		0.007	0.019	0.018
Interaction: P		NS	<0.10	<0.10

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

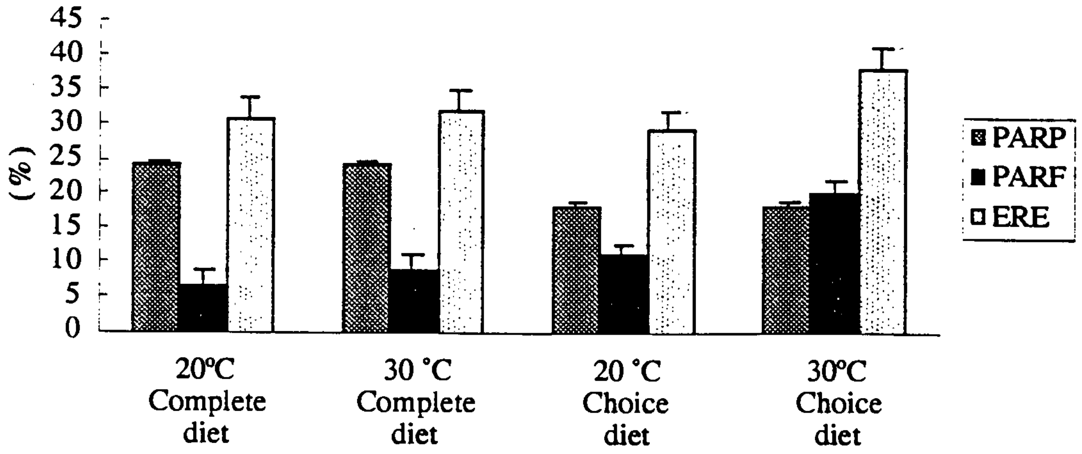


Figure 3.3. The effect of temperature and feeding system on the proportions of apparent metabolisable energy retained as protein (**PARP**), as fat (**PARF**) and on energy retention efficiency (**ERE**).

significantly increased ($p<0.05$) by elevated temperature. There was also a significant feeding system effect ($p<0.01$). The interaction between diet and temperature was significant ($p<0.10$).

Birds on the complete diet had similar efficiencies of total energy (**ERE**) retention (protein + fat retention energy) from apparent metabolisable energy (Table 3.9, Figure 3.3). However, the efficiency with choice-fed birds was 31% higher ($p<0.05$) with the birds reared at high temperature. Energy retention efficiency was 19% greater ($p<0.10$) with choice fed birds than with those on the complete diet when both were kept at high temperature. When the effect of temperature or the effect of feeding system on energy retention efficiency was tested separately, only temperature had a significant effect ($p<0.05$) being 17% higher with heat stressed birds. Diet and temperature interaction was barely significant ($p<0.10$).

3.3.7 Water and dry matter retention

Table 3.10 shows water and dry matter retention in the carcass. Water retention (**WRC**) was significantly (78%) greater ($p<0.05$) in the birds on the complete diet and kept at 20 °C than in those kept at high temperature (30 °C) on the same diet. No significant difference due to temperature was found in choice-fed birds, although water retention was 56% higher in the birds at 20 °C. Birds on complete diet and kept at 20 °C retained 60% more water ($p<0.10$) than choice-fed birds which were kept at the same temperature. No significant difference was noted between the birds kept at high temperatures and receiving different feeding systems, although it was 40% greater with the birds fed complete diet. The temperature effect was significant ($p<0.05$), a greater amount of water being retained by the birds at 20 °C. Feeding system also had an effect, birds on complete diet retained 53% more ($p<0.10$) water than choice-fed birds. The diet and temperature interaction was not significant.

Table 3.10. The effect of temperature and feeding system on water retention in th carcass (**WRC**) and growth rate as dry matter (**GRDM**). Means are presented as g/bird. (

Diet	Temperature	WRC	GRDM
Complete	**20 °C**	45.3*a	21.3a
	30 °C	25.4b	17.7ab
Choice	**20 °C**	28.3ab	16.9b
	30 °C	18.1b	18.3ab
SED		8.3	1.8
Temperature effect			
Moderate	**20 °C**	36.8a	19.1a
High	**30 °C**	21.8b	18.0a
Diet effect			
Complete diet		35.4a	19.5a
Choice diet		23.2a	17.6a
SED		5.9	1.2
Interaction: P		NS	<0.10

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

Increasing ambient temperature depressed growth rate as dry matter (**GRDM**) by 17% ($p<0.10$) in birds receiving the complete diet. No significant effect of temperature on this variate was noted when choice diet was offered, although slightly greater growth (+ 8%) was recorded with the birds housed at high temperature. Birds on complete diet had a higher growth rate (26%, $p<0.05$) than those on choice diet when they were kept at 20 °C. Birds kept at high temperature and receiving different feeding systems had similar growth rates. However, when the overall effect of temperature or of the feeding system was analysed, no significant difference was detected, although this value was 6% and 11% higher when the birds were kept at 20 °C or when they were fed complete diet, respectively. A significant interaction ($p<0.10$) between diet and temperature was found.

3.3.8 The composition of the body

The proportions of protein, fat, water and dry matter are displayed in Table 3.11 and Figure 3.4. This proportion was calculated by dividing the daily retention in grams of the observation by the total daily growth rate. The proportion of protein retention (**PRC%**) was not affected either by increasing ambient temperature or by changing feeding system, although a slightly higher ratio (not significant) was found with birds kept at high temperatures. No significant interaction was noted between diet and temperature.

The percentage of fat retention (**FRC%**) did not differ significantly with temperature in birds given the complete diet; however, this ratio was 64% higher with the birds kept at high temperature. Elevated ambient temperature with the choice-fed birds increased this ratio by 130% ($p<0.001$). Choice-fed birds had a higher proportion of fat (113%; $p<0.10$) than those on complete diet when they were kept at 20 °C. The difference between birds receiving different feeding systems and kept at high temperatures was 3-fold ($p<0.001$). There was a significant temperature

Table 3.11. The effect of temperature and feeding system on the proportions of prote retention (**PRC%**), fat retention (**FRC%**), water retention (**WRC%**) and growth rate dry matter (**GRDM%**) of the carcass.

Diet	Temperature	PRC%	FRC%	WRC%	GRDM%
Complete	**20 °C**	29.5a*	4.5b	66.0a	34.0b
	30 °C	34.2a	7.4b	58.4a	41.6b
Choice	**20 °C**	30.0a	9.6b	60.4a	39.6b
	30 °C	32.6a	22.1a	45.2b	54.8a
SED		4.2	2.6	4.7	4.7
Temperature effect					
Moderate	**20 °C**	29.8a	7.1b	63.2a	36.8b
High	**30 °C**	33.4a	14.8a	51.8b	48.2a
Diet effect					
Complete diet		31.9a	6.0b	62.2a	37.8b
Choice diet		31.3a	15.9a	52.8b	47.2a
SED		3.0	1.8	3.3	3.3
Interaction: P		NS	<0.05	NS	NS

* Measurements in the same column not sharing a common subscript are different at the $p<0.05$ level.

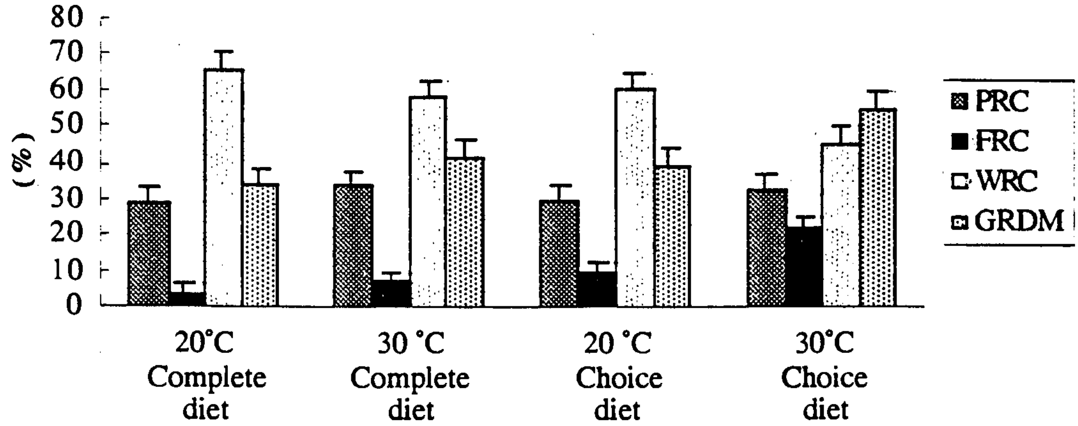


Figure 3.4. The effect of temperature and feeding system on the proportions of protein retention (**PRC%**), fat retention (**FRC%**), water retention (**WRC%**) and growth rate as dry matter (**GRDM%**) of the carcass.

effect (108%; $p<0.01$). The effect of feeding system was also significant (165%; $p<0.001$): higher with birds on the choice diet. The interaction between diet and temperature was significant ($p<0.05$).

Water retention proportion (**WRC%**) did not differ significantly with temperature in the birds on complete diet, although it was 12% less with those kept at high temperature. The proportion of water retention when the choice diet was offered decreased significantly (25%; $p<0.05$) in the birds kept at high temperature. However, birds receiving the complete diet had a 9% higher ratio (not significant) than choice-fed birds when they were kept at 20 °C, while a significant (29%; $p<0.05$) difference was recorded between the birds which were kept at high temperature and receiving different feeding systems. The temperature effect, when feeding system effect was removed, was significant ($p<0.01$), with water retention (%) being 22% higher with the birds kept at 20 °C. Also, the feeding system effect, was significant ($p<0.05$), the ratio being 18% higher with the birds on complete diet. Interaction was not significant.

The proportion of dry matter (**GRDM%**) in total growth rate was also calculated by the conventional method [dividing the weight of growth rate as dry matter in grams (Table 3.10) by the total daily growth rate in grams (Table 3.2)]. This proportion was, of course, negatively related to the proportion of water retention.

3.4 Discussion

3.4.1 Food, protein and water intakes and growth rate

Food intake (**FI**) was depressed (24%) by high temperature (Table 3.2) with birds given either the complete diet or the choice diet when compared with those fed on the complete diet and kept at 20 °C. Similar results have already been reported (Cowan and Michie, 1977, 1978; Mitchell and Goddard, 1990; Mitchell and Carlisle, 1992; Geraert *et al.*, 1993). However, it was surprising that birds kept at 20 °C and fed on the choice diet ate significantly less than those kept at the same temperature and given the complete diet.

Gleaves *et al.* (1968) found with laying hens that food consumption was reduced when the ratio of protein to energy was decreased and vice-versa. They attributed the greater food consumption when the (CP:ME ratio) increased to the increase in egg production, where egg production was associated with protein level. So, protein concentration acted on food intake in indirect way. They also suggested that energy in the diet should be adequate, otherwise protein would be used as a source of energy, but when energy is beyond the requirement level, it will serve as the main regulator of food intake. Similar results were reported by Meyer and Hargus (1959) in rats and by Shariatmadari and Forbes (1993) in broilers and laying hens, who found a reduction in food intake when these animals were given low-protein diets. They suggested that the food intake of the animals which were fed low-protein diets was limited by the excess of energy intake in relation to protein intake.

The birds fed on the choice diet and kept at 20 °C selected a mixture of feeds which gave a crude protein concentration (**PI**) of about 21% while those kept at 20 °C on the complete diet had 25% protein in their diet. It seems that increasing rather than decreasing the ratio of protein to energy in the diet (CP:ME ratio) is a good stimulator for increasing food intake with the condition that energy concentration is suitable to prevent the use of protein for energy. It is possible that the increase in food consumption with the birds kept at 20 °C and fed on the complete diet resulted from the greater demand for energy to incorporate the greater quantity of protein which was eaten. However, this suggestion may be valid when the birds are kept at 20 °C but not with those at high temperature (30 °C). The difficulty in increasing food intake at high temperature is still found even if protein level is high in the diet; food intake was similar between the groups kept at high temperature.

In the present work, the birds given the choice diet both at 20 °C and 30 °C significantly decreased their protein intake compared with the group fed on the complete diet and kept at same temperatures (Table 3.2). The concentration of crude protein with birds fed on a free-choice diet in this work was about 20%, similar to those reported by Cowan and Michie (1977) and Shariatmadari and Forbes (1993) when they offered a choice to broilers, where the concentration was about 19%. These results may suggest that when the birds are giving freedom to select their protein intake, they will not necessarily eat the amount which makes them grow most rapidly. The results obtained here are also in agreement with the work of Cowan and Michie (1977) who noted that broilers given a choice diet and kept at high temperature did not select to maintain their protein intake same as those kept at lower temperature, but not with that of Mastika and Cumming (1987).

Water intake (WI) was similar between the birds on complete diet and those fed choice diet and kept at high temperature (Table 3.2). These results were confirmed by Farrell and Swain (1977a) and Savory (1986). The similarities in water intake could be explained by the effects of food intake and temperature. There was greater food intake with the birds on the complete diet and kept at 20 °C which made the birds drink a lot of water and there was a heat load on the birds which were kept at high temperatures. The effect of increasing temperature on water requirements was discussed in Section (1.2.1); more water is required for respiratory evaporative cooling processes (Barott and Pringle, 1941; Sykes, 1977). However, the significant difference noted between the birds kept at 20 °C can be attributed to the difference in food consumption.

Growth rate (Table 3.2) was mainly affected by food intake, since, it will be seen in Section (3.4.7) that water retention also had an affect on growth rate. The greatest growth rate (**GR**) was in the birds on the complete diet and kept at 20 °C, where the greatest food intake also occurred. The reduction in growth rate as temperature increases was reported by Adams *et al.* (1962a, 1962b); Lei and Slinger (1970); Swain and Farrell (1975) and Cowan and Michie (1977, 1978).

In the present experiment, giving birds which are kept at 20 °C a complete high-protein diet was better for maximal growth than giving them a free-choice regime. Also, it is possible that this better growth might have been obtained by "forcing" the birds to increase their food intake because of a greater demand for energy. However, the same response may be impossible when the birds are exposed to high temperature, because the birds will not be able to increase their food intake even if protein level is high in the diet and a greater amount of energy is required to be eaten.

3.4.2 Metabolisable energy intakes

Metabolisable energy intakes (Table 3.3) were influenced by the total energy intake. So, the greatest apparent (**IAME**) and true (**ITME**) metabolisable intake values were with the birds on complete diet and kept at 20 °C because the greatest intake by weight and energy was with these birds (Table 3.2). However, the similarity in **IAME** intake between complete and choice fed birds, although a significant difference was recorded in the total food intake, resulted from the difference in the metabolisability of the diets (this will be discussed in Section 3.4.5).

However, the greater endogenous energy losses (**EEL**) with the birds kept at 20 °C (Table 3.3) than heat stressed birds is attributable to the demand for energy. At 20 °C, more energy is required to maintain body temperature and that increases nitrogen catabolism and excretion which in turn increases the value of endogenous energy losses. These results are in agreement with Farrell and Swain (1977b) and Geraert *et al.* (1992).

3.4.3 Energy expenditure and body temperature

Fed heat production (Table 3.4) kJ per bird per d (**HP kJ/d**) was affected by two factors, the temperature and the food intake (see Section 1.2.3). This was very clear in the birds on complete diet and kept at 20 °C; these birds ate most food and that in turn increased the heat increment. Also, these birds needed additional energy for thermoregulation. Together, food intake and ambient temperature induced the greatest heat production with this group. The higher heat production of choice-fed birds (kept at 20 °C) than either heat stressed group (although food intake was not significantly different between all these groups) confirmed the requirements of thermoregulation. Also, the difference in heat production between the groups kept at moderate temperature confirmed the effect of heat increment of the diet on this parameter.

However, when fed heat production (Table 3.4) was calculated per g of live weight (**HP kJ/g**), a significant difference was noted only between the groups kept at 20 °C and those at 30 °C, and that was of course due to the thermoregulation processes. Even if there was a difference in heat production (per bird per d) between the birds kept at 20 °C on different feeding systems, there was also a difference in growth rate and that led to similar heat production per g of live weight.

It is possible to enlarge on heat production by way of explanation. Heat will be produced according to the demand for energy. Any factor which will increase this demand for energy (such as the energy requirement for sustaining basic maintenance processes, thermoregulation and activity including feeding) will increase heat production. After using this energy, it can not be retained and it will leave the body as heat. So, the birds kept at 20 °C on different feeding systems had similar heat production (kJ/g), because each unit of live weight requires similar energy for basal metabolic rate and thermoregulation. Although the heat increment was greater (Table 3.5) with birds on the complete diet, there was also greater weight increase (Table 3.2). However, if the greater heat increment is divided by the greater body weight, similar heat production per g of live weight can be expected.

Results for fasting heat production (Table 3.4) when calculated per bird per day (**FHP kJ/d**) or per gram of live weight (**FHP kJ/g**) confirmed the previous suggestion. The greater thermoregulatory energy demand at 20 °C gave the significant difference.

The results reported here are in agreement with previous work (Kleiber and Dougherty, 1934; Farrell and Swain, 1977a; Farrell and Swain, 1977b; MacLeod, 1990, 1992) which noted reduced heat production at high temperature and also with Klandorf *et al.* (1981) and MacLeod (1990, 1992) who found lower heat production with fasted birds than with fed birds and with MacLeod and Shannon (1978) who reported greater heat production when calculated per bird but similar heat production when estimated per unit of body weight.

The greater heat increment (**HI kJ/d**) (Table 3.5) obtained with the group which were fed on the complete diet and kept at 20 °C than the other 3 groups (choice-fed kept at 20 °C and the birds kept at 30 °C and receiving different feeding systems) simply resulted from the greater food intake with that group (Li *et al.*, 1992; Zhou and Yamamoto, 1997). Also, it is worth mentioning here that the heat increment of the diet was similar between these three groups as a result of the similarities in food intakes, which indicates that heat increment of the diet with the birds at 20 °C and fed choice diet did not replace the heat produced by the birds for thermoregulation during fasting (Figure 3.1.a,b). To confirm this, heat increment was calculated per g (**HI kJ/g**) of food intake and as a fraction of apparent metabolisable energy (**HI kJ/kJ**) (Table 3.5). Results showed similar heat production (kJ/g) or (kJ/kJ), which gave more evidence on the suggestion of Kleiber and Dougherty (1934) and O'Neill *et al.* (1971) who reported that the heat increment of the diet was not used for thermoregulation process. However, the findings here are not in accordance with the work of Farrell and Swain (1977a) who suggested utilisation of heat increment in the cold.

The higher body temperature (**FBT °C**) recorded in the birds kept at high temperatures (Table 3.5) is attributable to their limitation in dissipating heat. Of course, this difficulty caused an increase in the heat content of the body. Similar results were reported by Grimes and Moreng (1965), Hayashi *et al.* (1992) and Waibel and MacLeod (1995).

3.4.4 Energy retention

Energy retention as protein (**REP**) (Table 3.6, Figure 3.2.a) was strongly related to protein intake, especially since the efficiency of protein retention did not differ (MacLeod, 1990, 1992) between the different treatments (discussed in 3.4.5). However, the efficiency of protein retention may decrease when the protein: energy ratio of the diet increases, because amino acids would function as an energy source.

Energy retention as fat (**REF**) was influenced by 3 factors, the first being diet composition, the second temperature and the third energy intake (Table 3.6, Figure 3.2.b). Fat retention was greatest with birds kept at high temperature and given the free-choice diet. This can be attributed to the effect of diet composition, since these birds selected a diet which gave about 19% protein. The increase in energy retained as fat, as protein level decreases in the diet, was reported by Adams *et al.* (1962a) and MacLeod (1990, 1992). The reduction in protein concentration means that a greater proportion of energy will be available from the diet to fuel the different processes which require energy. This in turn allows the animal to store a higher proportion of its energy intake as body fat. The second factor affecting fat deposition is ambient temperature. At high temperature less energy is required for thermoregulation (discussed in 3.4.3) and this leads to increased storage of energy as body fat.

The effect of the diet and temperature can be seen very clearly when comparison is made, respectively, between the birds kept at high temperatures on different feeding systems and between the birds on complete diet and kept at different temperatures. Comparison showed that even although the total food intake (Table 3.2) was nearly equal (117 v. 115 g) between both treatments at high temperature, fat retention differed significantly between them, which must have been due to the variation in the diet composition (CP:ME ratio), especially since similar energy intake, similar maintenance energy (fasting heat production) and nearly the same heat increment were shown by the birds (Tables 3.4 and 3.5).

