

AN EVALUATION OF
EFFECTIVE ENERGY IN THE
FORMULATION OF DIETS FOR LAYING HENS

MARION BELINDA YOUNG
B.Sc.AGRIC. NATAL

Submitted in partial fulfilment of
the requirements for
the degree of
MASTER OF SCIENCE IN AGRICULTURE

in the
Department of Animal Science and Poultry Science
PIETERMARITZBURG
1998

ABSTRACT

Emmans (1994) introduced a concept of energy utilisation applied across species, in which a heat increment in feeding is considered to be linearly related to five measurable quantities. Subtracting the heat increment of feeding from the metabolisable energy supplied defines the energy supply scale called effective energy.

Two trial protocols were developed and run in controlled environment chambers at hot and cold temperatures using laying hens in individual cages. The first trial tested the response of hens at temperatures of 18°C and 32°C to the dilution of a basal diet with ingredients selected to promote a heat increment in different manners, according to the effective energy system. Diluents were soy protein isolate, fishmeal, sunflower oil, husks and sugar and starch mix. Six diets were offered to Amberlink and Hyline Brown hens for two successive periods of six weeks at the two temperatures. Responses in performance and calculated heat production indicated that heat increments could be induced by particular diluents. These affected the response in laying performance of the birds, particularly at high environmental temperatures.

A second protocol tested the absolute value of the effective energy system by using Amberlink hens for three consecutive seven week periods at 30°C, 20°C and 30°C, respectively. High and low effective energy diets were formulated, and blended, and compared against commercial high and low density diets. The effective energy diets and the commercial diets were also offered as a choice to the hens. The data illustrate a marked linear response to the effective energy in the diet. High effective energy produced the same response as a high nutrient density at high temperatures. Highest performances in lay were achieved on the choice diets. The hens demonstrated the ability to change the proportion of the choice of the effective energy diets at the different temperatures.

Dynamic heat exchanges with the environment become significant, especially at higher temperatures in the thermally active hen. Effective energy considers this heat response,

and can assist in ameliorating the response of the laying hen to high environmental temperatures when incorporated into principles of feed formulation.

PREFACE

The experimental work described in this dissertation was carried out in the Department of Animal Science and Poultry Science, University of Natal, Pietermaritzburg, under the supervision of Professor R.M. Gous.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it has been duly acknowledged in the text.



M.B. YOUNG

LIST OF CONTENTS

	Page
1 INTRODUCTION	1
2 THE HEN	3
2.1 THE CONCEPT OF THERMAL NEUTRALITY	3
2.2 THE NATURE OF HEAT REGULATION	9
2.3 PARTITION OF FOOD ENERGY IN THE BODY: FLOW OF ORGANIC MATTER	16
2.4 FUNCTIONS WITHIN THE HEN	21
2.4.1 MAINTENANCE	21
2.4.2 GROWTH AND FATTENING	26
2.4.3 EGG PRODUCTION	27
2.5 NUTRITION : FEEDING THE HEN	32
2.6 THE EFFECTIVE ENERGY SYSTEM	34
3 EFFECTS OF ENVIRONMENTAL TEMPERATURE ON EGG PRODUCTION AND ENERGY BALANCE	38
3.1 INTRODUCTION	38
3.2 GENERAL	39
3.3 FEED INTAKE AND ME INTAKE	40
3.4 HEAT PRODUCTION	44
3.5 EGG PRODUCTION	47
3.6 BODY ENERGY	51

	Page
3.7 MEANS OF ALLEVIATING HEAT STRESS	52
3.8 CONCLUSIONS	59
4 RESPONSE OF LAYERS TO HEAT INCREMENT COMPONENTS IN THE DIET AT TWO ENVIRONMENTAL TEMPERATURES	 61
4.1 INTRODUCTION	61
4.2 MATERIALS AND METHOD	64
4.2.1 FACILITIES	64
4.2.2 BIRDS	68
4.2.3 TEMPERATURES	69
4.2.4 FEEDS	69
4.2.5 MEASUREMENTS	72
4.3 RESULTS	73
4.4 DISCUSSION	79
5 RESPONSE OF LAYING HENS TO EFFECTIVE ENERGY AT HIGH AND LOW ENVIRONMENTAL TEMPERATURES	 102
5.1 INTRODUCTION	102
5.2 MATERIALS AND METHOD	102
5.2.1 FACILITIES	102
5.2.2 BIRDS	103
5.2.3 TEMPERATURES	103

	Page
5.2.4 FEEDS	104
5.2.5 MEASUREMENTS	108
5.3 RESULTS	108
5.4 DISCUSSION	111
5.5 CONCLUSION	125
6 GENERAL DISCUSSION AND CONCLUSIONS	126
REFERENCES	134
APPENDIX	146