Also, nearly the same amount of fat was retained by the birds kept at 20 °C and 30 °C when the birds were fed on the complete diet (same composition), while there was a 29% difference ($p<0.001$) in food intake. This undoubtedly resulted from the greater demand for energy for thermoregulation in the birds kept at 20 °C, since, if the energy required for maintenance (fasted heat production of the birds kept at 30 °C; **FHP kJ/d**, Table 3.4) and for heat increment (**HI kJ/d**, Table 3.5) of the diet (which is almost constant in this experiment **HI kJ/g**, Table 3.5) were subtracted from the energy which was available, according to the equation below, it will be noted that much energy should be retained as fat with the birds on complete diet and kept at 20 °C as a result of the greater amount of energy eaten.

Energy retained as fat = I_{AME} - REP - (FHP at 30 °C + HI)

where IAME is apparent metabolisable energy intake, REP is energy retention as protein, FHP is fasted heat production at 30 °C and HI is heat increment of the diet.

However, the values of 119 and 128 kJ per bird per d were obtained with the birds on complete diet and kept at 20 °C and 30 °C (Table 3.6), respectively. The similar fat retention between the two groups, therefore, resulted from the greater thermoregulatory heat production with the birds kept at 20 °C.

However, it is difficult to find similar results when the data of choice-fed birds are used, since energy intake was similar between them but energy required for thermoregulation was greater with birds kept at 20 °C. Together, similar energy intake and greater energy required for thermoregulation led to decreased fat retention with the birds reared at 20 °C. The effect of temperature became very clear here.

Also, by using the above equation to calculate the effect of increasing protein level in the diet between choice-fed and complete diet birds both kept at high temperature, similar results will be noted (more fat will be retained with the low-protein diet).

The differences in energy retention as protein and as fat (Table 3.6, Figure 3.2.c) between the different treatments balanced out in total energy retention (**RE**), so similar amounts of energy were stored in the bodies. It is interesting to note that even if there was a significant difference in growth rate by weight between the different treatments (Table 3.2), there was similar energy retention (Figure 3.5). Also, the lowest growth rates with choice-fed birds which were kept at high temperature were associated with the greatest energy retention (not statistically significant). Greater growth rate by weight does not mean greater energy retention (Adams *et al.*, 1962a).

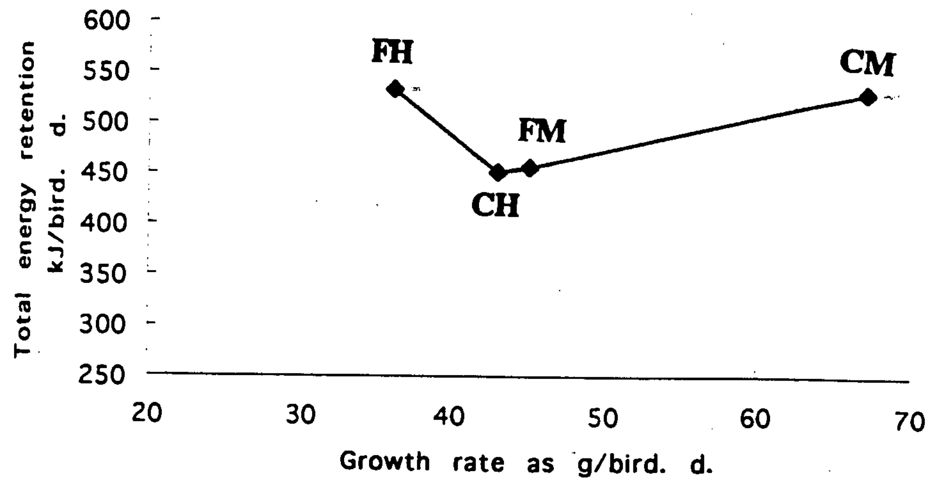


Figure 3.5. The relationship between growth rate and total energy retention; similar energy retentions were noted between different treatments although growth rate significantly differed from 36, to 43, to 45 to 67 g. Free-choice diet, high temperature (FH); complete diet, high temperature (CH); free-choice diet, moderate temperature (FM) and complete diet, moderate temperature (CM).

3.4.5 Food conversion efficiency and energy metabolisability

Food conversion efficiency (FCE) did not differ significantly between treatments (Table 3.7). No effect of increasing temperature on **FCE** was reported by Adams *et al.* (1962a), Wilson *et al.* (1980) or Savory (1986). However, food conversion efficiency was 15% higher with the birds kept at 20 °C and it was 18% greater with the birds on complete diet system. In this work it will be seen later (in Section 3.4.7) that an important factor affecting weight gain is water retention, and how this water is affected by temperature and protein retention.

Protein retention efficiency of total intake (**PRE**) was not affected by increasing temperature or by offering diet choice (Table 3.7). MacLeod (1990, 1992) noted no effect of increasing temperature from 20 °C to 32 °C or changing protein concentration on the efficiency of protein retention. Similar efficiencies of protein retention may have resulted partly from protein quality or amino acid balance for growth. However, these findings are not in agreement with Geraert *et al.* (1992) who found increasing protein retention efficiency or Farrell and Swain (1977a) who noted a decrease when temperature was increased.

Apparent metabolisability (**Amet kJ/g** or **Amet kJ/kJ**) was not significantly (Table 3.8) different between birds kept at 20 °C and those kept at 30 °C in each feeding system. However, it was 7% greater ($p<0.05$) with the choice fed group when compared with birds given complete diet and kept at 20 °C. This could be attributable to the different selection of the diet by choice feeding birds which resulted in different intakes of individual ingredients. For instance, protein intakes were, respectively, 25% and about 20% of total intake with complete diet and choice-fed groups.

Increasing protein level and decreasing low-protein source in the complete diet reduced metabolisability, especially when the efficiency of protein retention was similar between all treatments. This is because the metabolisability of the lower-protein ingredient (e.g. wheat) is higher than the metabolisability of the higher-protein ingredient (e.g. soybean). True metabolisability of complete diet, balancer and wheat feeds were 11.57, 9.71 and 12.8 kJ/g, respectively; since the proportion of the low-protein nutrient is higher in the diet of choice feeding than complete diet, that led to increase the amount of metabolisable energy in relation to the total intake with choice-fed birds and in turn the metabolisability increased. Similar results were noted by Sibbald *et al.* (1960), who found that metabolisability values increased when corn and soy contents of the diet increased and decreased, respectively. It is also possible that apparent metabolisability value of specific ingredients may change slightly with level of inclusion. Sell (1966) noted that metabolisable value of rapeseed was higher than that reported by Sibbald and Slinger (1963). He attributed this to the effect of dietary nutrient level, since he used rapeseed at levels 15 and 20% but Sibbald and Slinger (1963) used 20, 40 and 60%.

However, this significant difference in metabolisability could not be detected between choice fed birds and birds fed complete diet but kept at high temperature. Geraert *et al.* (1992) noted that elevating temperature from 22 to 32 °C caused an increase in metabolisability values. They suggested that the decrease of food passage rate as a result of elevating temperature (Wilson *et al*, 1980) may have increased the time for enzyme action. Another possible mechanism for the increased metabolisability values is the more efficient absorption of nutrients because of the longer stay in the intestine (Zuprizal *et al.*, 1993). Also, in the present study, it was noted that the values of metabolisability were greater (although not significantly so) with the birds kept at 30 °C than those kept at 20 °C in each feeding system. So, it seems that this small increase in metabolisability with the birds on complete diet and kept at high temperature was the reason for a reduction in the difference between them and the birds fed on the choice diet.

True metabolisability (**Tmet kJ/g, Tmet kJ/kJ**) was strongly related to apparent metabolisability values (Table 3.8), especially since endogenous energy losses were not effected by feeding system (Table 3.3).

3.4.6 Energy retention proportions and efficiencies

The proportion of apparent metabolisable energy retained as protein (**PARP**) (Table 3.9, Figure 3.3) was directly influenced by the concentration of protein in the diet, especially when the efficiency of protein retention from the total intake did not differ between the treatments (Table 3.7), and apparent metabolisability values were similar between the birds kept at different temperatures whether on complete diet or choice-diet (Table 3.8). The increase in protein level of the diet led to this nutrient forming a higher proportion of apparent metabolisable energy (**IAME**) compared with low-protein diet. So, the same values for **PARP** were found at both temperatures on each feeding system.

The proportion of apparent metabolisable energy retained as fat (**PARF**) (Table 3.9, Figure 3.3) was directly related to the effect of (CP:ME) ratio, to temperature and to energy intake (discussed in detail in 3.4.4). The greatest proportion of fat retention from apparent metabolisable energy (**IAME**) was with the birds kept at high temperature and given the choice diet. That is attributable, as mentioned above, to the reduction in the energy required for thermoregulation and to the composition of the diet (smaller proportion of protein and greater proportion of energy compared with complete diet). Also, the lowest proportion was recorded with the birds kept at 20 °C and fed on the complete diet (the treatment giving the greatest energy intake); probable reasons are the thermoregulatory costs and again the composition of the diet (a higher proportion of protein than in the choice diet).

The effect of the diet composition again appears (Table 3.9, Figure 3.3). Choice-fed birds kept at 20 °C ate less food (similar to the groups kept at 30 °C), and also used energy for thermoregulation. However, they had slightly higher proportion than the birds on complete diet at 30 °C which needed less energy for thermoregulation or the birds on complete diet and kept at 20 °C which ate the greatest energy. This is attributable to the effect of the diet composition (CP:ME ratios).

The efficiency of total energy retention (**ERE**) was effected by the proportions of apparent metabolisable energy retained as protein and fat (Table 3.9, Figure 3.3). Similar results have been found by MacLeod (1991a) at moderate temperature (26%) and by Kleiber and Dougherty (1934) and MacLeod (1992) at high temperature, 34 and 37%, respectively. Jones (1994) noted similar efficiencies (40%) at both 21 and 30 °C.

3.4.7 Water and dry matter retention

Water retention (**WRC**) was greatest with the birds on the complete diet and kept at 20 °C (Table 3.10) and least with choice-fed birds which were kept at high temperature (30 °C). Water retention is affected by two factors, protein retention and ambient temperature (see 1.2.1 and 1.2.5 for more details). The greatest water retention with complete diet birds when kept at 20 °C can be explained by the protein retention (Table 3.6) of these birds, which led to greater water retention (Adams *et al.*, 1962a; MacLeod, 1991a). Also, because these birds were not kept at high temperature, there was no need to use part of this water for evaporative cooling processes (Barott and Pringle, 1941; Sykes, 1977). The lowest water retention with choice-fed birds kept at high temperature is attributable to the low protein retention and to the greater water requirement for evaporative cooling processes.

The effect of increasing temperature on water retention was very clear when comparison was made between the birds on complete diet and kept at 30 °C and those fed on the choice diet but kept at 20 °C. Although the first group retained 19%

more protein than the latter one, water retention was greater with the choice-fed birds (not statistically significant). Also, although the difference in protein retention between the birds on complete diet and kept at different temperatures was nearly the same of that between complete diet and choice-fed birds when both were kept at high temperature (87 and 81 kJ, Table 3.6), water retention was significantly ($p<0.05$) different between the first two groups and the difference was about 20 g. However, the difference in the other group was only 7 g and it failed to show a significant difference.

When water retention was calculated per g of protein retention, it gave 2.5 and 1.8 g with complete diet birds when they were kept, respectively, at 20 °C and 30 °C. Similar results were obtained in choice-fed birds, 2.3 and 1.7 g with the birds kept at 20 °C and 30 °C, respectively. These results demonstrate the effect of temperature on water retention and on how much water may be used for the evaporative cooling processes.

It can be concluded from these results that, the strongest effect on water retention can be expected when both protein retention decreases and ambient temperature increases. The smallest effect on this parameter is expected when both groups of animals are exposed to heat stress because, even if there was a significant difference in protein retention, water would be evaporated for cooling the animal. This would reduce the amount of water retained and in turn the difference between the high temperature groups. Finally there is an intermediate effect when protein retention differs but animals are growing at moderate temperature.

Growth rate as dry matter (**GRDM**) exhibited very interesting information (Table 3.10). The lowest growth was with choice-fed birds which were kept at 20 °C. This can be explained by the reduction in food and protein intakes and by the greater demand for thermoregulatory energy (as those on complete diet and kept at 20 °C). So, a greater proportion of energy intake was used for maintenance and thermoregulation rather than growth. The less difference between the birds kept at 20 °C and given the complete diet and those on different feeding systems but kept at 30 °C temperature, although food intake was very different ($p<0.001$; Table 3.2), is attributable to the lower energy being used for thermoregulation.

Also, it is interesting to note that part of the large differences in growth rate by weight (Table 3.2) between the birds on complete diet and kept at 20 °C and those which were kept at 30 °C was due to the effect of water retention. When this effect was removed, the differences became less. That was clear when the ratios of growth rate (Table 3.2) were calculated between the birds. The difference in the ratio of growth rate between the birds on the complete diet and kept at different temperatures was 64%, and it was 54% between the birds on the complete diet and kept at 20 °C and those choice-fed and kept at 30 °C. However, when these ratios were estimated according to growth rate as dry matter, they were 83% and 86%, respectively. So, if the difference in growth rate was 24 g per d between the birds on complete diet (Table 3.2), we can estimate a difference of 960 g for 40 d (40 d is the period from 20 d, the age which was chosen for starting with the birds in this experiment), while the difference in growth rate as dry matter was only 3.6 g per d (Table 3.10), which would give a difference of 144 g for 40 d.

This evidence shows the effect of temperature on weight gain through decreasing the water content of the carcass as a result of the reduction in protein retention and the increase in water evaporation, and how growth rate differs less when calculated as dry matter.

3.4.8 The composition of the body

Body protein retention, fat retention, water retention and growth rate as dry matter (**PRC, FRC, WRC** and **GRDM%**) which were expressed as the proportions of growth rate per d were shown in Table 3.11 and Figure 3.4. To understand how the different proportions of body composition are influenced by increasing temperature, the effect of temperature on water retention (**WRC**, Table 3.10) and energy retention as protein (**REP**, Table 3.6, converted to g) were used here.

In Section (3.4.7) it was noted that each gram of protein is associated with the retention of about 2.4 and 1.8 g of water when the birds were kept at 20 °C and 30 °C, respectively. This difference was attributed to the effect of temperature (discussed in 1.2.1, 3.4.1, 3.4.7). From this information, it can be seen that the proportion of water and protein in the lean growth will decrease and increase, respectively, when ambient temperature increases.

Also, because growth is less with the birds kept at 30 °C than at 20 °C, and because the amount of fat retained is similar between the two groups, a higher ratio of fat will occur in the 30 °C group. The proportion of fat will be negatively related to the proportions of both water and protein, and that in turn, will decrease them. However, the ratio of water retention is more affected than the ratio of protein retention because of the higher proportion of water forming the growth. Also, it was mentioned above that water ratio will decrease and conversely protein ratio will increase as temperature increases and this will reduce the effect of fat retention on protein but not on water retention proportion. Finally, there was still a slightly higher proportion of protein retention with the birds kept at high temperature.

However, the significant increase in the proportion of fat retention (Table 3.11, Figure 3.4) with choice-fed birds which were kept at high temperature can be attributed to the effect of diet composition (smaller proportion of protein) and to the effect of temperature. The significant reduction in water retention ratio is due to the increase in fat retention proportion as explained above.

Also, it was mentioned earlier (3.4.4 and 3.4.6) that increasing temperature allows a greater part of the apparent metabolisable energy to be stored in the body as fat rather than being used for thermoregulatory processes. A higher proportion of fat by weight can, therefore, also be expected in the birds kept at high temperature than at moderate temperature when fed on the complete diet.

The proportion of growth rate as dry matter (**GRDM%**, Table 3.11, Figure 3.4) was inversely related to proportion of water retention. The highest observation was, therefore, recorded with choice-fed birds which were kept at high temperature where there was the lowest proportion of water retention; the lowest proportion of growth rate as dry matter was associated with the greatest ratio of water retention, in the birds on complete diet and kept at 20 °C. All these different relationships can be explained again by the effect of the diet composition and the effect of temperature.

As temperature increases, a greater amount of water will be used for evaporative cooling (discussed in 1.2.1, 3.4.1, 3.4.7). Also, by reducing protein level in the diet, less protein and more fat will be retained in the body and that will result in less water being retained in the body (Adams *et al.*, 1962a; MacLeod, 1991a). Together these factors act to reduce the proportion of water and, conversely increase growth rate as dry matter.

The results reported here on the different effects of high temperature on body composition are in agreement with the review of Howlider and Rose (1987). Since they used 17 published papers and one unpublished report which represented data from a total of 71 experiments, all the parameters were expressed as proportions (%) of the performance of the broilers kept at 21 °C. The results obtained showed an increase in fat retention and a decrease in water retention concentrations as ambient temperature increases. However, there was no relationship between protein concentration and rearing temperature. The effect of high ambient temperature on protein, fat and water proportions was discussed earlier (1.2.4 and 1.2.5).

3.5 Conclusions

An experiment was designed to test the effects of temperature on food utilisation by measuring energy metabolisability and expenditure, and to provide more information about which system can be used for more efficient growth at high temperature: giving a complete diet high in protein content or offering choice-feeding. The following were observed:

1- High temperature decreased food intake, growth rate, heat production and protein retention but increased fat retention (as a result of the reduction in total energy intake with choice-fed birds which were kept at moderate temperature) and had no effect on total energy retention.

2- High temperature had no effect on apparent metabolisability, food conversion efficiency or proportion of IAME retained as protein but increased energy retention efficiency and proportion of IAME retained as fat.

3- High temperature decreased the proportion of water retention but increased the concentrations of fat retention and dry matter, and had no effect on the proportion of protein retention.

4- Across temperatures, choice-feeding decreased food intake, growth rate, heat production and protein retention but increased fat retention and had no effect on total energy retention.

5- Choice-feeding increased apparent metabolisability, proportion of IAME retained as fat but decreased the proportion of IAME retained as protein and had no effect on food conversion efficiency or protein and total energy retention efficiency.

6- Choice-feeding decreased water retention but increased the proportions of fat retention and dry matter, and had no effect on protein retention concentration.

7- Including both factors (feeding-system and temperature) showed that choice feeding gave a lower growth rate than complete diet (especially with those kept at moderate temperature). The reduced growth rate was related to a reduced food intake and the proportion of protein in the chosen combination of feeds.

8- Heat increment per g of food intake did not differ between groups kept at 20 °C and those at 30 °C, supporting the suggestion that heat increment of the diet does not necessarily replace thermoregulatory heat production.

9- Although growth rate differed significantly, total energy retention did not, reflecting the energy densities of the different chemical components of the body.

10- The bird's "preferred" rate of protein growth may be lower than the industry's desired rate so choice feeding does not necessarily improve growth rate even at high temperature.

Chapter Four

The use of pair-feeding to analyse the effects of heat stress on growth

4.1 Introduction

4.1.1 Pair-feeding

It was noted from the results of the first experiment (Chapter 3) that the major effect of temperature increase on food utilisation was through the depression of food intake. However, previous authors' work has given a variety of results.

Smith and Oliver (1972) conducted a study for 4 weeks using laying hens maintained at temperatures of 21, 32 and 38 °C and fed *ad libitum*. Two other groups were kept at 21 °C and fed the same amount of food as that consumed by chickens at 32 and 38 °C. Results obtained from their experiment showed that as ambient temperature increased from 21 to 32 and 38 °C, body weight decreased by 12 and 25%, respectively. However, when birds in the 21 °C environment were restricted to the amount of food consumed by the 32 and 38 °C groups, reduction in body weight was only 4 and 20%, respectively of the control group. Mean egg weight was reduced by 2 and 17% at 32 and 38 °C, respectively, when compared with the control. Mean egg weight was not decreased when pair-fed to the hens in 32 °C, and decreased by 7% when food was limited to the amount consumed by the hens in the 38 °C environment.

Similar results were described by Fuller and Dale (1979) and by Mitchell and Goddard (1990). The latter authors found better growth when the same amount of food consumed by birds kept at high temperature was given to those kept at moderate temperature. The authors attributed this better production with pair-fed birds to the role of triiodothyronine (T3) on growth, since plasma concentration of this hormone decreases when ambient temperature is increased (this will be discussed in Section 4.1.2).