LIST OF FIGURES

Figure		Page
1.	Production Curve : Amberlink (Malan Chix, 1997)	1
2.	Simulated layer production curve (Emmans and Fisher, 1986)	3
3.	Relationship between heat production, evaporative heat loss, non-evaporative heat loss and deep body temperature in the homeotherm (after Mount, 1979)	7
4.	Sensible heat loss and evaporative heat loss at different environmental temperatures (Emmans, 1989)	8
5.	Heat loss in closely clipped sheep in relation to environmental temperature for all animals (Graham <i>et al.</i> in Blaxter, 1977)	12
6.	Partition of heat loss in the animal in Figure 5	12
7.	Diagrammatic representation of heat flow in the animal (Blaxter, 1977)	13
8.	Partition of food energy in the body (Macdonald, 1995)	18
9.	Gross chemical composition of food (Macdonald, 1995)	19
10.	Flow of organic matter in the monogastric above maintenance (Emmans, 1994)	20
11.	Energy balance at different feeding levels (Sykes, 1972)	31
12.	A scheme for predicting feed intake (Emmans and Oldham, 1988)	33
13.	Energy balance in layers at different environmental temperatures (after Marsden and Morris, 1987)	39
14.	Feed intake as a function of environmental temperature	40
15.	Metabolisable energy intake as a function of environmental temperature	42
16.	ME efficiency in relation to environmental temperature	43
17.	Heat production/kg metabolic body weight as a function of environmental temperature	45
18.	Feed intake and heat production at different environmental temperatures (after Li <i>et al.</i> , 1992)	46
19.	Energy balance as a function of ME intake (after Pesti, <i>et al.</i> , 1992)	47
20.	Egg energy as a function of environmental temperature	48
21.	Decline in rate of lay in relation to egg weight as temperature increases	49

Figure		Page
22.	Body energy change associated with increasing environmental temperature	51
23.	Relative changes in EE and ME intake as a function of feed intake	56
24.	Energy intake and its relation to egg output at environmental temperatures	57
25.	Internal dimensions of controlled environment chamber (after Paton, 1994)	64
26.	The relationship between heat production and egg output over 14 weeks of trial	89
27.	The relationship between egg output and EE intake	90
28.	Scheme of high and low effective energy diet blends	104
29.	Response in heat production to feed consumed by Amberlink hens	115
30.	Response in heat production to diet and feed intake by Amberlink hens	116
31.	Response in egg output to EE intake of Amberlink hens at 20°C and 30°C	117
32.	Response in bodyweight change to EE consumed by Amberlink hens at 20°C and 30°C	118

LIST OF PLATES

Plate I	Inputs and outputs within constraints determine the performance of the laying hen	59
Plate II	Controlled environments chambers at the University of Natal Research Farm	64
Plate III	Longitudinal view of the layer cages from the door of the chamber	65
Plate IV	Food and water supply to the hens within the chamber	66
Plate V	Electronic controller at the rear of the chambers	68

GLOSSARY OF TERMS

AFI	actual feed intake
AME	apparent metabolizable energy
AVE	available energy
B1	Blend 1 ($\frac{2}{3}$ low EE: $\frac{1}{3}$ high EE), experiment 2
B2	Blend 2 ($\frac{2}{3}$ high EE: $\frac{1}{3}$ low EE), experiment 2
BE	body energy
BMR	basal metabolic rate
BSL	basal diet, experiment 1
BW	body weight
CERU	controlled environment research unit
CF	crude fibre
CFI	constrained feed intake
CHO	carbohydrate
CP	crude protein
DCHO	digested carbohydrate
DCP	digestible crude protein
DE	digestible energy
DFI	desired feed intake
DFI _{EE}	desired feed intake for effective energy
DFI _{FLaa}	desired feed intake for the first limiting amino acid
DLIP	digested lipid
DM	dry matter
DOM	digested organic matter
DP	digested protein
EE	effective energy
EEC	effective energy content
EEi	effective energy intake
EEL	endogenous energy losses
EERQ	effective energy requirement
EHD	environmental heat demand

EHL	evaporative heat loss
EO	egg output
ER	energy retention
EW	egg weight
FE	faecal energy
FHP	fasting heat production
FI	feed intake
FIL	filler diet, experiment 1
FIS	fishmeal diet, experiment 1
FOM	faecal organic matter
FUN	fasting urinary nitrogen
GE	gross energy
H	high effective energy diet, experiment 2
H/L	high and low effective energy choice diet, experiment 2
HEX	heat of excretion
HI	heat increment
HIF	heat increment in feeding
HIM	heat increment at maintenance
HM	heat produced at maintenance
HP	heat production
H _{TN}	heat loss in a thermoneutral environment
L	low effective energy diet, experiment 2
LR	lipid retention
ME	metabolizable energy
MEi	metabolizable energy intake
MERQ	metabolizable energy requirement
MH	maintenance heat
MTHE	methane energy
N	Layer 95 diet, experiment 2
N/O	Layer 95 and Layer 125 choice diet, experiment 2
NE	net energy
O	Layer 125 diet, experiment 2

OIL	oil diet, experiment 1
OM	organic matter
OMM	organic matter at maintenance
PR	protein retention
RH	relative humidity
ROL	rate of lay
S/S	sugar/starch diet, experiment 1
SHL	sensible heat loss
SPI	soy protein isolate diet, experiment 1
T_A	ambient temperature
T_c	critical temperature
T_e	environmental temperature
TME	true metabolizable energy
TNZ	thermoneutral zone
UE	urinary energy
UN	urinary nitrogen
VR	ventilation rates

ACKNOWLEDGEMENTS

I have pleasure in expressing my sincere appreciation to the following persons and organizations for their contributions to this thesis.

The Foundation for Research Development for their financial support over many years,

The Protein Research Trust for their financial support,

Concord Trust for their financial support,

Columbit (Pty) Ltd and National Brands (Ltd) for the donation of soy protein isolate,

Gerry Emmans for numerous insights and perspectives on the work,

The technical staff at the Animal Science department for the analysis of material,

The staff at Ukulinga Research Farm for their assistance - "*ngiyabonga kakhulu ukungisiza kwakho*",

Neil Dominy for many *effective* discussions,

To those who have in some manner or means contributed to this work, and are no less appreciated,

To my Mom, for the tea, and for *effecting* its completion!

and particularly my supervisor, Prof. Gous, for his encouragement and advice and the willingness with which it was given.

*"Who was it that taught him knowledge or
showed him the path of understanding?"*

(Isaiah 40 v14)

CHAPTER ONE

INTRODUCTION

The aim of any hen in a productive environment is to describe certain production standards characteristic of her strain and type.

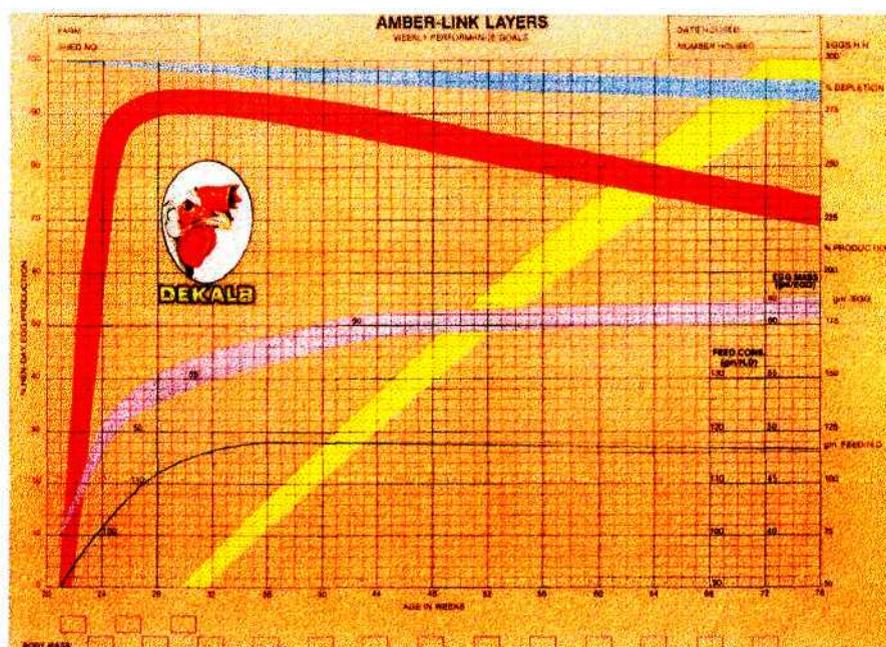


Figure 1 Production curve : Amberlink (Malan Chix, 1997).

These typical production (Figure 1) curves are provided by the breeding companies (eg. Lohmann Brown, Hyline Brown , Amberlink), as an indication of the potential to which they expect their stock to aspire. At any age, a certain number of eggs is expected from the flock to reflect, as a percentage, their current performance. This potential is however not always achieved. This reduction can be attributed to constraints, be they external or internal, which produce limits to performance. Examples are nutritional, environmental and genetic constraints. However, one cannot exclude other internal constraints from the equation. Indeed, the literature suggests an extensive interest in the explanation of external nature - how the environment can be manipulated, lighting programmes, feeding strategies, housing arrangements etc. Where one assumes the laying stock to have

advanced sufficiently genetically that low performance as a function of breed or strain can be excluded, the nature of internal heat production and digestive physiology can be investigated in an effort to explain the reduction in performance potential. Recent in its introduction to nutrition, the effective energy system of Emmans (1994) is highly relevant to the response of laying hens to high temperature, and it will be shown to be a truly invaluable aid to understanding the physiological mechanisms whereby the hens seek to partition their resources in response to a stress situation. An introduction to the evaluation of effective energy needs to describe the laying process accurately and performance standards where they are constrained by environmental factors - specifically that of environmental temperature. The hen's response in egg production to the environment and indeed any external circumstance, is usually reflected in feed intake (FI), as the literature will show, and it would be appropriate to consider explanations of the change in production in relation to nutritional adaptation.

An increase in nutrient density by changing the rations between winter and summer need not be the only alternative to maintaining performance in laying hens as the temperatures increase. It is the intention in this study to relate the hen's requirement for an increased nutrient intake to the balance that exists in the supply of nutrients. The Effective Energy system of Emmans (1994) offers an opportunity to study the relationship between feed ingredients and their interaction with the hen, by studying heat increments and heat productions in the laying hen. A keener sense of balance in feeding might promote the concept that there is scope for the provision of nutrients in such a manner that formulations are sensitive to the heat constraints that exist at high environmental temperatures.

'God grant me the serenity to accept the things I cannot change, the courage to change the things I can and the wisdom to know the difference'. Not strictly a poultry concept, but it may be a valuable tool instructing one to build upon a firm, well-researched foundation, while being prompted to expand horizons of thought to introduce innovative means of best mobilizing and realizing true potential where it exists.