However, it has also been noted (Olson *et al.*, 1972) that growth rate and energy retention were greater in heat-stressed birds than in those reared at moderate temperature when pair-feeding was carried out. The difference in carcass gain between the fully fed treatment in the warm environment and the group receiving the same intake in cool conditions was attributed to the added cost of temperature maintenance.

No difference in production when food intake was restricted to the same amount as that consumed by birds kept at high temperature was confirmed by Squibb *et al.* (1959). They reported that high temperature (37 °C) significantly depressed food intake and growth rate when compared with the control (25 °C). However, when pair-feeding was employed and food intake of the control birds restricted to that of the birds subjected to the 37 °C, weight gains of both groups were similar. The authors concluded that the observed depression in growth was due to the reduced food intake and not directly to the 37 °C temperature.

4.1.2 Thyroid hormones and energy demand

The thyroid hormones are thyroxine (T4) and triiodothyronine (T3). The thyroid gland secretes mainly thyroxine (T4) and lesser amount of triiodothyronine (T3) (Wentworth and Ringer, 1986). The majority of triiodothyronine (T3) is produced by peripheral conversion by 5'-monodeiodinase (5'-D) in the liver (Borges *et al.*, 1980) and also in the other tissues (Klandorf *et al.*, 1978).

Triiodothyronine (T3) is more potent than thyroxine (T4), and it is thought that T4 activity is due to its conversion to T3 (Srivastava and Turner, 1967; Bobek *et* *al.*, 1977; Klandorf *et al.*, 1981; Müller and Seitz, 1984; Rudas and Pethes, 1984; Ungar,1986; Decuypere and Buyse, 1988; Bartha *et al.*, 1989). T3 can be considered as an important hormone in the body and this is attributed to the great influence of this hormone on energy metabolism.

It is well known that T3 plays a very important role in growth (lean growth) and that this is due to its stimulation of ribosomes to increase the rate of formation of proteins; this hormone also acts on genes to increase RNA synthesis by the processes of transcription, which induces a generalized increase in the synthesis of many types of proteins within the cells (Guyton, 1987). On the other hand, it has also been suggested that triiodothyronine (T3) activates somatomedin-C (Sm-C) production (Decuypere and Buyse, 1988) and that this in turn acts on cartilage and bone to promote their growth (Guyton, 1987).

However, as it was mentioned above, T3 has an important function, other than its effects on growth, and that is its influence on energy metabolism. Any function in the body such as heart beat, breathing, physical activity or even eating requires energy. This energy is obtained from the compound adenosine triphosphate (ATP) which in turn is formed in the mitochondria in the presence of oxygen and nutrients. So, when there is demand for energy, ATP is used and, to be used, this compound must be broken down and the energy stored in it liberated. The importance of T3 is in activating the enzyme ATPase which breaks down ATP and makes the energy stored in it available for use (Ungar, 1986; Guyton, 1987). Eventually, this energy will leave the body as heat, and heat production therefore increases after T3 administration.

At the same time, T3 stimulates the consumption of oxygen. The increase in oxygen consumption is attributable to the increase in size and number of the mitochondria and also to the increase in oxidative enzymes which re-form ATP from ADP (Guyton, 1987). The importance of this process is to maintain steady concentrations of ATP. Hence oxygen consumption increases after the administration of T3.

The role of T3 in oxygen consumption and heat production is evident (Newcomer and Barrett, 1960; Bobek *et al.*, 1977; Klandorf *et al.*, 1981; Müller and Seitz, 1984; Decuypere and Kühn, 1984; Mitchell and MacLeod, 1986).

It can be concluded from the previous discussion that T3 concentration will increase when there is a demand for energy and, conversely, will decrease when that demand is reduced. Also, we can expect an increase or depression in oxygen consumption and heat production in relation to T3 concentration. Rudas and Pethes (1984) found with chickens that the rate of conversion of T4 to T3 by the deiodinase enzyme depends on the need for energy. They noted that the ratio of the conversion of T4 to T3 was 70%, while this ratio is 30% in mammals, and that this agrees with the theory that birds have a higher metabolic rate than large mammals. Oxygen consumption is about 9 ml/g/min in birds in comparison with the average of 2 ml/g/min in mammals). Similar results were reported by Hughes and McNabb (1986), since they noted that the activity of hepatic 5'-monodeiodinase (5'-D) increased in Japanese quail embryos at 16 d old and that this induced an elevation in T3 concentration. These authors suggested that the surge in T3 concentration was required to enhance lung surfactant production for pulmonary respiration which occurs at that age.

The effects of different factors such as elevating temperature and/or changing nutritional state (restriction or fasting) on thyroid hormone concentrations have been studied by many workers.

Increasing ambient temperature induced a reduction in the concentration of T3 but not of T4 (May, 1978; Klandorf *et al.*, 1981). However, these findings were not in agreement with those of Mitchell and Goddard (1990) or those of Kan (1994), since they reported a depression in T4 also as temperature increased.

The relationship between food intake and concentrations of these hormones is also very important. Fasting birds led to decreased T3 concentrations but conversely T4 increased (Klandorf *et al.*, 1981; Decuypere and Kühn, 1984). The increase in T3 after feeding was confirmed by Ingram and Evans (1980) and Dauncey *et al.* (1983) in piglets. However, not only feeding and fasting had an affect on T3 concentrations, but also less extreme variation in food intake. Barth *et al.* (1989) found with chickens at 28 d that restricting food to 70% of the total food consumed by control group induced a decrease in T3 and an increase in T4 levels when compared with the control. Similar findings were reported by Dauncey *et al.* (1983), who noted that T3 increased to greater concentrations when piglets at 8 weeks old were fed a meal of 600g compared with those on 300g. The authors concluded that the rhythms of T3 and T4 are totally or partly due to the meal-time-related shifts in 5'-monodeiodinase activity. The reduction in T3 hormone is a physiological adaptation to maintain nutritional reserves during fasting or lowering food intake (May, 1980; Decuypere and Kühn, 1984).

However, Mitchell and Goddard (1990) and Kan (1994) could not find any reduction in T3 or increasing in T4 concentrations when pair-feeding was employed (food intake was restricted to the amount consumed by birds kept at high temperature), and the concentrations of these hormones were similar to those in the birds fed *ad libitum* and kept at moderate temperature (the control).

4.1.3 High temperature and digestive tract

High temperature has been shown to increase the time required for food to pass through the digestive tract (Wilson *et al.*, 1980; Savory, 1986). However, Savory (1986) noted that increasing temperature up to 32 °C not only led to increase passage time of the diet through the digestive tract but also altered meal size. He found that number of meals/day did not differ between the birds kept at 8 and 32 °C although the total intake per day was different.

Since this project involved studying the effects of temperature on growth rate, and because the results of the first experiment indicated a close relationship between food intake and growth rate which is not in agreement with some of the previous work, a second experiment was designed.

This experiment was employed to answer the following questions:

1- Does high ambient temperature (30 °C) affect food utilisation and growth even when the high-temperature birds eat the same amount of food as birds kept at moderate temperature (20 °C) and pair-fed?

2- How are thyroxine (T4) and triiodothyronine (T3) concentrations related to temperature and feeding state? In other words: do pair-fed birds at 20 °C have same concentrations of T3 as those fed *ad libitum* and kept at same temperature? If the answer is yes, does that lead to better utilisation of dietary energy compared with heat stressed birds?

3- High temperature increases the time required for food to pass through digestive tract; however, does high temperature have any effect on the quantities of digestive tract contents?

4.2 Materials and methods

4.2.1 Experimental design

A 3 × 3 Latin square was employed, combining three replicate runs and three treatments: fed *ad libitum* at moderate temperature, 20 °C (control); fed *ad libitum* at high temperature, 30 °C (heat stressed) and fed an amount equal to that consumed by heat stressed birds but kept at 20 °C (pair-fed). Relative humidity ranged between 50% and 70%. Treatments were randomly assigned. A further two Latin squares were conducted in the same way as the previous one with the exception that the treatments in each Latin square were re-randomised. The second and third Latin squares were made to increase the number of replicates. Data were subjected to analysis of variance and the least significant difference (**LSD**) between means was calculated. It should be recalled that a $p<0.10$ level was considered significant.

4.2.2 Experimental procedure

Three 27-d-old Ross males of similar weight (1200 g) were chosen and put in calorimetry chambers (see Section 2.1) individually for 14 d. The first three days were an acclimatisation period. At 30-d-old, measurements such as food intake and growth rate were recorded daily until 40-d-old. The 10 d period was given to the birds to make sure that there was enough time to detect any differences, especially when the period of previous people's work (Section 4.1.1) was at least one week. However, oxygen consumption and heat production were calculated between 37 and 40 d; also, droppings were collected daily during these three days. Diet and droppings samples were treated in the same way as explained in Section (3.2.2) of the previous Chapter. The mean per d was then calculated either for the whole period (30-40 d) or for the energy and nitrogen measurement period (37-40 d).

Food of the same composition as in the previous experiment (Chapter 3) was given *ad libitum* both to the birds kept at moderate (20 °C) and high temperature (30 °C). Pair-fed birds (kept at 20 °C) were fed exactly the same amount of food as the heat-stressed birds had consumed on the previous day. The lighting pattern was 23 hours light: 1 hour dark.

At the end of the run (40-d-old) blood samples were obtained from each bird by venepuncture. The blood plasma was prepared by centrifugation and then stored frozen at -20 °C pending determination of thyroid hormone concentrations by radioimmunoassay (see Section 2.4). Finally the birds were killed and their digestive tracts removed. The contents of the upper part (crop, proventriculus and gizzard) and the lower part (small and large intestine) of each bird were collected separately and stored at -20 °C in sealed plastic tubs until they were oven-dried and weighed.

This work was replicated 9 times to represent 9 runs, so a total of 9 birds was exposed to each regime.

4.3 Results

4.3.1 Food and protein intakes and growth rate

Table 4.1 shows the food intake results, which were expressed as a mean of the10 d (**FI 10**) or as a mean of the last 3 d (**FI 3**) (see experimental procedure 4.2.2). Birds kept at moderate temperature (20 °C) and fed *ad libitum* (control) ate a greater amount of food (about 32% more; $p<0.01$) than the heat stressed birds. Protein intake recorded similar differences as with total food intake, about 30% ($p<0.01$) greater at 20 °C than with the heat stressed birds. It is interesting to note here that values calculated during the 3-d period were close to those recorded for 10 d, which indicates the sufficiency of 3 d as a period of measurement.

Growth rate (Table 4.1) over the 10 d (**GR10**) and 3 d (**GR3**) periods were also similar. Greater growth rates (38%; $p<0.05$) with those fed *ad libitum* and kept at 20 °C than with heat stressed birds was noted when measurements were made for 10 d. However, this difference was 45% ($p<0.01$) when measurements were done for 3 d. Growth of the pair-fed group was the same as that of the heat stressed group, and significantly less than the control.

4.3.2 Metabolisable energy intake, expenditure and retention

Metabolisable energy intake (IAME) was significantly more (32%; $p<0.001$) with the control than with the pair-fed and high-temperature groups. However, as designed, no difference could be detected between the latter two groups (Table 4.2).

The control group recorded the greatest heat production (**HP**) which was 23% ($p<0.001$) higher than that of the pair-fed group and 39% ($p<0.001$) greater than that of the heat stressed group (Table 4.2). Also, heat production was greater 13% ($p<0.001$) with the pair-fed than with the heat stressed group.

Table 4.1. The effects of temperature and pair-feeding (birds fed the same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on food utilisation. Food and protein intakes and growth rate for the 10 d period **(FI 10)**, **(PI 10)**, **(GR 10)**; also, food and protein intakes and growth rate for the final 3 d period **(FI 3)**, **(PI 3)**, **(GR 3)**. Means are presented as g/bird. d.

Observation	20 °C *ad libitum*	20 °C pair-fed	30 °C *ad libitum*	SED
FI 10	132a*	99b	100b	6.1
PI 10	35a	27b	27b	1.6
GR 10	55a	40b	40b	5.5
FI 3	139a	102b	102b	8.3
PI 3	37a	27b	27b	2.2
GR 3	55a	38b	38b	5.6

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

Table 4.2. The effects of temperature and pair-feeding (birds fed the same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on food utilisation. Apparent metabolisable energy intake (**IAME kJ**), heat production (**HP kJ**), energy retention as protein (**REP kJ**), energy retention as fat (**REF kJ**), total energy retention (**RE kJ**) and water retention of carcass in g (**WRC**). Means are presented/bird. d.

	Treatments			
Observation	**20 °C** ***ad libitum***	**20 °C** **pair-fed**	**30 °C** ***ad libitum***	**SED**
IAME kJ	1578a*	1187b	1197b	88.5
HP kJ	1058a	860b	759c	23.3
REP kJ	371a	275b	283b	29.7
REF kJ	149a	52a	155a	53.6
RE kJ	520a	327b	438ab	74.6
WRC	35a	25b	21b	3.8

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

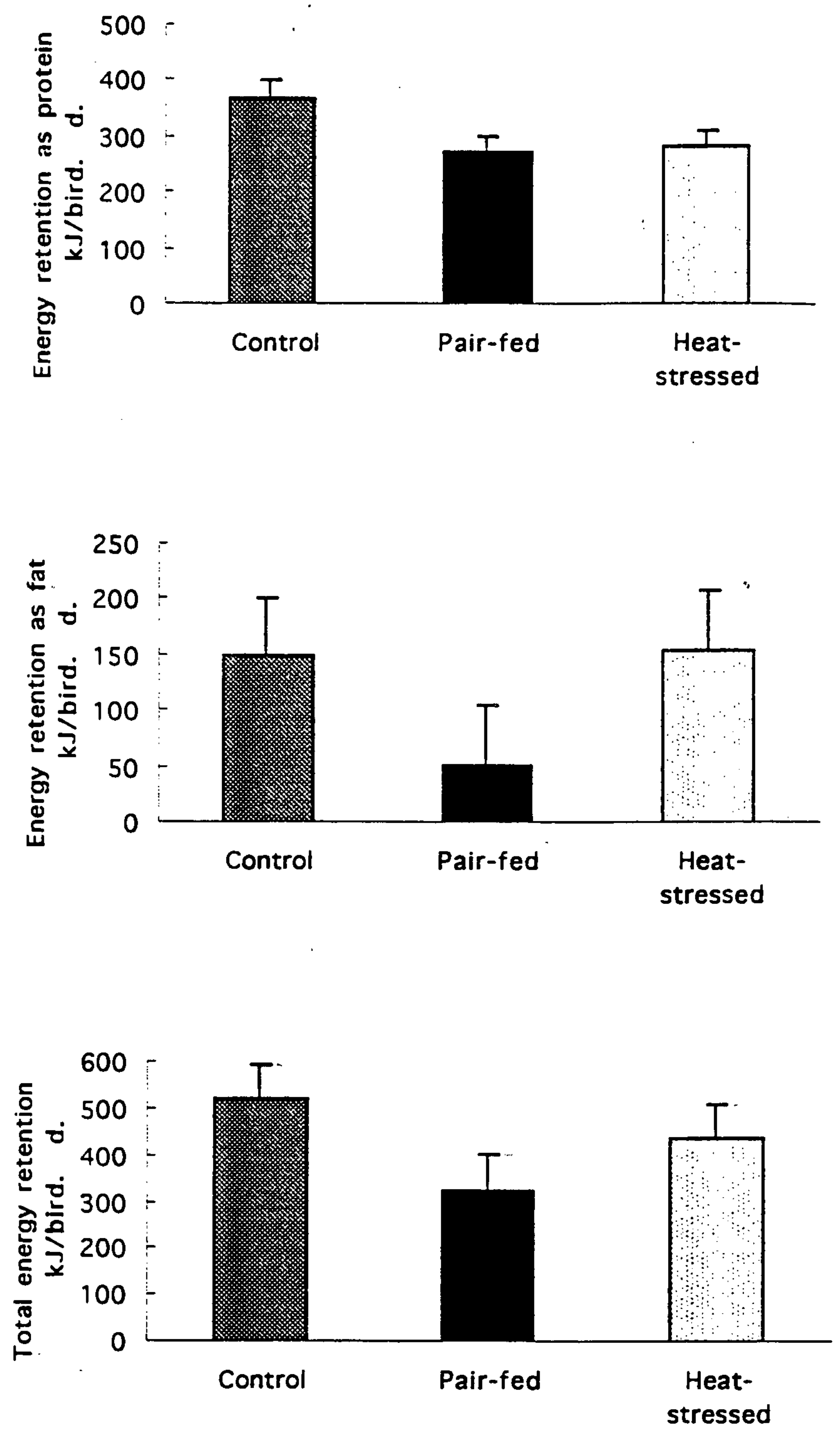


Figure 4.1.a,b,c. The effects of temperature and pair-feeding (birds fed same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on energy retention as protein, as fat and total energy retention.

No difference in energy retention as protein (**REP**) was recorded between heat stressed and pair-fed groups (Table 4.2 and Figure 4.1.a), which were 24% ($p<0.05$) and 26% ($p<0.01$), respectively, less than the control.

Energy retention as fat (**REF**) was similar between the control and heat stressed birds (Table 4.2 and Figure 4.1.b). However, these two groups had significantly greater fat retention (about 190%; $p<0.10$) than the pair-fed group.

Total energy retention (**RE**) although 19% higher in the control birds did not differ significantly (Table 4.2 and Figure 4.1.c) than the heat stressed group. Also, no significant difference was noted between the heat stressed and pair-fed birds. However, energy retention was significantly greater 59% ($p<0.01$) in the control compared with the pair-fed group.

Water retention in the carcass (**WRC**) was greater in the control compared with the other two groups (Table 4.2); 40% ($p<0.05$) and 67% ($p<0.01$) higher than in the pair-fed and heat stressed groups, respectively. Water retention was 19% more with the pair-fed than the heat stressed group, but this difference was not statistically significant.

4.3.3 Food conversion efficiency and energy metabolisability

No significant difference in food conversion efficiency (**FCE**) could be found when calculated either over the 10 d or the 3 d period (Table 4.3).

Protein retention efficiency (**PRE**) (protein retention/protein intake) behaved similarly to food conversion efficiency, since similar efficiencies were obtained in all different treatments (Table 4.3).

Apparent metabolisability values (**Amet**) did not differ significantly, although they were 3% higher with heat stressed and pair-fed groups than in the control (Table 4.3).

Table 4.3. The effects of temperature and pair-feeding (birds fed the same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on food conversion efficiency whether for the 10 d **(FCE 10)** or for the final 3 d **(FCE 3)** period. Also, on protein retention efficiency (protein retention/protein intake) **(PRE)** and on apparent metabolisability **(Amet)**.

	Treatments			
Observation	**20 °C** ***ad libitum***	**20 °C** **pair-fed**	**30 °C** ***ad libitum***	**SED**
FCE 10	0.42a*	0.40a	0.40a	0.032
FCE 3	0.39a	0.37a	0.37a	0.031
PRE	0.44a	0.45a	0.46a	0.026
Amet	0.68a	0.70a	0.70a	0.021

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

4.3.4 Energy retention proportions and efficiencies

The proportions of apparent metabolisable energy (IAME) retained as protein (**PARP**) and as fat (**PARF**) and total energy retention efficiency (**ERE**) are shown in Table 4.4. All treatments had similar proportions of energy retained as protein from apparent metabolisable energy.

However, the proportion of (IAME) retained as fat (**PARF**) was significantly greater (225%; $p<0.05$) with the heat stressed than pair-fed group and no significant difference was found between heat stressed and control groups, although it was 38% less with the control. This proportion was 100% higher with the control than pair-fed birds but this difference failed to reach significance.

Total energy retention efficiency (**ERE**) was of course affected by proportions of both protein and fat retentions. The only significant difference (33%; $p<0.01$) was between heat stressed and pair-fed groups and no significant differences could be noted elsewhere.

4.3.5 Energy contributions to gain

In this section energy concentrations to body weight were estimated by dividing energy retention as protein, as fat and total energy retention by growth rate, so the contribution of each component per g growth could be compared (Table 4.5, Figure 4.2).

Energy retention as protein per g growth (**REP kJ/g**) did not differ between treatments and ranged between 7.2 and 7.5 kJ/g.