CHAPTER TWO

THE HEN

2.1 THE CONCEPT OF THERMAL NEUTRALITY

The onset of lay occurs around 20 weeks of age in most commercial laying strains. It is well documented that the rearing regimes of the pullets will reflect greatly on the age at sexual maturity, and the subsequent production response during lay (Bolton, 1959; Kyarisiima, 1996). From the first egg, the pullet is expected to increase production to a level in excess of 90% at 25-26 weeks of age. Post-peak, a decline in production will occur. The function that describes this production curve is similar to that of a lactation curve (Figure 2), and is illustrated by the function describing the rate of yolk production:

$$y = a e^{-ct} \exp - [\exp(G_o - bt)]$$

where : y = rate of yolk production

t = time from first egg

a = a scalar

c = decay parameter

G_o = initial state parameter at $t=0$

b = growth rate parameter

(Emmans and Fisher, 1986)

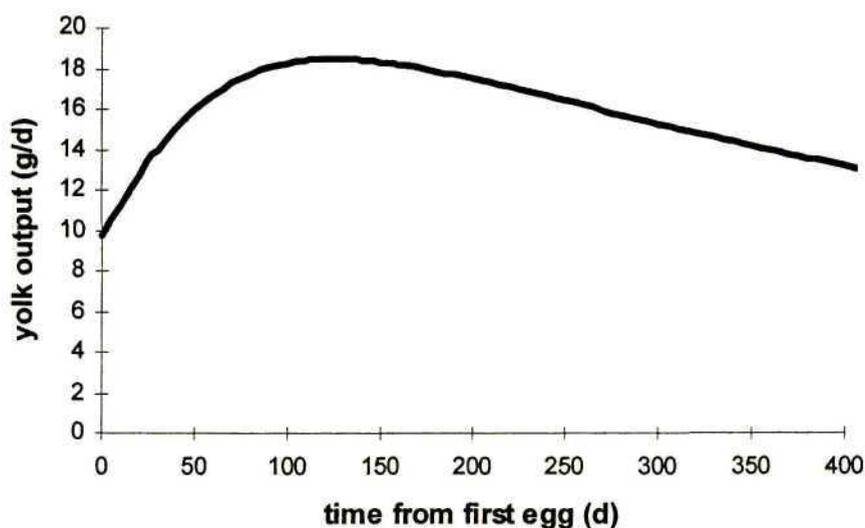


Figure 2 Simulated layer production curve (Emmans and Fisher, 1986).

The hen, as it exists, is a thermally active animal, with direct and indirect heat exchanges with the environment (Blaxter, 1977). It is necessary to define the environment to which the hen is exposed. The term 'environment' encompasses many factors such as relative humidity (RH), ventilation rates (VR), ammonia levels, as well as ambient temperature (T_A), though the term environmental temperature (T_E) is often used for comparative purposes. Emmans (1981) defines effective temperature as dry bulb temperature, radiant temperature (if different), air speed, and wet bulb temperature (only at high dry bulb temperatures), in order of importance. Payne (1967) and Cherry (1994) also define a concept of effective temperature by noting that the environmental temperatures experienced by the birds will depend on stocking densities, structural insulation, ventilation control. Climatic temperature is but a small part of the effective temperature concept. In defining a range of temperatures, a zone, where one expects the animal to be most comfortable, one is affording the objective measurement to a more subjective assessment, and it is indeed this quarrel that has precipitated re-definitions of the concept of thermal neutrality (Mount, 1974).

Of necessity, a zone should be defined by upper and lower bounds. The thermoneutral zone (TNZ) is usually described as a range of environmental temperatures within which the metabolic rate is a minimum and constant. Within this thermally neutral environment, the animal or man is expected to exhibit prescribed physiological and behavioural responses that indicate that it is within its preferred environment, and is able to be productive and unstressed within that range of temperatures. The lower limit of the zone is the lower critical temperature (T_{cl}), below which the metabolic rate must increase if the deep body temperature is to be maintained (Mount, 1974). The upper limits of the zone seem to be defined as the region beyond the increase in metabolic rate or the increase in evaporative heat loss (EHL). The relative bounds of this zone are important in so far as they define a 'region' where the animal's heat production is minimal, where its body temperature is normal and remains normal while sweating and panting do not occur. For this reason, it is often referred to as the zone of minimal thermoregulatory effort. This region provides the sensation of maximum comfort and is the animal's preferred thermal environment. The optimal thermal environment need not necessarily be synonymous

with the above, in that there may be an environment which better promotes health and production, and indeed, is economically optimal too.

'It seems that poultry investigators deny the existence of a TNZ' (Dr van Es in Mount, 1974). There is evidence to suggest a variability in the TNZ of birds. After the age of three weeks, birds become homeotherms and are capable of producing their own body heat, no longer relying on the application of an external heat source. There is variability in the TNZ, and this depends on the animal and the stage of acclimatization of the bird. The lower critical temperature changes with species of bird. Acclimatization has the effect of changing the lower T_C . Small birds have a narrower TNZ. Their surface area to volume ratio dictates that a drop in the T_E will drive them to enter hypothermia at a higher temperature as a result of their greater capacity to lose heat to the environment. Once birds have acclimatised to a particular environment, however, there no longer exists a TNZ where heat production is minimal; rather, their rate of heat production will depend on the T_E (Meltzer, 1987; Gous, 1993, pers. comm.).

An environment is effectively cold if the heat that the bird would have produced in a thermally neutral environment (equal to the ME intake - energy retention (ER) including eggs) is insufficient to meet the environmental heat demand. Whether the environment is cold or not depends not only on its physical characteristics (air temperature, radiant temperature, air velocity), but also on the bird and how it is fed.

In immature birds, the problem of predicting whether a given environment is effectively cold or not is particularly difficult since characteristics that are relevant - size, feathering, growth rate, body composition, rate of intake- all rapidly change with time. As the effects of feeds with particular nutrient to energy ratios are affected by whether the environment is cold or not, and if so, how cold, the prediction of a thermally neutral environment for a given case is of considerable practical importance. This problem has not been satisfactorily solved (Emmans and Fisher, 1986).

An idea of the ranges proposed in thermal neutral zones for poultry are the following :

- 16-28°C in chickens (Brody in Ahmad, 1974)
- 28-26°C, and 16.5-27.5°C for fasting birds (Waring, 1967).

Waring (1967) supports the notion of it being difficult to define a zone in birds, since feeding in essence reduces the lower T_c by virtue of a heat increment in feeding.

However, the birds will accommodate the change in T_E by changing their feed intake and by dropping the metabolic rate to create a new neutral zone. It would therefore be the researchers endeavour to define which temperatures would best suit the bird (the optimal thermal environment), where feed intake ensures the correct assimilation of nutrients for optimal production. This zone can also be defined in terms of a 'minimal material demand', where exchanges in water and food or heat are minimal because the bird is in a neutral state, neither requiring or giving off materials to the environment. The position of the zone and its limits depend on diet and activity.

Figure 3, a diagrammatic representation of the relationship between heat production, evaporative and non-evaporative heat loss and deep body temperature in the homeotherm, schematically depicts a region (CE on the figure) of minimal metabolism, bounded on either side by raising metabolic rate. There exists also a region of least thermoregulatory effort (CD) coinciding with minimal material demand, bounded by an increasing metabolic rate (cold) or increasing EHL (hot). The optimal, comfort or preferred temperature ranges need not necessarily coincide with the ranges described as neutral.

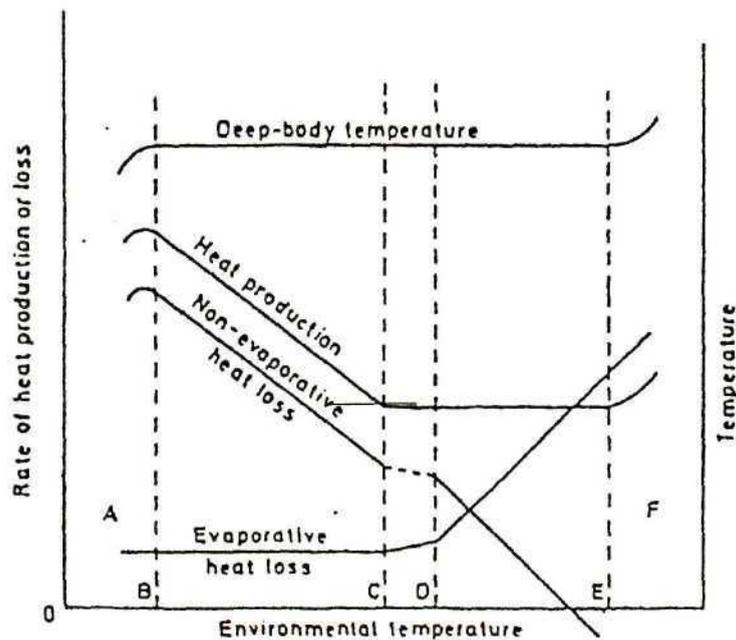


Figure 3 Relationship between heat production, EHL, non-evaporative heat loss and deep body temperature in the homeotherm (after Mount, 1979).

The region CD on the figure depicts a region of least thermoregulatory effort, where the bird's heat production is minimal. Marsden and Morris (1987) also identify this region in relation to a cubic model of heat production per unit metabolic body size with increasing temperature. A sigmoidal model would imply that the slope of the heat production curve was lower in the region of the 'comfort zone' than at temperatures higher or lower. This is consistent with the idea of least thermoregulatory effort in the TNZ as defined by Mount (1974).

In an environment where hotness varied spatially, the bird might be expected to move to an area where it was most comfortable, if that area existed. In an environment that does not provide such pockets of comfort, it is the environment that largely determines the rate at which the bird can lose and therefore, produce heat (Emmans, 1989). For a given bird in a given state the relationship between heat loss and T_E may be as shown in Figure 4.

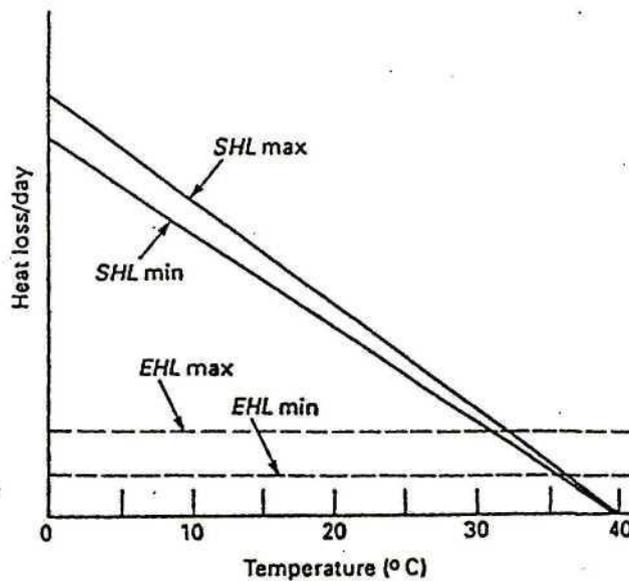


Figure 4 Sensible heat loss (SHL) and evaporative heat loss (EHL) at different T_E (Emmans, 1989).