However, when energy retention as fat per g growth (**REF kJ/g**) was calculated, there was a significant difference (156%; $p<0.10$) between pair-fed and heat stressed birds; it was greater with the latter group. Energy retention as fat per g

Table 4.4. The effects of temperature and pair-feeding (birds fed the same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on the proportions of apparent metabolisable energy retained as protein (**PARP**), as fat (**PARF**) and energy retention efficiency (**ERE**).

	Treatments			
Observation	**20 °C** ***ad libitum***	**20 °C** **pair-fed**	**30 °C** ***ad libitum***	**SED**
PARP	0.23a*	0.23a	0.24a	0.014
PARF	0.08ab	0.04b	0.13a	0.036
ERE	0.32ab	0.27b	0.36a	0.030

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

Table 4.5. The effects of temperature and pair-feeding (birds fed the same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on the amounts of energy retention as protein (**REP kJ/g**), as fat (**REF kJ/g**) and total energy retention (**RE kJ/g**) per g growth.

	Treatments			
Observation	**20 °C** ***ad libitum***	**20 °C** **pair-fed**	**30 °C** ***ad libitum***	**SED**
REP kJ/g	7.2a*	7.4a	7.5a	0.8
REF kJ/g	2.3a	1.6a	4.1a	1.2
RE kJ/g	9.4b	8.9b	11.7a	1.0

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

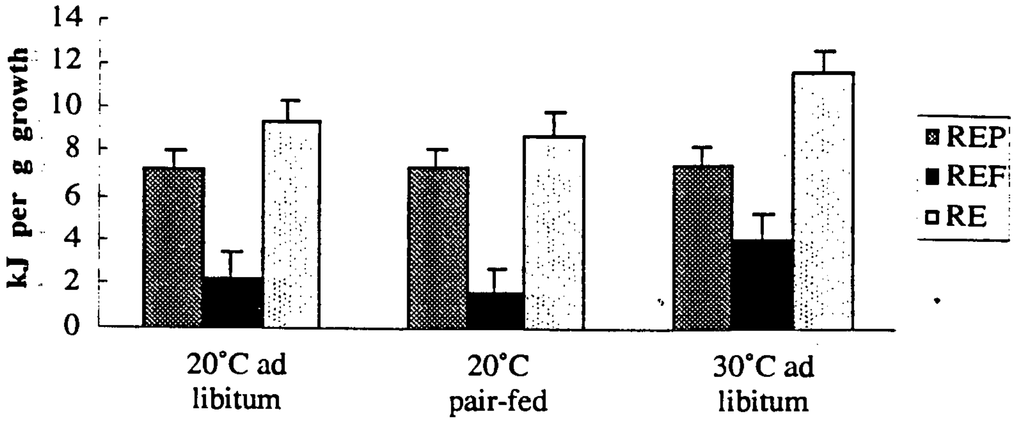


Figure 4.2. The effects of temperature and pair-feeding (birds fed the same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on the amounts of energy retention as protein (**REP** **kJ/g**), as fat (**REF kJ/g**) and total energy retention (**RE** **kJ/g**) per g growth.

growth was 44% (not significant) higher with the control than with pair-fed birds. Also, this measurement was 78% higher with heat stressed than with control birds but this was not significant also.

Total energy retention per g of weight gain (**RE kJ/g**) was greatest with the heat stressed group, and it was about 28% ($p<0.05$) greater than pair-fed and the control groups. No significant difference was noted between the last two groups.

4.3.6 Thyroid hormones and oxygen consumption

Table 4.6 shows thyroid hormone and oxygen consumption results. Thyroxine concentration (**T4 ng/ml**) was significantly greater (49%; $p<0.05$) in the pair-fed group than in the control; it was also 27% higher (not significant) than in the heat stressed group. The latter group had a 17% greater concentration of T4 than the control, but this difference was also not significant.

Triiodothyronine concentrations (**T3 ng/ml**) were similar between pair-fed and heat stressed groups (Table 4.6), which were in turn 51% less than the control ($p<0.001$).

Oxygen consumption (**O_2 ml/d**) was greatest with the control group (Table 4.6); it was 19% and 31% higher than pair-fed and heat stressed groups, respectively ($p<0.001$). Also, oxygen consumption was 11% ($p<0.05$) more with the pair-fed than the heat stressed group.

4.3.7 Digestive tract contents of food

It was mentioned in Section (4.2.2) that food was collected from the digestive tracts of the birds. It is expressed here in g (dry matter). Also, it is worthy of note that when the food was collected from the upper part of digestive tract (crop, proventriculus and gizzard) no food was found in the crop, and all the food which

Table 4.6. The effects of temperature and pair-feeding (birds fed the same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on the concentrations of thyroxine (**T4 ng/ml**) and triiodothyronine (**T3 ng/ml**) hormones and also, on the oxygen consumption (**O_2 ml/d**). Means are presented/bird. d.

	Treatments			
Observation	**20 °C** ***ad libitum***	**20 °C** **pair-fed**	**30 °C** ***ad libitum***	**SED**
T4 ng/ml	8.6b*	12.8a	10.1ab	1.77
T3 ng/ml	3.3a	1.7b	1.5b	0.33
O_2 ml/d	44.8a	37.7b	34.1c	1.40

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

was collected was found either in the proventriculus or in the gizzard. Food was always found in the gizzard and was found in the proventriculus in (30-40%) of cases.

Food in the upper part (FU) was significantly ($p<0.001$) greater with the control than pair-fed and heat stressed groups (Table 4.7), being 400% and 100% higher, respectively. Food retained was significantly 150% ($p<0.01$) greater with heat stressed than pair-fed birds.

Food in the lower part of the digestive tract (FL) gave similar results to food in the upper part (Table 4.7); it was significantly greater ($p<0.001$) with the control than the other two groups, 225% and 94% higher than pair-fed and heat stressed birds, respectively. The latter group had 68% more ($p<0.10$) food than the pair-fed group.

When food retained in the upper and lower parts were combined (FW) (Table 4.7), the greatest amount ($p<0.001$) was recorded in the control, 247% and 95% higher than pair-fed and heat stressed groups, respectively. A 78% greater amount ($p<0.05$) was recorded with heat stressed than pair-fed group.

Table 4.7. The effects of temperature and pair-feeding (birds fed the same amount of food as that consumed by heat stressed birds on the previous day, but kept at 20 °C) on the amount of food retained (dry matter) in the upper part (**FU**), lower part (**FL**) or whole (**FW**) digestive tract. Means are presented as g/bird. d.

	Treatments			
Observation	**20 °C** ***ad libitum***	**20 °C** **pair-fed**	**30 °C** ***ad libitum***	**SED**
FU	2.0a*	0.4c	1.0b	0.20
FL	9.1a	2.8b	4.7b	1.04
FW	11.1a	3.2c	5.7b	1.04

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

4.4 Discussion

4.4.1 Food and protein intakes and growth rate

Food intake (Table 4.1) was depressed by elevated ambient temperature, whether measured for 10 or for 3 d periods (**FI 10 and FI 3**). These results confirmed previous findings (Chapter 3).

Growth rate for 10 or for 3 d periods (**GR 10 and GR 3**) also decreased as ambient temperature increased (Table 4.1), and that of course is mainly attributable to the reduction in food intake. However, as was noted in the choice-feeding experiment (previous Chapter), water retention had some effect on this parameter and this is discussed in Section (4.4.2). The suggestion of the role of food intake as the major factor influencing temperature effects on growth rate is supported by the similarities in growth rate between heat stressed and pair-fed groups, which had same amount of food.

These findings are in agreement with Squibb *et al.* (1959), who noted similar growth between pair-fed and heat stressed groups, but not in agreement with Smith and Oliver (1972), Fuller and Dale (1979) and Mitchell and Goddard (1990), who reported better production by the pair-fed group. They are also not in agreement with Olson *et al.* (1972), who found more rapid growth with heat stressed birds kept at cycling high temperature (26- 40.5 °C) than those kept at cycling cool temperature (13- 24 °C).

4.4.2 Metabolisable energy intake, expenditure and retention

Metabolisable energy intakes (**IAME kJ/d**) were closely linked to gross energy intake (Tables 4.1 and 4.2), especially since the energy metabolisabilities were similar between all groups (Table 4.3). Similar metabolisable energy intakes between pair-fed and heat stressed groups was obtained as a result of the similarity in gross energy intake. It was noted from choice-feeding experiment (previous Chapter, 3.4.5) that apparent metabolisability (**Amet**) may differ when the composition of the diet changes; however, all birds in this experiment had same diet and that of course led to similar digestibilities and metabolisabilities.

Heat production (**HP kJ/d**) was greatest with the control (Table 4.2). That can be explained by the greater demand for energy, since it can be expected that all treatment groups have similar basal metabolic rate. Additional energy was required by the control birds for thermoregulation processes, since it was evident from the results obtained from choice-feeding experiment that heat increment of the diet was not used for thermoregulation. Also, a greater heat increment was produced by these birds as a result of the greater energy intake. Together these factors have produced greatest energy expenditure (for more details see 1.2.3 and 3.4.3). However, the greater energy expenditure by the pair-fed than by the heat stressed group, although the same energy was consumed by these birds, is simply attributable to thermoregulatory processes.

Energy retention as protein (**REP kJ/d**, Table 4.2, Figure 4.1.a) behaved in a similar way to metabolisable energy intakes, since these values were governed by the total protein intake, especially when efficiencies of protein retention were similar between all treatments (Table 4.3). It is interesting to recall that similar efficiencies in protein retention were found in the choice-feeding experiment (Table 3.7, previous Chapter). Again, that could be explained partly by protein quality or amino acid balance for growth.

Control and heat stressed groups (Table 4.2, Figure 4.1.b) had same energy retention as fat (**REF kJ/d**). It was explained in the discussion of the choice-feeding experiment that energy retention as fat was influenced by three factors: food composition, environmental temperature and energy intake (see 3.4.4, previous Chapter). Control birds lost more energy as heat, but at the same time there was a greater energy intake; heat stressed birds ate less energy than the control (102 v. 139 g/bird per d), since less energy was required for thermoregulatory processes. The reduction in energy demand with these birds therefore allowed them to store this energy as body fat. However, pair-fed birds needed energy for thermoregulation and at the same time their energy intake was restricted (equal to those consumed by heat stressed birds), so less energy was stored as fat. Similar results were found in restricted birds at 20 °C by MacLeod and Shannon (1978).

The differences in energy retention as protein and as fat between the control and heat stressed groups balanced out in total energy retention (**RE kJ**, Table 4.2, Figure 4.1.c), so similar amounts of energy were stored in the bodies. Again, as noted in the choice feeding experiment, even if there was a significant difference in growth rate by weight between the control and heat stressed groups, there was similar energy retention. However, as a result of the reduction in energy retention as protein, which resulted from the reduction in total intake, and as a result of the greater energy required for thermoregulatory processes, pair-fed birds had the lowest energy retention.

Water content of carcass (**WRC**, Table 4.2) was greatest with the control, which can be attributed to the strong correlation with protein retention. The association between water retention and protein retention was reported by Adams *et al.* (1962a) and MacLeod (1991a). However, water retention was 19% higher (not significant) with pair-fed than heat stressed birds (25 v. 21 gram) although the same energy retention as protein was measured in the two groups; similar results were noted in the choice-feeding experiment. This can be attributed to the greater demand for water at high temperature. The effect of temperature on evaporative water loss was reported by Barott and Pringle (1941) and also reviewed by Sykes (1977), (see Section 1.2.1 for details).

From Table 4.2, it can be understood that the similarity in growth rate by weight between pair-fed and heat stressed groups was due to the balance in fat retention and water retention. More fat was retained by heat stressed birds, while that was compensated for by the greater water retained by the pair-fed group. Therefore, similar weight gain was obtained, especially since protein retention was similar between the two groups.

4.4.3 Energy retention proportions and efficiencies

The efficiency of retention of metabolisable energy (Table 4.4) was greatest with the heat stressed group and lowest with the pair-fed group. The higher efficiency can be attributed to the greater proportion of apparent metabolisable intake retained as fat in the case of the heat stressed birds. The reduction in this proportion with pair-fed birds is as explained by the portion of metabolisable energy used for thermoregulation processes. However, because the control birds ate more energy (139 v. 102 g) compared with the heat stressed group, these birds were able to store a great amount of energy and finally to have a similar efficiency to that obtained with heat stressed birds.

4.4.4 Energy contributions to gain

Table 4.5 and Figure 4.2 show the composition of the body. The results from the Table and Figure also explained the effect of temperature on energy stored. The greatest energy retention per g growth was found with heat stressed birds. This was attributable to the higher fat retained per g in these birds.

From the previous results, it is very clear that high temperature affected food utilisation through its effect on the total food intake only. Also, as was mentioned in the choice-feeding experiment, high temperature had a positive effect on efficiency of food utilisation, since less energy is required for thermoregulation and more energy can therefore be retained as fat.

Also, there was no evidence that pair-fed birds could utilise their energy intake more efficiently than heat stressed birds. These two groups retained similar amounts of protein (as a result of the similarities in intake), and conversely, greater fat was retained in the heat stressed birds. These results are in agreement with Squibb *et al.* (1959), who noted similar growth between the two groups and with Olson *et al.* (1972), who confirmed less energy retention with pair-fed birds as a result of the greater demand for energy to maintain body temperature. However, they were not in agreement with Smith and Oliver (1972), Fuller and Dale (1979) and Mitchell and Goddard (1990), who reported better production with pair-fed than heat stressed birds consuming the same amount of food.

4.4.5 Thyroid hormones and oxygen consumption

Triiodothyronine concentrations (T3) were greatest in the control group (Table 4.6). That can be explained simply by the greater demand for energy in these birds. Birds in this treatment were kept at moderate temperature and also had free access to food. These factors, along with the basic requirements for energy (the energy required for maintenance processes), induced the greatest concentrations of T3. This hormone is responsible for providing the energy to be used in different processes. The role of T3 in energy provision has been discussed in Section 4.1.2.

The similarities in the concentrations of T3 between heat stressed and pair-fed groups could be attributed to the similarity in some aspects of energy demand. Heat stressed birds had free access to food, so these birds needed energy for maintenance and for the activities associated with food intake, such as picking up, digestion, absorption and finally growth processes.

However, it was noted that pair-fed birds had finished their food about 3 h before blood samples were taken, and that of course led to a decrease in the energy required for feeding processes and in turn T3 decreased (Mitchell and MacLeod, 1986). Also, this more rapid clearance of the food led to a smaller amount of food retained in the digestive tracts of these birds (Table 4.7, discussed below) and that led to decreased energy required for dealing with this food. On the other hand, these birds were kept at 20 °C, so energy was needed for thermoregulation, and the production of that energy of course was modulated by T3 hormone. Similar concentrations of T3 between these two groups can, therefore, be expected.

Thyroxine (T4) concentration was higher in the pair-fed birds than in the controls (Table 4.6). The reason for this increase is the reduction in the conversion of T4 to T3, which, as explained above, can be attributed to the reduction in energy demand. The concentrations of T4 in the heat stressed group were intermediate between the control and pair-fed birds. As it is known that T4 is secreted from the thyroid gland, however, this secretion is under the control of thyroid-stimulating hormone (thyrotropin, **TSH**) which is secreted from pituitary gland and, in turn, this hormone is under the control of thyrotropin-releasing hormone (**TRH**), which is secreted from the hypothalamus (Klandorf *et al.*, 1978; Guyton, 1987).

Also, it is known that the hypothalamus is the major centre responsible for temperature regulation (Wilson, 1979; Guyton, 1987). So, when the hypothalamus is overheated, as a result of the increase in ambient temperature, it decreases the secretion of TRH and, in turn, TSH is decreased (Winchester, 1940; Guyton, 1987), the final result being that less T4 is produced. However, at the same time the conversion of T4 to T3 was less with heat stressed birds as a result of the reduction in energy demand (less thermoregulation and food intake); together these factors (the reduction in T4 secretion and the reduction in the conversion to T3) may have produced the intermediate concentrations of T4 with these heat stressed birds.

The depression in T3 and the increase in T4 concentrations by restriction or fasting were reported by Ingram and Evans (1980); Klandorf *et al.* (1981); Dauncey *et al.* (1983); Decuypere and Kühn (1984) and Bartha *et al.* (1989). However, these results were not in agreement with Mitchell and Goddard (1990) and Kan (1994), who noted similar concentrations of T4 and T3 in pair-fed and control birds. Also, the reduction in T3 and not in T4 by elevating ambient temperature which was noted here was confirmed by Klandorf *et al.* (1981) and May (1978), but not by Mitchell and Goddard (1990) and Kan (1994), who noted a reduction in T4 concentrations as ambient temperature increased.

The greater consumption of oxygen by the control birds than by the heat stressed birds (Table 4.6) is related to the concentrations of T3. As mentioned in Section (4.1.2), this hormone increases the size and number of the mitochondria and also increases the oxidative enzymes. Pair-fed birds consumed more oxygen than heat stressed birds, although T3 concentrations were similar between these groups (Table 4.6). The similarities in T3 concentrations between these groups do not mean that T3 concentrations with pair-fed birds were the same as those of heat stressed birds throughout the day. The reduction in T3 concentration with pair-fed birds during blood sampling may be temporary, as explained above (no feeding activity).

The correlation between T3 concentration and oxygen consumption was confirmed by Newcomer and Barrett (1960) and Müller and Seitz (1984). Also, it is important to remember that there was a correlation between the concentration of T3, heat production and oxygen consumption (Table 4.2 and 4.6). These results support the previous work (see Section 4.1.2), which suggested the effect of T3 on heat production (as a result of the breakdown of ATP compounds), and also on oxygen consumption (through the activation of oxidative enzymes and the increase in the size and number of the mitochondria). The relationship between T4 or T3 with heat production or oxygen consumption is summarised in Figures 4.3.a,b and 4.4.a,b.

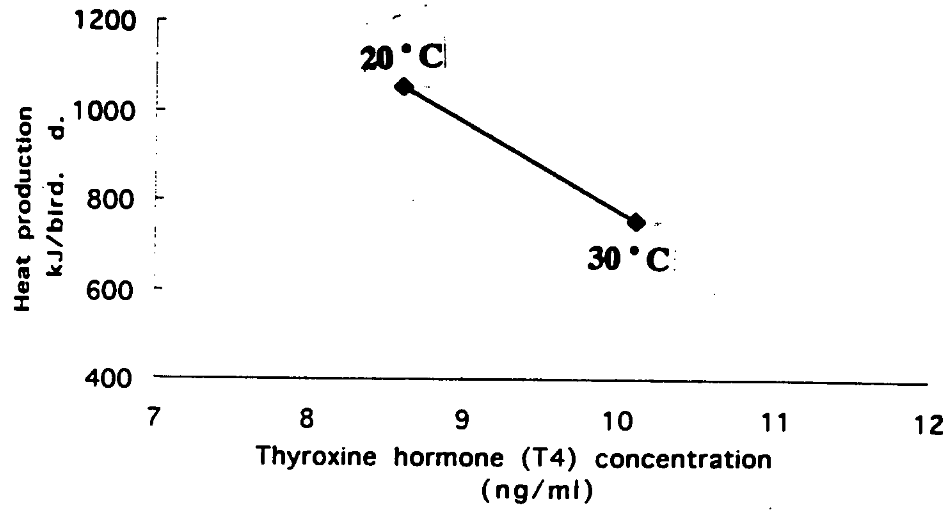


Figure 4.3.a. The inverse relationship between thyroxine (T4) hormone concentrations and heat production; high concentrations of T4 were not associated with high levels of heat production.