Total heat loss is the sum of the sensible and evaporative losses. The value of the evaporative heat loss is constant at 20-30% of total heat loss (Romijn and Lokhorst, 1966), while the sensible heat loss is dependent on the environment, and decreases as a proportion of the total heat loss as the T_E increases. While Figure 4 in itself poses several questions, it also provides an alternate means to the description of the thermoneutral zone that we have been discussing. If we were to draw in a horizontal line at the value of the calculated maximum heat loss of the hen, we would intersect the slopes of the minimum and maximum sensible heat losses. The temperatures that correspond to these minimum and maximum heat losses define a range within which the bird is able to lose the heat that it produces.

The accuracy of this representation demands the following considerations :

- at what T_E is SHL zero?
- what is the value of the slope relating SHL_{min} to T_E , and in what ways does this vary between birds?
- what is the value of EHL_{min} and in what ways does this vary between birds?

- what is the ratio of SHL_{max} to SHL_{min} ?
- what is the ratio of EHL_{max} to EHL_{min} ? (Emmans, 1989).

Limits to performance might be summarised as environmental temperatures that are too hot, poor nutrient:energy ratios, both in combination, or an upper limit to the bird's capacity to lose heat in the given environment (Emmans, 1989).

2.2 THE NATURE OF HEAT REGULATION

Having explained that there exists a range of environmental temperature within which the bird would physiologically 'prefer' to be, it is appropriate to consider natural responses should the bird move outside that relative zone of neutrality.

Below the critical temperature, there exists the need to increase the basal metabolic rate to maintain deep body temperature (by definition). The main cause of the heat increment of feeding after maintenance is the energetic inefficiency of the reactions by which the nutrients are metabolised. The decrease in the lower critical temperature can also be attributed to feeding, where the energy provided in the diet provides the energy required in cold thermogenesis, in addition to the heat increment experienced in feeding (MacDonalds, 1995).

Above the TNZ, by definition, the rate of EHL increases. Having produced sufficient heat through feeding, activity and physiology below the temperatures where EHL becomes important, it is now appropriate to consider heat loss mechanisms available to the bird. At temperatures above the upper T_C , the temperature of incipient hyperthermia, the bird needs to dissipate heat, especially from the food processing organs. The liver generates most heat; a transfer of energy from the inside to the outside for loss to the environment is required (MacDonalds, 1995).

Transfer within the body is achieved by conduction, convection and counter current heat exchange mechanisms (Blaxter, 1977; Peguri *et al.*, 1993). Conduction is the direct

transfer of heat/energy from molecule to molecule, the rate depending on the thickness of the tissue and its thermal conductivity.

- fat 0.75
- skin 1.21
- muscle 1.80 kJ/m/hr/°C

The low conductivity of the fat layer makes it the primary concern under conditions of high T_E , and in birds acclimatised to higher temperatures, the fat layer is that much thinner (Blaxter, 1977). Convection is important over the TNZ where heat production is constant, and the blood acquires heat and transports it to the extremities where a temperature gradient will ensure direct exchange with the environment.

Heat loss from the body is sensible or evaporative. Sensible heat loss (SHL) is effected by means of conduction, convection and radiation, all of which depend to a large extent on the formation of a gradient between tissues and the external environment to which the heat can be transferred. This mechanism of heat loss is constant, such that no further increase in SHL can occur through an increase in the ambient temperature.

EHL, however, increases with ambient temperature. Also dependent on a gradient, evaporative losses rely on a humidity differential, in that moisture is evaporated more effectively off the surface of the skin or mouth (panting) where the ambient environment is dry and can facilitate evaporation. Having no sweat glands, the bird relies heavily on panting. Behavioural adaptations also include wetting of the wattles, holding wings away from the body to expose the featherless portion under the wing, consuming more water, less feed, and decreasing activity to a minimum (Peguri *et al.*, 1993; Meltzer, 1987). The higher rate of heat loss achieved through the skin would be dependent on the thickness of the skin layer and the rate of filtration of fluid from the blood capillaries at the surface of the skin. Adaptations also exist in feather loss or gain, and the accumulation of fat reserves as insulation (Peguri *et al.*, 1993). The nature of the diet to the largest extent motivates many of the behavioural and physiological adaptations.

It is important that the methods of temperature control within the bird be noted to

understand the influence of conditions outside the bird. The discussions that follow will largely assume knowledge of the mechanisms of heat loss while we more intimately discover the operations at work within the bird leading to productions of heat.

The problems of heat production and heat loss would largely be obviated were there not a system against which they work, and in this study, the antagonism is environmental temperature. Some assume ambient temperature under conditions of 50% RH (Mount, 1974), though the influence of humidity is undoubtedly significant as a purveyor of environmental temperature (with respect to differentials in heat loss). The ambient temperature tests their ability to adjust physiology, nutrition and behaviour as it provides an environmental constraint.