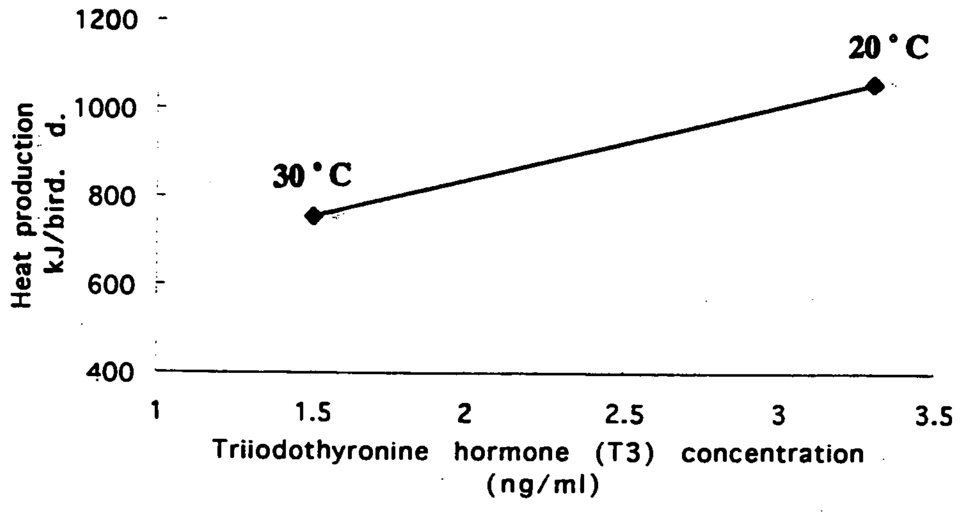


Figure 4.3.b. The relationship between triiodothyronine (T3) hormone concentrations and heat production; as T3 increases heat production increases, so direct relationship between these two measurements was obtained.

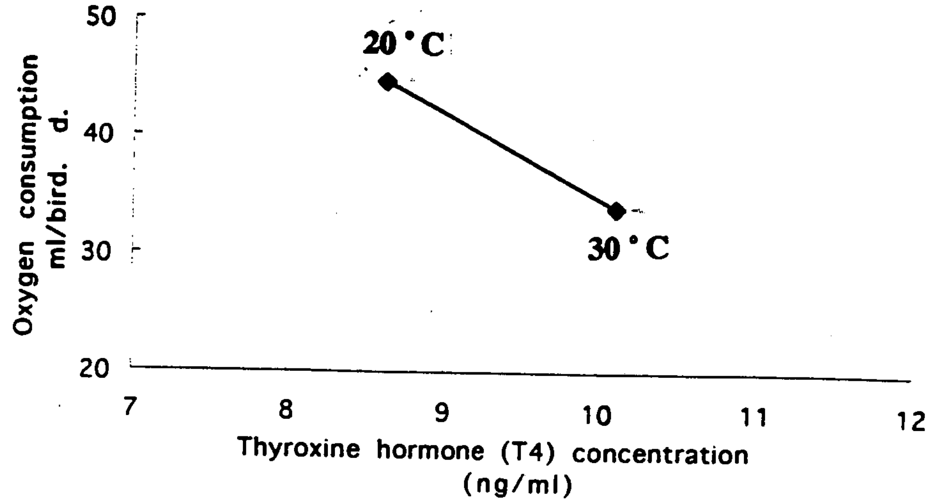


Figure 4.4.a. The inverse relationship between thyroxine (T4) hormone concentrations and oxygen consumption; high concentrations of T4 were not associated with high levels of oxygen consumption .

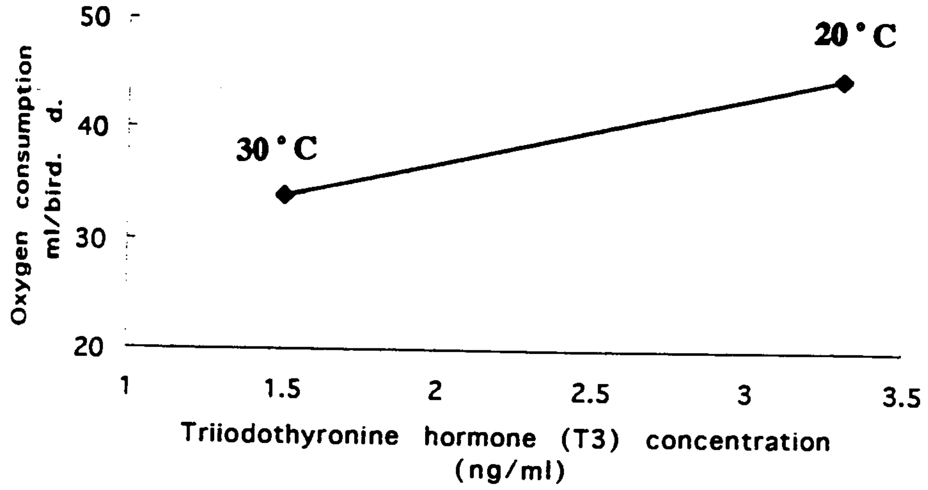


Figure 4.4.b. The relationship between triiodothyronine (T3) hormone concentrations and oxygen consumption; as T3 increases oxygen consumption increases, so direct relationship between these two measurements was obtained.

It can be concluded that as energy demand increases, T3 concentrations increase, and in turn heat production and oxygen consumption also do so (4.1.2). Also, it can be suggested that there is no especial role of T3 on food utilisation or growth when food intake is restricted and the most important factor affecting growth is the amount of energy intake, on condition that all essential nutrients are present in the diet.

4.4.6 Digestive tract contents of food

As was mentioned in Section (4.3.7) no retained food was found in the crops of the birds during the collection of gut contents. However, this was not surprising, since Richardson (1970a) concluded that the main importance of this organ is during periods of food deprivation. He noted that surgical removal of the crop did not affect food intake or body weight when food was given continuously. However, when the food was restricted to 2 h or less per d, food intake was less with cropectomized birds. Also, these findings can add further weight to the hypothesis that meal initiation (hunger) may be associated with partial gizzard emptying and meal termination (satiety) may be associated with varying degrees of gizzard filling (Savory, 1985).

There was a significant difference in food retained in the upper part (proventriculus and gizzard) of the digestive tract (Table 4.7) between the control and heat stressed birds, although they both had free access to food. These results support the findings of Savory (1986) who noted a reduction in meal size of chickens exposed to 32 °C when compared with those kept at 8 °C. It would be expected that the control group showed normal feeding behaviour, but there is the question of why heat stressed birds did not act the same as the control. In other words, why did they reduce food quantity in the upper part of their digestive tract and, in particular, in the gizzard?

Kan (1994) found with broilers that T3 production was inhibited when those birds were exposed to high temperature (35 °C). He attributed that inhibition to the reduction in the number of growth hormone receptors or that these receptors may be non-receptive to growth hormone stimulation during heat stress. However, if this suggestion is correct, less food would be expected in the upper part of the digestive tract, since as was mentioned above (Sections 4.1.2 and 4.4.5) T3 hormone is required when there is a demand for energy. Any factor which decreases the availability of this hormone may in turn lead to a reduction in the power of the function of any organ needing more energy, such as the proventriculus and gizzard after a meal. The depression in T3 production might, therefore, reduce the work rate of the upper part of the digestive tract, especially the gizzard, where energy is required for grinding the diet and making it suitable to be transported to the remainder of the digestive tract. Food in the gizzard will not leave to the duodenum until it is ground to very small particles, since the gizzard functions as a sieve preventing large or hard materials from entering the intestine (Henry *et al.,* 1933; McLelland, 1979).

The effect of T3 on food intake was studied by Blakely and Anderson (1949) and Snedecor (1971). They noted that food intake decreased when the diets included 1 or 2% of thiouracil (which blocks peripheral conversion of T4 to T3).

Another possible mechanism for the reduction in food quantity is the depression in blood flow to the digestive tract. It is well known that blood flow to specific body parts changes according to the activity of the part. So, when glandular secretion or motor activity of the gut increases, blood flow to this system does also. The increase in blood flow to the active gut is a result of the needs for oxygen, nutrients and hormones which should be supplied for providing the energy required for muscle contractions and the synthesis of macromolecules; the increase in blood flow is also required for the quick removal of metabolic waste products to the places where they can be excreted (Wilson, 1979; Guyton, 1987).

Studies of Wolfenson *et al.* (1981) on heat stressed laying hens showed that blood flow increased to organs active in heat dissipation such as comb and wattle. Upper parts of the respiratory tract had a marked increase in blood flow, ranging from 320 to 430% of the control level. However, blood flow to the digestive tract was, conversely, reduced by hyperthermia, with the effect being greater in the upper parts of the gut, decreasing to 44 and 48% of control values in the proventriculus and gizzard, respectively. In the duodenum and jejunum it decreased to 69 and 71% of the control levels, while in the ileum the reduction noted was non-significant. The authors attributed the increase in blood flow to upper respiratory tract during hyperthermia to the need to maintain the evaporative capacity of the respiratory tract during panting, and this redistribution is controlled by sympathetic activity which also cause skin vasodilatation and mesenteric vasoconstriction. If the second possibility is the most likely, it can be concluded that the depression in T3 concentrations with heat stressed birds was a result of the reduction in food intake, which in turn occurred because of the decrease in blood supply to the digestive tract in general, and in particular to the gizzard. The reduction in blood flow to the digestive tract in response to heat stress (35-45 °C) was also documented by Arad *et al.* (1993).

However, the role of hormones in the nervous system can not be ignored. Morrow *et al.* (1994) noted that the injection of thyrotropin-releasing hormone (TRH) into the paraventricular nucleus of the hypothalamus (PVN) in rats significantly increased the amplitude of gastric contractions. Also, they noted that the excitatory action of TRH on gastric contractions was completely abolished by subdiaphragmatic vagotomy and suggested that TRH acts within the PVN to stimulate gastric contractility via vagal-dependent pathways. It was mentioned in

Section 4.4.5 that TRH is depressed at high temperature, so it can be expected that there may be less vigour in gizzard contractions and, therefore, less food processed in the gizzard.

The smallest quantity of food retained in the upper digestive tract, which was recorded with pair-fed birds (Table 4.7), can be explained in two ways. First, the amount of food intake, which was significantly less than the control and secondly to the normal ability of this tract (at 20 °C, the same as the control) to deal with food. So, these birds could consume their food about 4 h before they were killed and in turn could also empty their digestive tracts of most of the food.

From the previous discussion, it can be suggested that a possible reason for the decrease in the amount of food, especially in the upper part of the digestive tract, when the animal is exposed to high temperature might be the reduction in the ability of digestive tract to deal with this food. In other words, to the lesser ability to digest the meal (by mechanical and chemical processes) and send it to the remainder of digestive tract. This suggestion can be confirmed by the slower rate of food passage when ambient temperature increases (Wilson *et al.*, 1980; Savory, 1986).

One of the most important factors which regulates food intake is digestive tract capacity, so that it can be expected that the reduction in digestive tract ability when ambient temperature increases might be a reason for the depression in food intake. Further studies are required to investigate this suggestion and will be tested and discussed in the next Chapter.

4.5 Conclusions

Results from this experiment indicated the following points:

1- As was noted in the choice-feeding experiment in the previous Chapter, high temperature decreased food intake and growth rate; however, it had no further effect on food utilisation, other than the direct effect of reducing food intake.

2- High temperature had a positive effect on proportion of apparent metabolisable energy intake retained as fat; this resulted from decreased heat production. However, water retention was decreased by elevating temperature.

3- The differences in fat retention and water retention between pair-fed controls and heat stressed birds equalised growth rate by weight, especially since protein retention did not differ between these groups.

4- High temperature depressed plasma triiodothyronine hormone (T3) concentration, but had no effect on thyroxine (T4) concentration. However, it is not certain whether that depression in T3 was due to temperature itself or to the decrease in food intake.

5- T4 hormone concentration was highest with the pair-fed group as a result of the reduction in its conversion to T3. The lower concentration of T3 in pair-fed birds was due to the decrease in energy demand, as compared with the birds kept at 20 °C and fed *ad libitum*.

6- High temperature decreased the quantity of digestive tract contents. It was suggested that the reason might be the reduction in digestive tract ability.

Chapter Five

Dietary modifications to increase food utilisation and growth rate in broiler chickens exposed to high ambient temperature (30°C)

5.1 Introduction

Results from choice-feeding (Chapter 3) and pair-feeding (Chapter 4) experiments have indicated the over-riding effect of food intake on growth, and how this growth is depressed when food intake is reduced in response to high temperature. Also, it was noted that although there was a negative effect of high temperature on protein and water retention, which contribute to total growth, high temperature at the same time had a positive effect on fat retention. So, it can be concluded that increasing food consumption or the utilisation of the food intake is required for obtaining a higher rate of growth when animals are exposed to heat stress.

5.1.1 Factors affecting food intake

There are many factors which affect food consumption, such as, size, age, environmental temperature, activity and the availability of food and water (Duke, 1986a). Food intake can be also influenced by dietary factors, such as diet composition (CP:ME ratios) and the volume of ingesta (Meyer and Hargus, 1959; Gleaves *et al.*, 1968; Shariatmadari and Forbes, 1993). Blood glucose concentration has been found to have no effect on food intake in the fowl. Richardson (1970b) noted no correlation between blood glucose fluctuations and feeding behaviour.

However, birds which have been used in the choice-feeding experiment (birds given complete diet and kept at different temperatures) and also those used in the pair-feeding experiment both have had similar circumstances except the temperature factor. They were of the same age and similar weights, food and water were available throughout the day and their diet had the same composition which gave the same CP:ME ratios and the same density.

From the previous discussion, it can be seen that the only factor which has changed between the birds used in the choice-feeding and pair-feeding experiments and which led to depressed food intake is the temperature. The question that remains is why animals reduce their food intake at high temperatures? The review of Sykes (1977) discussed this question; he mentioned that the conventional explanation for the reduction in food intake as temperature increases is the decrease in energy required for maintenance. For example, when laying hens were given diets which had different energy contents (11.97, 12.80, 13.60, 14.43 MJ/kg) and kept at 20 °C and 30 °C, their energy intake was decreased by elevating temperature. However, at 30 °C their energy intake had a large range from 1280 to 1452 kJ per d, whereas their food intake in grams was more or less constant (107 to 101). If the birds decreased their energy intake when temperature increases because less energy was required for maintenance, why did they have large differences in total energy intake? Also, why did the birds on a low energy diet not try to increase their food intake in grams to maintain an energy intake similar to the birds on a high energy diet? Sykes (1977) also raised this question: if the birds decrease their food intake as a result of the reduction in energy demand, why do they allow their bodyweights to decrease by use as an energy source when temperature increases? This question can be also asked about the reduction in gains that occurred in the birds which were kept at 30 °C in the choice-feeding and pair-feeding experiments; why did they not increase their energy intake to maintain their growth rate equal to the birds kept at 20 °C? Finally Sykes (1977) asked are there then other factors controlling food intake which become more important at higher temperature? The hypothesis that birds may decrease their food intake at high temperature to reduce the heat increment and, in turn, the heat stress should also be remembered.

However, several authors have reported the capacity or throughput of digestive tract as an important factor affects in food intake. Duncan *et al.* (1970) found with Brown Leghorn females between 10 and 16 week-old that there was a relationship between the amount of food eaten per meal and the intervals between the meals, giving large intervals with birds which had large meals. Also, they noted that the birds which were fed on mash visited the feeder about 35 times per d, while those fed on a pelleted diet visited 27 times. These authors concluded that there was an 'activating mechanism' which depended upon the amount of food in a specific part of the digestive tract, and that the initiation of the next meal was when the level of food in this organ decreased below a threshold value. Boorman (1973) reported in his review that the primary influence on food intake, on an hour-to-hour basis, in the fowl resulted from the gut. Similar findings were reported by Savory (1980), who found with Japanese quail, given diluted mash (standard mash + 40% cellulose powder) thereby reducing nutrient density, that these birds ate more per day and had shorter mean interval length when compared with those given undiluted standard mash. It was noted also that the shorter interval with birds fed on diluted mash was associated with the faster passing of food through the gut than the birds fed on undiluted mash. Savory and Hodgkiss (1984) reported with vagotomised birds between 13 and 15 week-old that intervals between meals increased by up to 16% more than the control and this increase was accompanied by a 19% difference in the food passage rate, being slower in the vagotomised group. Savory (1980) and Savory and Hodgkiss (1984) concluded that it is possible that meal initiation is concerned with the emptying of part of the alimentary tract. The question now is which part of the digestive tract is most responsible for the initiation of the meal. Savory (1985) reported that meal initiation (hunger) may be associated with partial gizzard emptying in all birds and meal termination (satiety) during most of the day is associated with partial crop filling in birds eating larger, less frequent meals, and with varying degrees of gizzard filling in birds eating smaller meals.

However, building on the above discussion, a relationship between ambient temperature and food intake can be proposed. It is well known that at high temperature food passage rate through the digestive tract is decreased (Sleeth and Van Liere, 1937; Wilson *et al.*, 1980; Savory, 1986). The longer time required for food to pass through the digestive tract means this food remains in the gut longer and, in turn, no space is available for a new meal, which leads to longer intervals between meals and finally less food consumed per unit of time.

The reduction in food passage rate through the digestive tract as temperature increases could be explained by many possibilities which were mentioned in the previous Chapter (pair-feeding experiment, see 4.4.6). These possibilities have involved the role of triiodothyronine (T3) in the provision of energy which is required for tissues such as muscles or glands to function actively and how high temperature depresses the production of this hormone (see 4.1.2 for detail). In an early study Fetter and Carlson (1932) found that daily feeding to dogs of 0.4 gram per kg body weight of desiccated thyroid increased the activity of the empty stomach (hunger contractions and gastric motor activity). After thyroid feeding was discontinued there was a lowering of gastric activity. They also noted that during thyroid feeding the emptying time of the stomach was decreased and food passed quickly through digestive tract, however, when the administration of thyroid was stopped the speed of the meal through the digestive tract returned to its former rate. Guyton (1987) concluded that an increase in the motility of the gastrointestinal tract is accompanied by increased appetite and food intake when thyroid hormone is administered. The reduction in blood supply to the digestive tract when temperature increases is another possibility which might reduce the ability of this tract

(Wolfenson *et al.*, 1981). A decrease in blood flow to the digestive tract, in general, and to the gizzard, in particular, may reduce the supply of oxygen, nutrients and hormones which are required by this organ, especially during feeding (see 4.4.6). Of course the normal response would be a reduced work rate, fatigue. Moreover, thyrotropin-releasing hormone (**TRH**) which was injected into the hypothalamus, as mentioned in Section 4.4.6, increases gastric contractions via vagal-dependent pathways in rats (Morrow *et al.*, 1994), and at high temperature TRH secretion decreases (4.4.5). In birds, the role of vagal innervation in gizzard movements was reported by Hill (1971) and on digestive tract motility by Savory and Hodgkiss (1984). Therefore, the reduction in TRH which results from increasing temperature may lead to a decrease in the ability of the digestive tract to deal with the food, for the reasons explained above.

It seems, therefore, that a major reason for the depression in food intake when ambient temperature increases, is the reduction in the digestive tract's ability to deal with this food, in other words, to digest (mechanically and chemically) the food in the gizzard (see 4.4.6; the role of gizzard in food digestion) and make it ready to proceed to the remainder of the digestive tract to be absorbed in the intestine. Following this suggestion, some solutions were tested in this experiment which may allow the birds to increase their consumption of food and in turn their growth, especially when the second aim of this thesis (mentioned in the Introduction) is to explore methods of improving growth at high ambient temperature.

5.1.2 Proposed solutions

5.1.2.1 Grinding and wetting the diet

The digestive tract has the function of mechanically breaking down the diet, as well as chemical digestion, to allow absorption and utilisation. Some authors have studied the relationship between the nature of the diet and food passage rate. Heuser

(1944) found with hens that oats were retained in the crop longer than corn and wheat. Whole corn remained in the crop longer than cracked corn, which in turn was retained longer than corn meal; also when oats were boiled, they passed from the crop faster than dry oats. Wet mash also passed from the crop faster than dry mash. He concluded that food passage rate through the digestive tract is related to the amount of grinding and hence the time required for this food to remain in the gizzard. Also, any processes which will facilitate the passage of food such as grinding, softening or moistening the diet will hasten the passage rate, since soft foods require less muscular activity of the gizzard than hard foods. Recent studies have confirmed the effect of wetting the diet on food consumption and utilisation. Forbes and Yalda (1995) and Yalda and Forbes (1995a, 1995b, 1995c) noted that wetting diets significantly increased food intake, weight gain, food conversion efficiency and metabolisability. They also found that the greater gains in body weight due to wet feeding did not significantly affect fat deposition but that energy retention as protein was significantly increased.

However, do grinding and wetting diet increase food consumption and in turn growth in birds kept at high temperature? It was mentioned above (5.1.1) that initiation of a meal (hunger) is associated with partial gizzard emptying; if food passes more quickly through the digestive tract, shorter intervals between meals can be expected and finally a greater food intake per unit of time is obtained than with coarse meal diet.

5.1.2.2 Sodium concentration

Supplementation of the diet or drinking water with inorganic ions has been noted to improve growth. Smith and Teeter (1989) noted significant increases in food consumption, water intake and growth rate with broilers at 4 weeks old kept at cyclical temperature (26.6 to 36.7 °C) when they received 0.38% sodium chloride (NaCl) or 0.48% potassium chloride (KCl) in their drinking water. These authors suggested that the increase in water consumption caused an increase in food intake and finally weight gain. Sodium bicarbonate (NaHCO3) supplementation of the diet (16.8 g/kg) or drinking water (5.6 g/l) of finishing broilers improved food intake and weight gain when these birds were kept at 30 °C (Balnave and Oliva, 1991). More recently, Belay and Teeter (1995) found that adding bicarbonate to drinking water of broilers kept at high temperature (22-35 °C) induced an increase in water intake, food consumption and weight gain, when compared with control. However, it has been noted no response to sodium bicarbonate supplementation on the performance of guinea fowls raised at 23.8 to 33.9 °C, when compared with the control (Fuentes *et al.*, 1996). The different effects of high ambient temperature on mineral metabolism and excretion in broilers were shown by Belay and Teeter (1996). These authors noted lower urinary chloride and higher potassium, phosphorus, sulphur, sodium, magnesium, calcium and manganese excretion when broilers were exposed to 35 °C compared with those kept at 24 °C. Sodium ions (Na^+) may have another important function. It is known that glucose and amino acids in chickens are actively absorbed from the intestine (Lin and Wilson, 1960; Holdsworth and Wilson, 1967; Fearon and Bird, 1968; Basova and Kushak, 1986). The theory of 'active transport' means that energy from adenosine triphosphate (**ATP**) should be provided to maintain suitable concentrations of sodium inside the epithelial cells which should be less than the concentrations of sodium in the lumen. Then sodium ions can be transported into the epithelial cells and in turn the absorption of glucose and amino acids is facilitated (Wilson, 1979; Guyton, 1987).

Does increasing sodium concentrations by elevating sodium chloride content in the diet induce an increase in food intake and possibly the absorption of nutrients and lead to improved utilisation of the diet (greater metabolisability)?

5.1.2.3 Protein content in the diet

Results from the choice-feeding (Chapter 3) and pair-feeding (Chapter 4) experiments have indicated the similarities in the efficiencies of protein retention (protein retention/protein intake) between the different treatments. Also, it was noted that water retention was associated with protein retention (3.4.7, 4.4.2). The increase in protein retention will increase the weight of the animal and this effect will be magnified if water retention accompanies this protein. However, the difficulty which may result with high protein content is a reduction in protein retention efficiency. Evans and Scholz (1971) noted that chickens are able to use amino acids as a source of energy when high-protein diets are offered. They found that giving a diet containing 88% protein did not prevent these chicks having normal concentrations of blood glucose compared with the control group on 32% protein diet. In the choice-feeding experiment, it was noted with the birds kept at 30 °C, that the relatively high protein concentrations in the complete diet (25%) did not improve total food intake when compared with the birds receiving a free-choice diet and that they selected a mixture of feeds which gave a crude protein concentration of 19% (Table 3.2). However, the average growth rate in g per d was greater with the birds fed on the complete diet (43 v. 36, Table 3.2), and that was attributable to the greater protein and water retention. Does increasing protein content (up to reasonable level) improve growth by elevating protein retention and then water retention?

5.2 Materials and methods

5.2.1 Experimental design

A 5 × 5 Latin square was employed, combining five replicate runs and five treatments. Treatments were randomly assigned. A second 5 × 5 Latin square was run in the same way, with the treatments re-randomised. The second Latin square was conducted to increase the number of replicates. Data were treated by analysis of variance and least significant difference (LSD) between means was calculated. A $p<0.10$ level was considered significant.

5.2.2 Experimental work

Five 47-d-old Ross males of similar weight (1800 g) were put in calorimetry chambers (see 2.1) individually for 6 d. The first 3 days were for acclimatisation. The second period of 3 d was the fed measurement period, when food and water intakes, growth rate and heat production were recorded.

Constant high temperature (30 °C) was imposed on all the birds during the period of 6 d. Relative humidity ranged between 50% and 70%. The light pattern was 23 hours light: 1 hour dark. Five diets were offered to five groups of birds to represent five treatments as follow:

Treatment 1. The control diet was a typical, coarsely ground mash (diet 1).

Treatment 2. This diet was prepared by soaking the control diet freshly each day in twice its weight of water (diet 2, wet diet).

Treatment 3. The same feed was finely ground to pass a 1 mm screen before being mixed daily with twice its weight of water (diet 3, wet-ground diet).

Treatment 4. To make up diet 4, sodium chloride (20 g/kg) was added to diet 3 (diet 4, wet-ground-high-salt diet).

Treatment 5. The high-protein formulation (381 g/kg), which was also ground and soaked (diet 5, wet-ground-high-protein diet).

The diet compositions are summarised in Table 5.1. The following comparisons were made: between the first and second treatments to test the effect of wetting; between the second and third treatments to test the effect of grinding; the effect of sodium can be studied when comparison is done between third and fourth treatments ; and to test the effect of protein, the comparison is between treatments three and five. Food and water were available during the 6 d period. The remainder of the food in the feeders was collected daily during the measurement period and dried in an oven at 60 °C for 48 h; this was done to allow calculation of intakes as dry matter. Droppings were collected daily during the feeding measurements days. This was used for calculating apparent metabolisable energy. Energy retention as protein, as fat and total energy retention and also water and dry matter retention were estimated (see Section 2.3). The samples of diets and droppings were treated in the same way as explained in Section (3.2.2). The mean of the measurement period (3 d) was taken and the results were expressed per bird per d.

It should be noted that this work was repeated 10 times to give 10 runs. A total of 10 birds was, therefore, exposed to each regime.

Table 5.1. Diet compositions. A coarse meal diet was given to the birds as the contr diet. The control diet was also mixed daily with twice its weight of water, and given to th second group as wet diet. The third group received the same formulation as the contr but it was ground to 1 mm and wet (**wet-ground diet**). The fourth and fifth groups ha the high-salt and high-protein diets, also ground to 1 mm and wet, to represent (**we ground-high-salt diet**) and (**wet-ground-high-protein diet**).

Ingredients g/kg	**Coarse meal diet**	**High-salt diet**	**High-protein diet**
Wheat meal	600	582	270
Fish meal	23	23	-
Soyabean	300	300	560
Meat & bone meal	50	50	40
Maize gluten meal	-	-	85
Vegetable oil	-	-	13
Limestone	20	20	20
Salt	2	20	2.5
Dicalcium phosphate	-	-	4
Vitamin mix	2.5	2.5	2.75
Mineral mix	2.5	2.5	2.75
Crude protein	256	256	381
ME (kJ/g dry matter)	12.9	12.7	12.7

5.3 Results

5.3.1 Food, protein and water intakes and growth rate

Food intake as dry matter (**FI**) was greatest with the birds on the wet-ground diet and lowest with the group receiving the coarse whole meal diet (the control) (118 v. 84 g, $p<0.001$), and it was similar in the other 'processed' diets (Table 5.2, Figure 5.1). However, when comparison between the groups on the control and wet diets was made to test the effect of wetting, a significant difference was noted, birds on the wet diet consuming 27% more food ($p<0.001$) than those on the control diet. An effect of grinding was detected when wet diet was compared with wet-ground diet; intake was 10% greater ($p<0.10$) with the latter. No significant difference could be found between wet-ground and wet-ground-high-salt diets. Increasing protein content decreased food intake by 12% ($p<0.05$) compared with that on the wet-ground diet.

Table 5.2 and Figure 5.1 show the results for protein intake as dry matter (**PI**). The greatest intake (39 g) was by the birds fed on the wet-ground-high-protein diet, while the lowest intake was recorded with the control (22 g). Individual comparisons showed a significant difference ($p<0.01$) between the birds on control and wet diets; it was 23% more with the latter group. Also, grinding had a significant effect, it was 11% ($p<0.10$) greater with wet-ground diet than wet diet. Similar intakes of protein were found with the wet-ground and wet-ground-high-salt diets, 30 and 29 g, respectively. However, birds given the wet-ground-high-protein diet consumed 30% ($p<0.001$) more than those on the wet-ground diet.

The greatest water intake (**WI**) was detected (Table 5.2) with the birds on wet-ground-high-salt diet, which drank 250 ml per d; birds fed on the wet diet had the lowest value (31 ml). The control group consumed 535% ($p<0.001$) more water than the group on the wet diet. Birds receiving wet-ground diet drank 155%

Table 5.2. The effect of the nature and composition of the diet on food utilisation when broilers were exposed to high temperature (30 °C). Food intake (**FI**), protein intake (**PI**) as dry matter (**DM**), water intake, ml (**WI**) and growth rate (**GR**). Means are presented as g/bird. d.

	Diets					
Observation	**Coarse meal (control)**	**Control + wet**	**Control + ground + wet**	**Control + ground + wet + high-salt**	**Control + ground + wet + high-protein**	**SED**
FI (DM)	84c*	107ab	118a	114ab	104b	6.3
PI (DM)	22c	27b	30b	29b	39a	1.7
WI	197b	31c	79c	250a	76c	24.1
GR	27c	36bc	50ab	59a	50ab	7.8

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

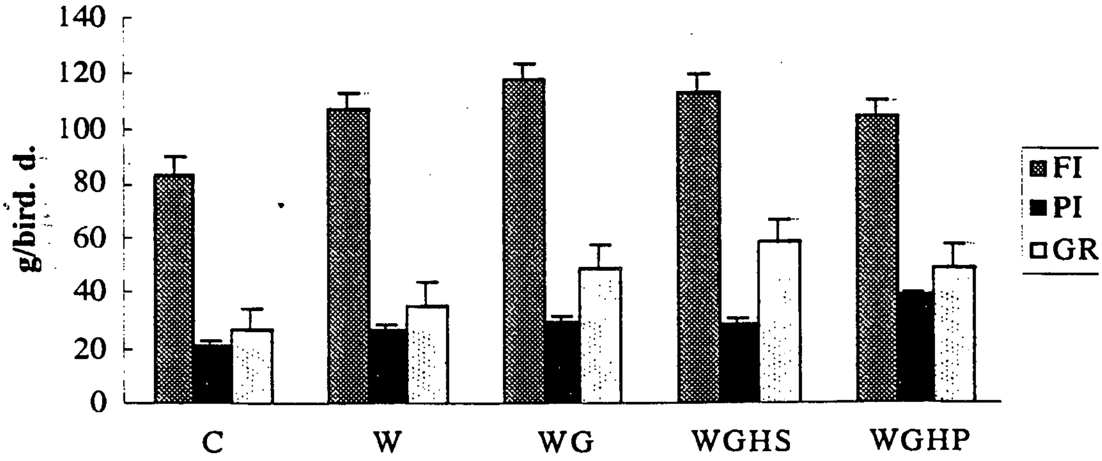


Figure 5.1. The effect of diet nature and composition on food intake (FI), protein inta (PI) and growth rate (GR) when broilers were exposed to high temperature (30 ° Control diet (C), wet (W), wet-ground (WG), wet-ground-high-salt (WGHS) and w ground-high-protein diets (WGHP).

($p<0.10$) more than those on wet diet. Much more water (216%; $p<0.001$) was drunk by birds on wet-ground-high-salt diet than the birds on the wet-ground diet. No significant difference was noted between the birds on wet-ground and wet-ground-high-protein diets.

Growth rate (**GR**) is shown in Table 5.2 and Figure 5.1. It was greatest with birds fed on wet-ground-high-salt diet (59 g/d). The control group had the lowest growth rate (27 g/d). Birds on wet diet grew 33% more rapidly than the control but this difference was not significant. Grinding the diet produced a significant difference ($p<0.10$), with birds on the wet-ground diet growing 39% more than on the wet diet. There was no significant difference between the high-salt diet and the wet-ground diet. Also, the same growth rate was noted in the birds on the wet-ground-high-protein diet and those on wet-ground diet.

5.3.2 Metabolisable intake, expenditure, oxygen consumption and energy retention

The greatest metabolisable energy intake (**IAME**) was found with birds fed on the wet-ground and wet-ground-high-salt diets, while the lowest value was recorded with the control group (Table 5.3). However, comparison between control and wet diets showed a significant difference ($p<0.01$), with IAME 21% greater with birds on wet diet. There was an effect of grinding, since birds on the wet-ground diet consumed 11% ($p<0.10$) more metabolisable energy. No significant difference was recorded between wet-ground and wet-ground-high-salt diets. Birds on the wet-ground-high-protein diet consumed 14% ($p<0.05$) less metabolisable energy than those on the wet-ground diet.

Energy expenditure (heat production, **HP**) is shown in Table 5.3. No significant difference was noted between the birds on wet, wet-ground, wet-ground-high-salt and wet-ground-high-protein diets. However, birds on control diet had a significantly lower heat production than the other groups. Taking the results as a whole, there was a clear trend for heat production to increase with food intake (Figure 5.2.a).

Oxygen consumption (O_2) gave the same trend as heat production (Table 5.3, Figure 5.2.b). No significant difference was noted between the birds on wet, wet-ground, wet-ground-high-salt and wet-ground-high-protein diets. However, birds on the control diet had a significantly lower oxygen consumption than the other groups.

Energy retention as protein (**REP**) was greatest with birds on the wet-ground-high-salt diet (Table 5.3, Figure 5.3.a) and lowest with those on the control diet (307 v. 197 kJ/d). No significant difference was detected between the birds on control and wet diets, although the latter had 9% greater energy retention as protein. REP was 23% greater with birds on the wet-ground diet than with the birds on the wet diet. Birds on the wet-ground-high-salt diet retained 17% more energy as protein than birds on the wet-ground diet. Similar values were obtained between birds given wet-ground-high-protein and wet-ground diets.

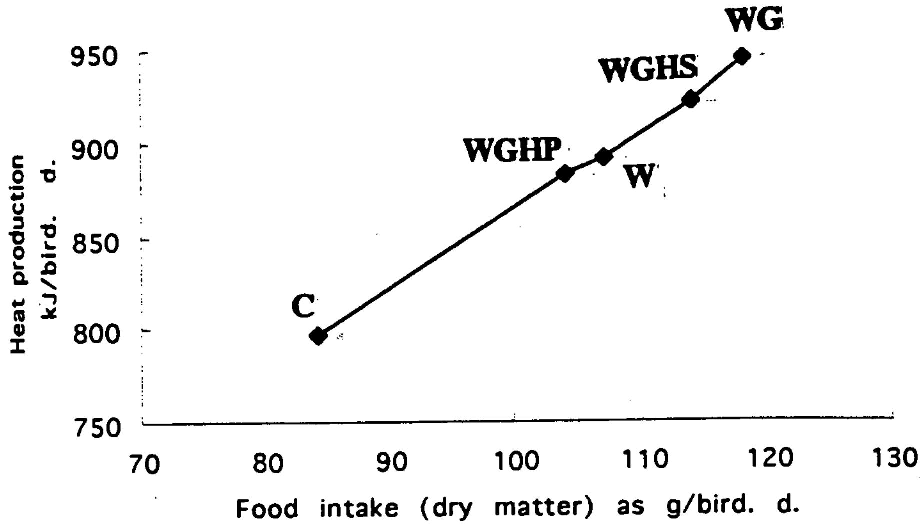
Energy retention as fat (**REF**) was greatest with birds on the wet-ground diet (170 kJ/d) and lowest (28 kJ/d) in the control (Table 5.3, Figure 5.3.b). When direct comparisons were made, a difference ($p<0.10$) was found between birds on control and wet diets, with REF being more than 4 times greater with the latter group. Birds on the wet-ground diet had 31% (not significant) greater energy retention as fat than those on wet diet. REF was 31% more with the birds on wet-ground diet than those on wet-ground-high-salt diet. Birds on the wet-ground-high-protein diet had 80% ($p<0.05$) less fat retention than the birds fed on the wet-ground diet.

Total energy retention (**RE**) was greatest with the birds on wet-ground-high-salt and wet-ground diets, and lowest in the control group (Table 5.3, Figure 5.3.c). Wetting the diet increased this value by 52% ($p<0.10$) compared with the control

Table 5.3. The effect of the nature and composition of the diet on food utilisation when broilers were exposed to high temperature (30 °C). Apparent metabolisable energy intake (**I_{AME} kJ**), heat production (**HP kJ**), oxygen consumption (**O_2 ml**), energy retention as protein (**REP kJ**), energy retention as fat (**REF kJ**) and total energy retention (**RE kJ**). Means are presented/bird. d.

	Diets					
Observation	**Coarse meal (control)**	**Control + wet**	**Control + ground + wet**	**Control + ground + wet + high-salt**	**Control + ground + wet + high-protein**	**SED**
I_{AME} kJ	1023c*	1235ab	1377a	1360a	1190b	75.3
HP kJ	798b	892a	946a	923a	884a	41.6
O_2 ml	39b	43a	45a	44a	43a	1.9
REP kJ	197c	214bc	263ab	307a	273ab	32.3
REF kJ	28b	130ab	170a	130ab	34b	50.4
RE kJ	225b	343ab	431a	437a	307b	58.5

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.



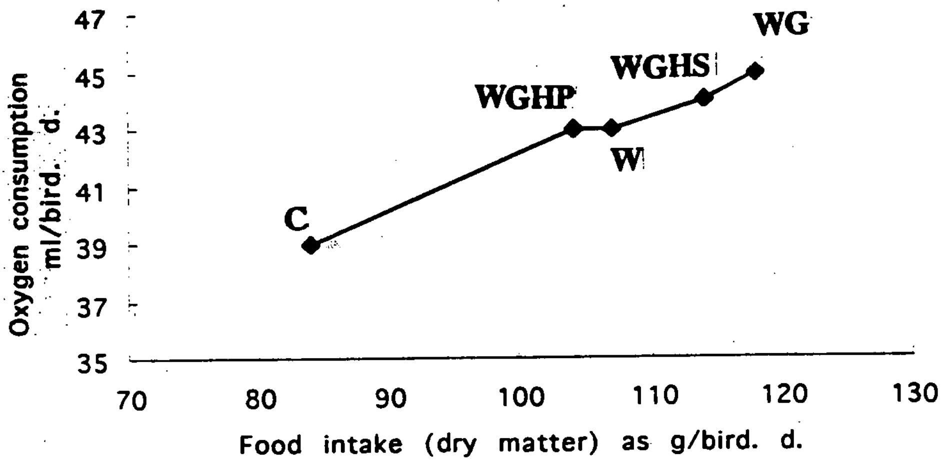


Figure 5.2.a,b. The relationship between food intake, heat production and oxygen consumption in birds kept at high temperature (30 °C); it is clear how heat production and oxygen consumption increased to high levels with increasing food intake although all the birds were kept at high temperature. Control diet (C), wet (W), wet-ground (WG), wet-ground-high-salt (WGHS) and wet-ground-high-protein diets (WGHP).