The study that follows will detail the energy balance within the laying bird, describing how gross energy (GE) ingested is partitioned within the bird, and how needs for maintenance, growth and feathers and egg production are met. The effective energy system will be introduced and discussed in detail, since the ramifications of this system explain more comprehensively the response of laying birds to T_E . Mapping the trends in ME intake, egg production, effective energy (EE), and feed intake (FI) to temperature and the trends in EE should elucidate dietary manipulations that exist to decrease heat production in layers such that performance need not be compromised as greatly as is currently the case at high T_E .

Effects of environmental factors on animal production are both direct and indirect, indirect in that they affect the amount of food available and direct in that they affect the energy needs of the animal. There exists an interaction between these two effects : the nutritional status affects the animal's response to its environment.

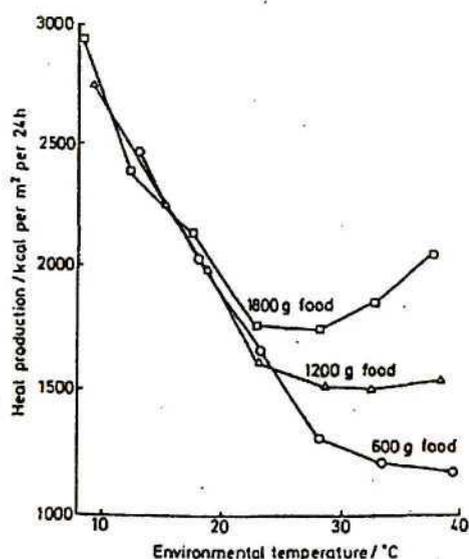


Figure 5 Heat loss in closely -clipped sheep in relation to T_E (for all animals) (Graham *et al.* in Blaxter, 1977).

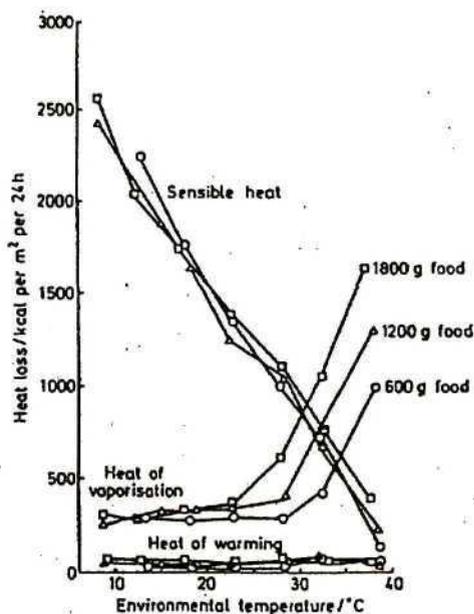


Figure 6 Partition of heat loss of the animal in Figure 5.

Figure 5 indicates that below 25°C, heat production is independent of the food supply, and is defined by the environment. In Figure 6, below 25°C, there is an invariant nature to the heat loss by sensible means (convection, conduction and radiation) which increases by a constant amount for each °C decrease in temperature. Also, EHL is invariant at low T_E such that heat production will be independent of food supply at low temperatures. This is applicable for all animals, and is similar in humans.

The lower critical temperature (T_C) is that temperature below which heat production must increase in response to the decrease in T_E .

$$T_C = T_R - 1/c(H - E')$$

where : $1/c$ = reciprocal of the negative slope
 = total insulation = resistance to heat flow
 placed between deep body and air.

T_R = rectal temperature

H = heat production

E' = minimal heat loss by evaporation

At temperatures below T_C , heat production increases by 'c' for every 1°C decrease in temperature.

$1/1/c$ = reciprocal of insulation = heat loss/°C = amount of ME which should be given for every °C that its environment is lower than the lower critical temperature to maintain productivity characteristic of lower temperatures.

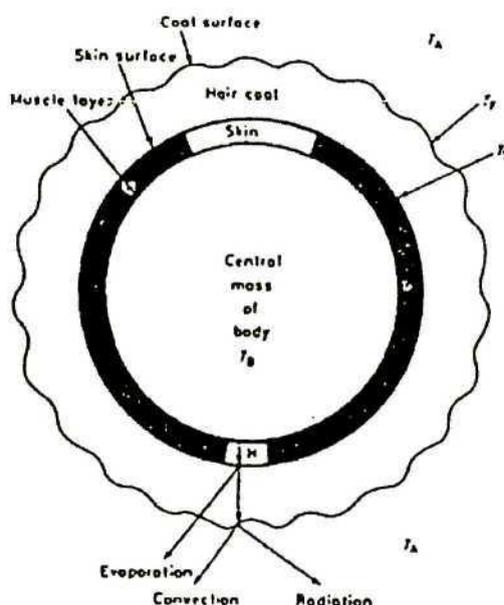


Figure 7 Diagrammatic representation of heat flow in the animal (Blaxter, 1977).

Heat is produced centrally and is convected to the surface of the body in the blood (Figure 7). The animal controls this flow by opening and closing the capillary network in the skin. At the skin surface, some heat is used to vaporize moisture and the rest is

transferred through the coat surface, where it is transferred to the environment by radiation and convection.