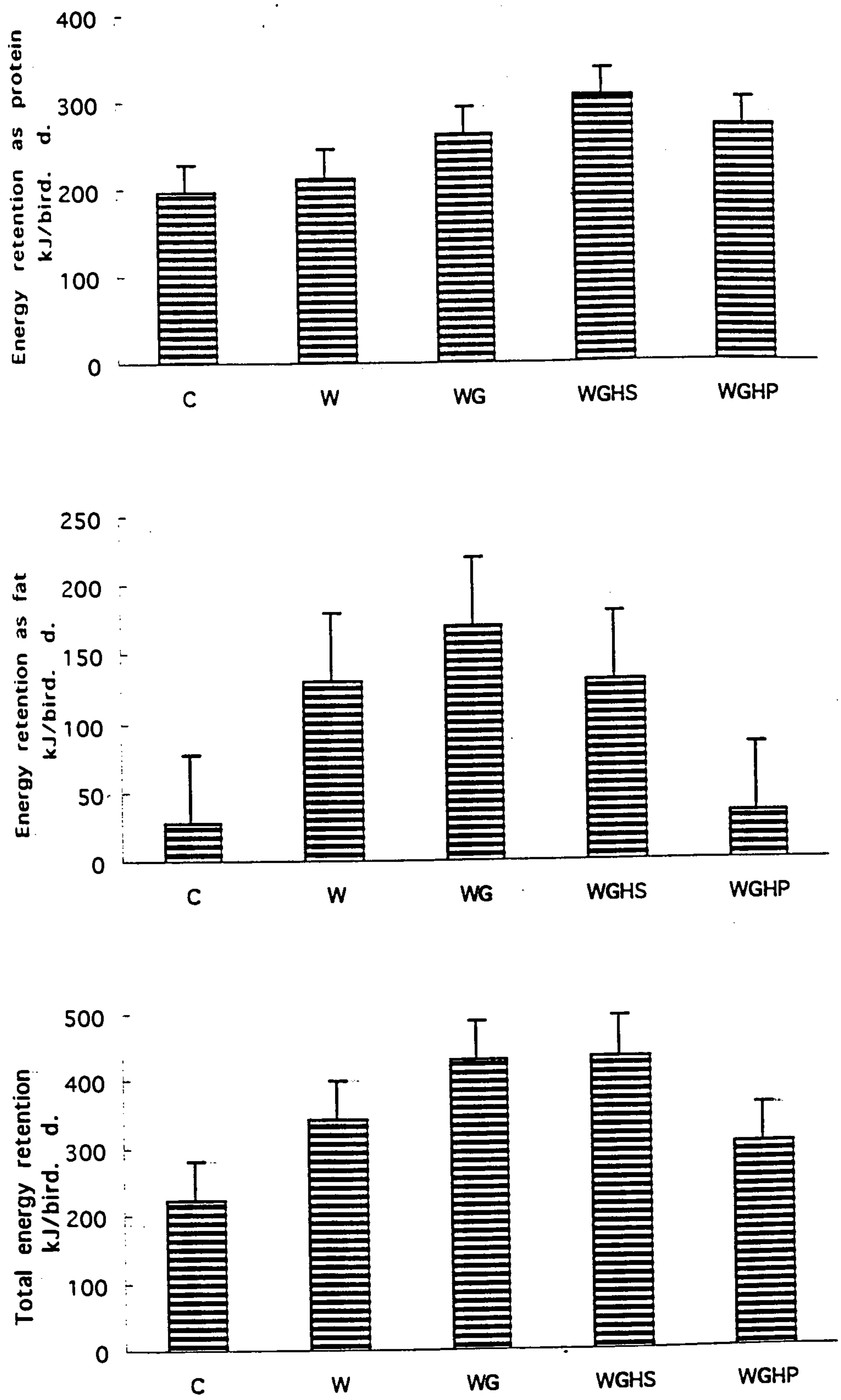


Figure 5.3.a,b,c. The effect of diet nature and composition on protein, fat and to energy retention when broilers were exposed to high temperature (30 °C). Control d (C), wet (W), wet-ground (WG), wet-ground-high-salt (WGHS) and wet-ground-hig protein diets (WGHP).

diet. Also, grinding increased energy retention by 26%; it was greater with the birds on the wet-ground diet than those on the wet diet. Similar energy retention was noted between birds on wet-ground-high-salt and wet-ground diets. Increasing dietary protein content decreased this value; it was 29% ($p<0.05$) less when compared with wet-ground diet.

5.3.3 Food conversion efficiency and energy metabolisability

Food conversion efficiency (FCE) was highest with the birds on the wet-ground-high-salt diet and lowest with those on the control diet (Table 5.4). Wetting the diet increased this efficiency by 13% compared with the control. Grinding the diet also increased this value; it was 23% higher than in the birds on the wet diet. Birds on the wet-ground-high-salt and the wet-ground-high-protein diets had 19% and 14% greater FCE than those on the wet-ground diet. However, these differences were not statistically significant.

Protein retention efficiency (**PRE**) was not significantly affected by wetting or grinding diet when compared with the control (Table 5.4). Increasing salt content in the diet led to a 24% ($p<0.10$) increase in this efficiency when compared with the wet-ground diet. However, increasing the protein content of the diet caused a reduction, the efficiency being 18% (not significant) less than on the wet-ground diet.

Apparent metabolisability (**Amet**) is shown in Table 5.4. The highest metabolisability values were recorded with the birds on the control and wet-ground-high-salt diets, while lowest values were noted with those on wet-ground-high-protein diet. Direct comparisons show a significant difference between the birds on the control and wet diets, since it was 4% ($p<0.01$) less with birds on the wet diet. The same values were found with wet and wet-ground diets. However, the wet-ground-high-salt diet had higher metabolisability (4%; $p<0.01$) than those on wet-

Table 5.4. The effect of the nature and composition of the diet on food utilisation when broilers were exposed to high temperature (30 °C). Food conversion efficiency (**FCE**), protein retention efficiency (**PRE**) and apparent metabolisability (**Amet**).

	Diets					
Observation	**Coarse meal (control)**	**Control + wet**	**Control + ground + wet**	**Control + ground + wet + high-salt**	**Control + ground + wet + high-protein**	**SED**
FCE	0.31c*	0.35bc	0.43abc	0.51a	0.49ab	0.072
PRE	0.40ab	0.35b	0.38ab	0.47a	0.31b	0.047
Amet	0.72a	0.69b	0.69b	0.72a	0.64c	0.009

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

ground diet. Increasing protein content in the diet decreased Amet (7%; $p<0.001$) when compared with birds on wet-ground diet.

5.3.4 Water and dry matter retention

Water and dry matter retention are shown in Table 5.5. The greatest water retention (**WRC**) was detected with the birds on wet-ground-high-salt diet (41.6 g/d), while those on control diet had lowest value (17.2 g/d). No significant difference was produced by wetting the diet, although the group on the wet diet had 37% more carcass water retention than the control group. Birds on the wet-ground diet recorded 44% greater water retention (not significant) than those on wet diet. Water retention was also 23% and 11% greater with the birds on wet-ground-high-salt and wet-ground-high-protein diets than with those on the wet-ground diet.

The greatest growth rate as dry matter (**GRDM**) was noted with the birds on the wet-ground-high-salt diet, and the control recorded the lowest value (Table 5.5). However, wetting the diet did produce an effect, growth rate as dry matter being 36% ($p<0.10$) greater with the birds on the wet diet than the birds on the control diet. Birds on the wet-ground diet had 24% greater growth as dry matter than those on wet diet. Birds on the wet-ground-high-salt and wet-ground-high-protein diets had 6% more and 19% less when compared with those on wet-ground diet.

Table 5.5. The effect of the nature and composition of the diet on food utilisation when broilers were exposed to high temperature (30 °C). Water retention in the carcass (**WRC**) and growth rate as dry matter (**GRDM**). Means are presented as g/bird. d.

	Diets					
Observation	**Coarse meal (control)**	**Control + wet**	**Control + ground + wet**	**Control + ground + wet + high-salt**	**Control + ground + wet + high-protein**	**SED**
WRC	17.2c*	23.5bc	33.8ab	41.6a	37.4ab	7.0
GRDM	9.4c	12.8bc	15.9ab	16.9a	12.9bc	1.9

* Measurements in the same row not sharing a common subscript are different at the $p<0.05$ level.

5.4 Discussion

5.4.1 Food, protein and water intakes and growth rate

The effect of wetting and grinding diets on food consumption (FI) as dry matter was very clear (Table 5.2, Figure 5.1). It is suggested that this increase was achieved by the facilitation which was given to the digestive tract in dealing with the diet. The food was mechanically broken down by grinding and also softened, lubricated and possibly made less viscous by wetting. Less energy was therefore required from the digestive tract, in general, and from the gizzard, in particular, to grind this diet (Heuser, 1944; Forbes and Yalda, 1995; Yalda and Forbes, 1995a, 1995b, 1995c). This softness and grinding allowed this food to pass through the digestive tract faster than the coarse meal diet. Since the gizzard is the main organ responsible for the grinding process, it seems that the food left the gizzard and entered the remainder of the digestive tract in a shorter time than with the diet of normal consistency. In turn, this left space in the gizzard for a new meal, so that the‘activating mechanism’ was stimulated (Duncan *et al.*, 1970). A shorter interval between meals therefore resulted and consequently greater food intake per d (Savory, 1980; Savory and Hodgkiss, 1984; Savory, 1985). However, it seems that increasing sodium chloride content had no special effect on food consumption, since the birds on this treatment did not eat more than the birds on wet-ground diet. These results are not in agreement with Smith and Teeter (1989) who reported greater food intake with birds which received 0.38% NaCl in their drinking water when compared with the control (no salt supplementation). It was surprising that the birds on wet-ground-high-protein diet decreased their consumption (12%; $p<0.05$) less than those on wet-ground diet although, both of these groups had diets which were ground and wet to the same level. The explanation of this might be that increasing protein content in the diet may have led to an increase in the time required for the gizzard to digest this food, especially since the first stage of protein digestion is made in this organ (Duke, 1986b).

Protein intake (PI) as dry matter (Table 5.2, Figure 5.1) was of course affected by the amount of food consumption. The greater protein intake which was noted with the birds on wet-ground-high-protein diet was attributable to the concentration of this nutrient in the diet.

Water intake (WI) was greatest with the birds on wet-ground-high-salt diet, which was expected (Table 5.2), as it is well known that an increase in dietary salt intake induces an increase in osmolarity in the extracellular fluid. Receptors (the thirst centre) in the hypothalamus are then activated, causing the feeling of thirst and the desire to drink (Guyton, 1987; Villee *et al.*, 1989). Similar results were reported by Smith and Teeter (1989) who found greater water consumption when NaCl was increased. The greater water intake by the birds on the coarse meal diet (the control) ($p<0.001$) compared with other treatments (except the high-salt treatment) may be attributable to the fact that drinker was the only source of water for these birds, while the birds on the other treatments also had the water which was mixed with their diets. Water intake was 155% ($p<0.10$) greater with the birds on the wet-ground diet than those on the wet-unground diet; this greater intake was probably due to the difference in food consumption, which was 10% ($p<0.10$) more with wet-ground diet. However, it was interesting to find that water intake was similar between the birds on wet-ground and wet-ground-high-protein diets although, food intake was 13% ($p<0.05$) greater with those on wet-ground diet. It is possible that the increase in protein intake led to increased water intake. Gastric acid secretion is affected by many factors such as vagal stimulation (Gibson *et al.*, 1974) and the hormone gastrin (Hill, 1983), which is secreted from specialised cells located in the pyloric region of the fowl (Polak *et al.*, 1974). Gastrin is secreted in response to the distension of the stomach wall and in response to the chemical nature of the food ingested with particular response to protein. However, the postulated mechanism for the secretion of hydrochloric acid suggests that water, which is supplied from the blood, contributes to the formation of hydrochloride acid. Moreover, some water will pass to the stomach in response to increased osmolarity (Guyton, 1987). Therefore, it may be that increasing protein content in the diet induced an increase in hydrochloric acid secretion which, in turn, led to greater amount of water transported to the lumen with an increase in extracellular osmolarity and a need for more water. Another possible mechanism responsible for increased osmolarity is the greater quantity of N compounds produced by the birds on the high protein diet. A greater amount of water was, therefore, used to excrete these products.

The high growth rate (**GR**) which was recorded in the birds on wet-ground and wet-ground-high-salt diets (Table 5.2, Figure 5.1) is simply attributable to higher food intake with these groups; also, the slightly better growth with the birds on wet-ground-high-salt diet than those on wet-ground diet, although food intake was slightly greater with the birds on wet-ground diet, can be explained by the greater water retention (this is discussed in 5.4.4). However, birds on the wet-ground-high-protein diet had similar growth rate to those on wet-ground and wet-ground-high-salt diets, although their food intake was 12% ($p<0.05$) and 9% less than the previous groups, respectively. This similar growth is attributable to the similarities in energy retention as protein which resulted from the great intake of this nutrient and is also a result of the similarities in water retention. The association between protein retention and water retention is well evident (Adams *et al.*, 1962a; MacLeod, 1991a). The lowest growth rate, noted with the control group, resulted from the temperature-induced depression in food consumption, which was the lowest of any treatment.

5.4.2 Metabolisable intake, expenditure, oxygen consumption and energy retention

Apparent metabolisable energy intake (IAME) generally followed the same trend as food intake by weight (Tables 5.2, 5.3). However, apparent metabolisability had an effect on apparent metabolisable intake values, since there were some differences in apparent metabolisability between the different treatments. This is discussed below.

Heat production (HP) was strongly correlated with food intake (Table 5.3). The greatest heat production was in birds on the wet-ground diet, which also had the greatest food intake; the lowest heat production was associated with the lowest food intake, in the control group. The factors which may affect heat production such as body size, environmental temperature and food intake were discussed in Section 1.2.3. However, the birds which had been used in this experiment had similar body weights about (1800 g) and were all kept at 30 °C. Similar energy expenditure for maintenance can therefore be expected. The differences in heat production can, therefore, be attributable to variations in food intake, especially when it was noted from choice-feeding experiment that each g of food intake cost nearly same energy whether with the birds kept at 20 °C or 30 °C (see Section 3.3.3, Table 3.5).

The pattern of oxygen consumption (O_2) was similar to that of heat production, as expected (Table 5.3). However, the most important information which can be concluded from heat production and oxygen consumption results is that, the reduction in both HP and O_2 when temperature increases may be attributable to the reduction in food intake and not to the inhibition of triiodothyronine (T3) production as suggested by Kan (1994). Kan (1994) suggested that at high temperature T3 production is inhibited, and this inhibition may resulted from the reduction in the number of growth hormone receptors or their response to growth hormone stimulation. If this was correct, similar heat production would be expected in all treatments in this experiment. However, heat production and oxygen consumption varied to a great extent between treatments, from 798 to 946 kJ/d and from 39 to 45 ml/d with the control and wet-ground diets groups, respectively (Table 5.3, Figure 5.2.a,b). Also, it was clarified (4.1.2) that heat production and oxygen consumption are stimulated by T3 hormone. Therefore, greater heat production and oxygen consumption would be expected to be linked to greater production of T3, although all the birds were kept at the same high temperature (30 °C). Again, it seems likely that the reduction in T3 which occurs at high temperature is a result of the depression in food intake and not the opposite. Also, it seems that the other possible explanation for the reduction in food intake when temperature increases (the reduction in digestive tract ability that results from the depression in blood flow to this system, 4.4.6) might be more probable. Evidence for this is that food intake greatly increased, from 84 g/d on the control diet to 118 g/d when the same diet was ground and wet, functions which are normally performed by the digestive tract. These results suggest that the domestic fowl reduces its food intake at high temperature not to reduce or limit heat production, but because the gut is limited in the amount of food it can process. If the gut is 'assisted' by providing ground or wet food, food intake and heat production both increase.

Energy retention as protein (**REP**) was influenced by several factors (Table 5.3, Figure 5.3.a). The greatest retention was with the birds on wet-ground-high-salt diet, although these birds ate a similar amount of protein to those on wet-ground diet. The explanation for this greater retention was the greater metabolisability which occurred with these birds (discussed in Section 5.4.3). The similarity in protein retention between wet-ground and wet-ground-high-protein diets although there was a significant difference in food intake between these groups was due to the greater protein intake with the latter group. So, the increase in protein intake allowed these birds to retain a great amount of protein. The relatively low protein retention in the control group resulted from the reduction in intake of this nutrient.

The similar energy retention as fat (**REF**) obtained between the birds on wet, wet-ground and wet-ground-high-salt diets would be expected from the similarity in food intake (Table 5.3, Figure 5.3.b). The low fat retention with the control birds also resulted from the relatively low food intake with these birds; however, it was unexpected to find similar fat retention between the groups on control and wet-ground-high-protein diets, although food intake was significantly (24%; $p<0.01$) greater in those on the wet-ground-high-protein diet. The explanation of the similar fat retention between these groups is the diet composition (CP:ME ratios). There was an increase in the proportion of protein and a decrease in the proportion of non-protein sources, which reduced the proportion of energy stored as fat.

Total energy retention (**RE**) was of course the sum of energy retained as protein and as fat (Table 5.3, Figure 5.3.c). However, it was very clear that grinding and wetting the diet helped the birds not only to have more rapid growth but also greater energy retention. That of course, resulted from the greater energy intake with these birds. Also, it should be remembered that the high protein content in the wet-ground-high-protein diet induced a significantly greater (85%; $p<0.05$) growth rate when compared with the control; however, this greater growth rate was accompanied by a much smaller (36%) increase in energy retention, which was not significant. The significantly greater weight gain without significantly increasing energy retention is because of the large (89%) proportion of protein in total energy retention. This large protein retention was associated with much water retention and led to greater growth as weight gain.

5.4.3 Food conversion efficiency and energy metabolisability

It was mentioned in the choice-feeding experiment (Chapter 3) that an important factor affecting weight is water retention, and how this water is associated with protein retention (3.4.7). Similar findings were recorded in this experiment, the greatest protein retention with the birds on wet-ground-high-salt diet resulting in the greatest water retention (**WRC**), which gave the greatest food conversion efficiency (**FCE**) (Tables 5.3, 5.4, 5.5). The lowest (FCE) was noted with the control group, which had the lowest protein and water retention (Tables 5.3, 5.4, 5.5).

The greatest protein retention efficiency (**PRE**) was noted with the birds on the wet-ground-high-salt diet (Table 5.4); it seems that increasing the sodium chloride of the diet led to greater absorption of amino acids. The role of sodium in nutrient absorption is well defined (Lin and Wilson, 1960; Holdsworth and Wilson, 1967; Fearon and Bird, 1968; Basova and Kushak, 1986). The increase in the absorption of amino acids led to increased utilisation for protein synthesis. However, the lowest efficiency of protein retention, which was found with wet-ground-high-protein diet, is probably attributable to the increased proportion of dietary energy supplied as protein. This increase means that protein functions as a source of energy (Evans and Scholz, 1971).

It appears that apparent metabolisability (**Amet**) was affected by many factors (Table 5.4). The greatest metabolisability was found with the birds on the wet-ground-high-salt diet which may be attributable again to the effect of sodium ions on nutrient absorption. However, it was interesting to find the same apparent metabolisability in the birds on the control and the wet-ground-high-salt diets which was, in turn, significantly greater than those on wet and wet-ground diets. It seems that the reduction in food passage rate which would be expected to occur with the birds on the control diet at high temperature (Sleeth and Van Liere, 1937; Wilson *et al.*, 1980; Savory, 1986) led to increased efficiency of digestion (Geraert *et al.*, 1992) or absorption (Zurpizal *et al.*, 1993) and, in turn, metabolisability. The lowest metabolisability, recorded with the birds on the wet-ground-high-protein diet can be attributed to the increased content of protein in the diet. It was demonstrated earlier (in choice-feeding experiment, 3.4.5) that increasing the amount of high-protein ingredients in the diet led to reduced metabolisability; this is because the metabolisability of the low-protein ingredients is greater than that of the high-protein ingredients.

5.4.4 Water and dry matter retention

Water retention (**WRC**), as discussed above (5.4.3), was directly related to protein retention (Table 5.5, Figure 5.4).

Growth rate as dry matter (**GRDM**, Table 5.5) demonstrated that the best utilisation of the diet was with the birds on the wet-ground-high-salt diet, since they had the best growth rate as dry matter, although their intake of the diet was slightly less than those on the wet-ground diet. Again, this better utilisation of the diet could be attributable to the effect of sodium ions on nutrient absorption. Also, growth rate as dry matter confirmed that the most important factor affecting total growth rate and food conversion efficiency with the birds on the wet-ground-high-protein diet was the water retention which was associated with this protein retention. When the weight of the water was subtracted, their growth rate was the same as those on the wet diet, although the difference was 39% when calculated as total weight gain.

It can be concluded from this experiment that grinding and wetting diet can lead to great improvements in growth rate (from 27 g with the birds on coarse meal diet to 50 g per d with those on the wet-ground diet); this more rapid growth, in turn, was obtained by increasing food intake. However, increasing salt content (to a reasonable level) in the diet which is ground and wet may also improve the efficiency of food utilisation to some extent. In relation to increasing protein content in the diet, good growth rates might be obtained, but this may not be associated with greater energy retention and the increase in protein content of the diet may also lead to lower efficiency of protein retention and metabolisability.

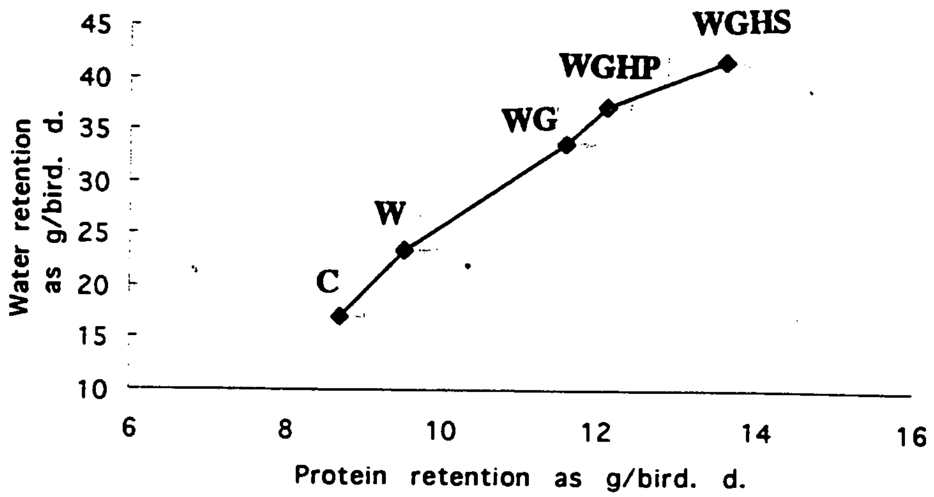


Figure 5.4. The relationship between protein retention and water retention; a linear relationship was obtained between these two measurements. Control diet (C), wet (W), wet-ground (WG), wet-ground-high-salt (WGHS) and wet-ground-high-protein diets (WGHP).

5.5 Conclusions

An experiment was designed to investigate if wetting, grinding and wetting, increasing salt content and/or increasing protein content in wet-ground diets, can help broilers to increase their food consumption and, in turn, their growth when they are exposed to high ambient temperature (30 °C). Results from this experiment indicated the following points:

1- Grinding and wetting diet led to increased food consumption, growth rate and total energy retention.

2- Increasing salt content in wet-ground diet improved the metabolisability.

3- Increasing protein content in a wet-ground diet induced a growth rate similar to that of birds on wet-ground or wet-ground-high-salt diets, but decreased total energy retention, protein retention efficiency and metabolisability.

4- It is usually assumed that reduced food intake at high temperature results firstly from a decrease in energy requirements for thermoregulation and secondly from the need to minimise heat stress by reducing the heat increment of feeding. However, results in this work suggested that the domestic fowl reduces its food intake at high temperature not to reduce or limit heat production, but because the gut is limited in the amount of food it can process. If the gut is 'assisted' by providing ground and/or wet food, food intake, growth rate and heat production all increase.

5- It was also suggested that the increase in apparent metabolisability in the birds on high-salt diet may have resulted from the effect of sodium ions on the absorption process.

Chapter Six

General discussion

6.1 Effects of high ambient temperature on food utilisation and growth rate

It is well known that high ambient temperature leads to depression of food intake and this, in turn, decreases growth rate in farm animals. Therefore, this project was designed to investigate, firstly, the effects of high ambient temperature on the utilisation of the diet through energy metabolism and energy retention, secondly, the mechanisms which might be responsible for the reduction in food intake and, thirdly, nutritional methods that may help the animals to sustain food intake and growth.

The first experiment was designed to serve the first aim of this project and to test the efficacy of a choice-feeding system in improving food intake and growth in heat-stressed broilers. From this experiment, it was concluded that high temperature (30 °C) had no effect on the efficiency of food utilisation, but it decreased growth rate significantly. This reduction was attributable to a depression in food intake which, in turn, decreased the retention of protein; the retention of water associated with protein deposition also decreased, magnifying the growth depression effect. However, energy retention as fat was not affected by high temperature despite the reduction in food intake. The similarities in fat retention were attributable to the lower need for energy to support thermoregulatory processes with the birds kept at high temperature (see 3.4.3, 3.4.4). The second reason responsible for the reduction in growth rate at high temperature is the additional decrease in water retention, since water is lost in evaporative cooling processes. Therefore, it can be said that high temperature will act negatively on growth rate by decreasing food intake, protein retention, the water retention associated with protein deposition and also by the additional reduction in water retention which results from the greater demand for water for thermoregulatory processes. However, at the same time, the reduction in energy demand for thermoregulation with birds kept at high temperature led to a slightly but not significantly greater proportion of metabolisable energy intake being retained as fat, which led to a positive effect of high temperature on the proportion of energy intake retained as fat. There was no indication of a positive effect of a choice-feeding system on growth rate at high temperature. Moreover, this system led to decreased growth rate with the birds kept at 20 °C when compared with those given complete diet. This was attributable to the animal's selection of the amounts of protein and energy intakes, and to the effect of the ratio of protein to energy (CP:ME ratio) in total food intake (see 3.4.1).

In the first experiment (discussed above) it was clear that high ambient temperature affected food utilisation mainly by reducing intake, although there was also a positive effect of high temperature (30 °C) on the proportion of energy intake retained as fat. However, some previous work has suggested that high temperature had a negative effect on food utilisation even if food intake was the same as of the lower temperatures. This was demonstrated by use of a pair-feeding method (see 4.1.1, 4.2.2). They suggested that the lower utilisation of food at high temperature was related to concentration of triiodothyronine hormone (T3) which is depressed at high temperature. A second experiment was, therefore, designed to test the effect of high temperature under pair-feeding design. Results from the pair-feeding experiment confirmed those found in the first experiment, which suggested no negative effect of high ambient temperature on food utilisation, other than its effect on intake. Also, as mentioned above, the proportion of metabolisable energy retained as fat increased in the birds kept at high temperature. In addition to this, T3 secretion was related to with the demand for energy, so similar concentrations of triiodothyronine (T3) were found in the birds kept at 20 °C and at 30 °C but receiving the same amount of food (see 4.4.5). From this experiment, it was also concluded that the digestive tract contents decreased with the birds at high temperature and it was suggested that this may be attributable to either inhibition in triiodothyronine (T3) production and/or to a reduction in blood flow to the digestive tract which, in turn, would lead, respectively, to a decrease in the energy provision or to a reduction in the supply of substances which are required for energy for this system to work actively (see 4.4.6). Therefore, a hypothesis was formed that the reduction of food intake at high temperature may result, at least partially, from the lower power of this system to deal with the diet. This would act in addition to the commonly offered explanation that food intake is decreased initially because of reduced maintenance and finally to minimise heat stress by reducing heat increment of feeding. The next experiment therefore included, as one of its aims, the separation of the heat production and digestion effects of high temperature, by measurement of heat production in birds fed on diets treated in ways which would be expected to affect the amount of work done by the alimentary tract.

6.2 Dietary modifications and their effects on food intake, food utilisation, growth rate and heat production

Exploring nutritional methods of improving growth rate at high temperature was a second aim of this project. Results from the third experiment showed that the reduction in food intake when birds are exposed to high temperature is, at least partially, attributable to the reduction in the rate at which the digestive tract can deal with the food (in other words, to the lower work rate of this system in breaking down the food mechanically and chemically, and also in propelling the food through it). This, in turn, may lead to an increase in the time spent by the food in different parts of digestive tract. For instance, the time required for the food to stay in the gizzard until ground to the small particles which are allowed to proceed to the duodenum will be greater with the birds kept at high temperature. Of course this, in turn, will induce longer intervals between the meals and finally less food intake per unit of time, especially when the association between meal initiation and partial gizzard emptying is well defined (see 5.1.1). Therefore, it can be concluded that modifications of the food, such as grinding and wetting the diet, will help the digestive tract to deal with this food and to expel it from the gizzard more rapidly, so that greater numbers of meals can be consumed, leading finally to greater food intake. Also, this experiment suggested greater metabolisability of the food when dietary sodium chloride was increased, and this led to greater growth rate. The increase in the metabolisability of the high-salt diet may be attributable to the more efficient absorption of nutrients which may have resulted from the role of sodium ions in the absorption mechanism. Heat production increased significantly with increased food intake and growth rate on the modified diets. The results were, accordingly, consistent with the explanation that gut function and not heat production places a limit on food consumption at 30 °C.

6.3 Summary

High temperature decreased food intake, growth rate, energy retention as protein and water retention but had no effect on energy retention as fat and little effect on total energy retention. High temperature did not affect the proportion of apparent metabolisable energy retained as protein or the efficiency of energy retention from apparent metabolisable energy. However, it increased the proportion of apparent metabolisable energy retained as fat. The latter effect was attributable to the reduced energy requirement for thermoregulation. Offering the birds a choice between a "high-protein" and a "high-energy" diets did not improve growth when the animals were exposed to high temperature. Moreover, this system led to decreased food intake and, in turn, growth rate with the birds kept at moderate temperature (20 °C) when compared with those given a complete compound diet.

Dietary modifications such as grinding and wetting food led to increased food consumption and, in turn, growth rate in broilers kept at high temperature (30 °C). Also, increasing salt content in a wet-ground diet improved the metabolisability. This increase may have resulted from the effect of sodium ions in the absorption mechanism.

Contrary to the common assumption that reduced food intake at high temperature results firstly from a decrease in energy requirements for thermoregulation and secondly from the need to minimise heat stress by reducing the heat increment of feeding, results in this work suggested that the domestic fowl reduces its food intake at high temperature not to reduce or limit heat production, but because the gut is limited in the amount of food it can process. If the gut is 'assisted' by providing ground and/or wet food, food intake, growth rate and heat production all increase.

6.4 Potential application of the findings in the thesis to poultry industry

It was mentioned earlier (Section 1.1) that commercial poultry production faces difficulties in tropical countries as a result of high ambient temperature. Artificial cooling systems help birds to increase their food intake and, in turn, improve their growth but building and running such systems are expensive.

According to the results from this work, it can be suggested that offering ground and wetted diets to heat-stressed broilers will allow an increase in growth rate. Grinding and wetting diets can potentially be done by commercial poultry producers or feed compounders. Increasing salt content in these ground and wetted diets increased metabolisability; however, further studies are required to assess a practical level of sodium chloride addition which does not have a negative effect in the long term.

6.5 Further applied research aims

Improving food intake and, in turn, production in broilers housed at high temperature was achieved by grinding and wetting the diet. However, other possible solutions can still be tested, which may lead to increased growth rates under high temperature regimes. The use of exogenous enzymes, such a polysaccharidases and proteases, may be particularly beneficial at high ambient temperature. Enzymes may add to the effectiveness of wet-ground diets.

It is also important to do more studies on sodium chloride to confirm, firstly, if the increased metabolisability which occurred with the birds fed on the high-salt diet is attributed to the effect of sodium ions on the absorption mechanisms. Secondly, to investigate if there is a negative effect of this compound on poultry health when it is used in the long term and, thirdly, to test the maximum level which may be added to the diet.

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Appendix

ANALYSIS OF HEAT STRESS EFFECTS ON GROWTH BY PAIR-FEEDING

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It is well known that high ambient temperature decreases growth rate in broilers. It is less clear, however, if growth rate is depressed simply by the decreased food intake or if there are direct effects of high temperature on growth. Previous work (Squibb et al., 1959; Olson et al., 1972; Mitchell and Goddard, 1990) has given a range of answers. Since weight gain in itself is not a good indicator of the mechanisms involved, this study was planned to analyse the growth responses in terms of energy metabolism and of protein and fat deposition.

Precise pair-feeding was used to compare male Ross broilers on the same food intake kept at moderate (20°C) and high (30°C) temperatures. There were 3 treatments: (1) 20°C with *ad libitum* feeding; (2) 30°C with *ad libitum* feeding; (3) 20°C but receiving exactly the same amount of food as the heat-stressed bird had consumed on the previous day. The diet contained 260 g crude protein and 11.6 MJ ME per kg. During experiment, the birds were housed individually in calorimeter chambers. A total of 9 birds was exposed to each regime, with the treatments arranged in 3 successive 3 (chamber) x 3 (time) Latin Squares. Measurements were made while the birds were 37 - 40 d old, after a 3-d adjustment period. The following were among the variates measured: food intake, growth rate (GR), heat production (H), apparent metabolisable energy by total collection (AME), energy retention (ER), ER as protein (REP) and fat (REF). The results were subjected to analysis of variance.

AME intake (I_{AME}) was 25% lower ($p<0.001$) in the 30°C and pair-fed birds than in the 20°C control group (Table). *Ad-libitum*-fed birds at 20°C gained more weight ($p<0.01$) than the 32°C and pair-fed groups. It is important to note that there was no difference in weight gain between the latter two groups. H was greatest in the 20°C control group, while the 20°C pair-fed birds had a significantly higher H than birds on the same food intake kept at 30°C ($p<0.001$). The balance between I_{AME} and H led to the control 20°C birds having the greatest ER, with the pair-fed birds lowest and their 30 C counterparts intermediate. Protein retention was similar in birds eating the same amount of food at 20 and 30°C; however, fat retention was significantly greater in the 30°C treatment.

The results indicated the following points. (1) There was no difference in growth rate (as measured by weight gain) between 30°C heat-stressed birds and those given the same food intake at 20°C. (2) Heat-stressed and 20°C pair-fed birds had the same protein retention but the high-temperature birds had markedly greater fat retention. (3) It can therefore be stated that, in this experiment, the effect of heat stress on growth rate could be explained in terms of the direct effects of reduced food intake and reduced heat production.

Table. Effects of high temperature and pair-feeding on weight gain and energy and protein metabolism in growing broilers

	20°C	30°C	20°C	SED	P
	ad libitum	*ad libitum*	pair-fed	(26 df)	(ANOVA)
Weight gain (g/d)	55.0_{a}*	37.9_{b}	38.0_{b}	5.57	<0.05
AME intake (kJ/d)	1578_{a}	1197_{b}	1187_{b}	88.5	<0.001
Heat production (kJ/d)	1058_{a}	759_{b}	860_{c}	23.3	<0.001
Energy retention (kJ/d)	520_{a}	438_{ab}	327_{b}	74.6	<0.10
E retention as protein	371_{a}	283_{b}	275_{b}	29.7	<0.05
E retention as fat	149_{a}	155_{a}	52_{b}	53.6	>0.10
Water deposition (g/d)	34.8_{a}	21.4_{b}	24.5_{b}	3.77	<0.01

* Measurements in the same row not sharing a common subscript are different at the p<0.05 level.

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Free-choice feeding and energy metabolism of growing broilers at moderate (20°) and high (30°) ambient temperatures.

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Offering broiler chickens a choice between low- and high-protein diets has been tested several times as a way of alleviating the growth depression associated with high ambient temperature. The responses of the birds have been variable, as has the success of the technique if judged by production criteria (Cowan & Michie, 1977; Mastika & Cumming, 1987). In the present experiment, two dietary treatments (a complete compound diet and a choice between wheat meal and a high protein concentrate) were applied at each of two temperatures (20° and 30°). The complete diet contained 250 g crude protein (CP) and 11.6 MJ apparent metabolisable energy (AME) per kg. The choice-fed birds were offered wheat meal (110 g CP and 12.8 MJ AME/kg) in one feeder and a high protein mixture (460 g CP and 9.7 MJ AME/kg) in the other. The latter diet contained all the ingredients of the complete diet other than wheat meal. Eight 40-d-old male broilers were exposed individually to each treatment combination for a total of 6 d in open-circuit calorimeters (Lundy *et al.* 1978). The first 3 d were allowed for the birds to become accustomed to the experimental set-up and the measurements tabulated below are the means of the second 3 d period.

	20°		30°		Standard error
	Complete diet	Free choice	Complete diet	Free choice	of difference
Food intake (g/d)	151^{a}	124^{b}	117^{b}	115^{b}	6.2
Protein intake (g/d)	38^{a}	26^{bc}	30^{b}	22^{c}	1.8
Growth rate (g/d)	67^{a}	45^{b}	43^{b}	36^{b}	9.5
AME intake (kJ/d)	1692^{a}	1494^{b}	1370^{b}	1402^{b}	68.8
Heat production (kJ/d)	1162^{a}	1036^{b}	917^{c}	867^{c}	41.0
E retained as protein (kJ/d)	412^{a}	274^{bc}	325^{b}	244^{c}	24.0
E retained as fat (kJ/d)	119^{b}	184^{b}	128^{b}	291^{a}	39.0
Total energy (E) retained (kJ/d)	531^{a}	458^{a}	453^{a}	535^{a}	54.0

^{abc} Values in the same row not sharing a common superscript were significantly different, $P<0.05$ (ANOVA).

Free choice feeding gave lower food and protein intakes than the complete diet, especially at 20° (Table). Choice feeding also produced a lower rate of weight gain, as a consequence of the reduced total food intake and the reduced proportion of protein in the chosen combination of foods. The latter effect also led to a significant decrease in the quantity and proportion of energy retained as protein and contributed to a corresponding increase in the proportion of energy retained as fat. Energy retention as fat was influenced by three factors: energy intake, diet composition (CP:AME ratio) and ambient temperature. The greatest fat retention was, therefore, obtained in the birds on choice feeding and kept at 30°, which selected a lower CP:AME ratio and also had lower thermoregulatory heat production. The bird's "preferred" rate of protein growth may be lower than the target set by the poultry industry and attained by commercial compound diets, so choice feeding does not necessarily sustain maximum growth rate even at high temperature.

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Dietary modifications to increase food utilization and growth rate in broiler chickens exposed to high ambient temperature (30°).

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High ambient temperature decreases food intake and consequently growth rate in broiler chickens. It is usually assumed that the reduced food intake results firstly from a decrease in energy requirements for thermoregulation and secondly from the need to minimize heat stress by reducing the heat increment of feeding. However, there is an alternative hypothesis that high temperature reduces the ability of the alimentary canal to break down and propel food, possibly because of the redirection of blood flow to the periphery. An indication of this is that food passage rate is decreased by high ambient temperature (Savory, 1986). The present experiment aimed to separate the heat production and digestion effects of high temperature by measurement of heat production in birds fed on diets treated in ways which would be expected to affect the amount of work done by the alimentary tract. A further treatment was to increase dietary protein concentration, which would be expected to permit greater protein synthesis on reduced food intake. The control diet was a typical, coarsely ground mash containing 256 g crude protein (CP) and 11.6 MJ apparent metabolizable energy (AME) per kg. Diet 2 involved soaking the control diet freshly each day in twice its weight of water. For diet 3, the same feed was finely ground to pass a 1 mm screen before being mixed daily with twice its weight of water. To make up diet 4, NaCl (20 g/kg) was added to diet 3 (Na ion concentration is known to affect absorption). Diet 5 was a high-protein formulation (380 g CP and 11.4 MJ AME per kg), which was also ground and soaked. Ten individual Ross Broiler males were given each diet from 47 to 54 d of age, while continuously housed in open-circuit calorimeter chambers (Lundy *et al.* 1978) controlled at 30°. AME was measured by total collection.

	Diet 1 Control	Diet 2 Wetted (W)	Diet 3 W+ ground (G)	Diet 4 W+G+NaCl	Diet 5 W+G+ high protein	SED
Food intake (g DM/d)	84^{c}	107^{ab}	118^{a}	114^{ab}	104^{b}	6.3
Growth rate (g/d)	27^{c}	36^{bc}	50^{ab}	59^{a}	50^{ab}	7.8
AME intake (kJ/d)	1023^{c}	1235^{ab}	1377^{a}	1360^{a}	1190^{b}	75.3
Heat production (kJ/d)	798^{b}	892^{a}	946^{a}	923^{a}	884^{a}	41.6
Energy retention (kJ/d)	225^{b}	343^{ab}	431^{a}	437^{a}	307^{b}	58.5
Apparent metabolizability	0.72^{a}	0.69^{b}	0.69^{b}	0.72^{a}	0.64^{c}	0.01

^{abc} Mean values within a row not sharing a common superscript were significantly different, $P < 0.05$.

Wetting and grinding the diet led to increased food consumption, growth rate and energy retention (Table). Elevated NaCl content increased the metabolizability of the diet compared with the corresponding diet 3. High protein content (diet 5) produced a similar weight gain to the lower-protein diet 3, but with decreased energy retention. Heat production increased significantly with increased food intake and growth rate on the "processed" diets. The birds were, therefore, shown to have been able to increase food intake, growth rate and heat production when their diet was treated appropriately. The results were, accordingly, consistent with the explanation that gut function and not heat production places a limit on food consumption at 30°.

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