Total insulation or resistance to heat flow = tissue insulation, external insulation (coat, boundary layer of the coat surface, skin surface where there is no hair).

$$I_T = \text{tissue insulation} = \frac{(\text{rectal} - \text{skin temperature})}{\text{rate of heat loss/m}^2/\text{d}}$$

$$I_E = \text{external insulation} = \frac{(\text{temperature gradient : skin to air})}{\text{rate of SHL/m}^2/\text{d}}$$

$$I_E = I_F + I_A = \text{fleece insulation and air insulation.}$$

I_E is defined in terms of the temperature of the air, though this is not the sole index of the coldness of the environment - air movement, precipitation, and the short and long-wave radiation environment are also considerations.

Radiant heat losses are the most important heat losses below 30°C (Peguri *et al.*, 1993), with evaporation or conduction predominant above 35°C (Wilson in Deaton, 1983). The amount of radiation depends on the temperature of the radiant surface, the relative positions of the two surfaces and the radiating quality of the surface. Heat loss by convection above 30°C is aided by higher air velocities, the increase in heat loss being proportional to the square of the air velocity, but once T_A is above 41.5°C (body temperature), an increase in air velocity is detrimental (Bouchillon in Deaton, 1983). A ventilation rate of 0.0043m³/bird/second is recommended (Oluyemi *et al.* in Deaton, 1983).

Respiratory evaporation is a very important route of heat dissipation above 30°C, but panting in itself is a heat producing mechanism, and depends on the vapour pressure and the differential is therefore important, and this response is therefore less effective for layers held at a high humidity (Peguri *et al.*, 1993; Bouchillon in Deaton, 1983). Birds have no sweat glands and there is no active pumping of water onto the skin surface. Water loss from the skin is less than that loss from the respiratory surfaces. SHL is

inversely proportional to the T_E , such that when T_E increases, SHL decreases and EHL increases (Blaxter in Li *et al.*, 1992). A maximum amount of heat loss through sensible means requires an increase in EHL where possible. The increase in EHL at high T_E depends on respiratory evaporation, and this EHL increases at $T_E=31^\circ\text{C}$, accounting for 40% of total HP at 34°C . The limited capacity for EHL makes the birds susceptible to HP associated with feed intake (HIF) at high T_E . Therefore HIF add to the heat load above 28°C (Li *et al.*, 1992). HIF is not directly linked to thermoregulation at the lower T_A , but becomes an additional heat load at higher temperatures. Thus behavioural adaptations exist in an attempt to lose heat by any means possible.

Emmans and Fisher (1986) identified a general principle relating to attaining a “potential” production or output - the birds have a purpose which is to achieve their potential. This potential should be defined as the upper limit to the rate of protein production and the desired level of fatness, rather than the output of weight in the case of the immature bird. As a female in lay, the approach is more tentative and untested, suffice it to say that one is considering a manner in which it can be predicted how the animal would behave if nothing were to stop it, i.e. in a non-limiting environment, such that it attained the potential output.

This concept of potential production/output is central to the problem of nutritional theory, since the potential, once defined, presents no problem provided the stock are capable of reaching this level. But this level rarely concurs with a practical production potential determined by cost and the level of nutrient supply. However, the hens have a purpose, and under non-limiting conditions, would seek to realize the potential inherent to them.

It is appropriate now to discuss energy balance within the hen - what becomes of organic matter ingested, with associated heat production and inefficiency in utilization. Having understood how the hen is able to lose heat, we need to understand where the heat originates.

2.3 PARTITION OF FOOD ENERGY IN THE BODY : FLOW OF ORGANIC MATTER

Major organic nutrients are required as material for the construction of body tissue and the synthesis of product as well as sources of energy for work done by the animal. A unifying feature of these divergent functions is that they involve the transfer of energy -

- chemical to heat/mechanical energy (nutrients oxidised)
- chemical to chemical energy (body fat from carbohydrates).

The ability of food to supply energy determines its nutritive value.

The dietary energy consumed by the bird is required for four processes, those of body maintenance, body growth, feather growth and egg production. The growth in BW of the hens after the first egg is usually small and in relation to the resources required for maintenance and egg production, can probably be ignored, as in done by Emmans and Fisher (1986). Animals deprived of food continue to require energy for functions of body maintenance - functions immediately necessary for life that include mechanical work (essential muscular activity), chemical work (movement of substances against a concentration gradient) and for the synthesis of expended body constituents (enzymes and hormones). Starving animals catabolize body reserves of glycogen followed by fat and protein to meet these maintenance requirements. The primary demand on the food fed is meeting this body maintenance requirement to prevent the catabolism of body tissues, though no function has an absolute priority for food energy, not even maintenance.

When the chemical energy of the food is converted to the muscular and chemical work of maintenance, the animal does no work on its surroundings, and the energy used is converted to heat. Energy converted to heat is regarded as having been expended, as heat energy is useful only in the maintenance of body temperature. In a fasting animal, heat production is the energy of tissue catabolized and this constitutes the basal metabolism. Energy supplied by the food in excess of that required for maintenance is used in various forms of production.

The potential energy supplied to the animal by its diet is equal to the heat of combustion of that diet, since the maximum quantity of chemical energy which any substance can furnish for vital activity by its oxidation is measured by its heat of combustion (Armsby and Fries in Emmans, 1994). It is only the organic matter (OM) which yields energy on its combustion (Emmans, 1994), such that the potential energy supply is determined by the (rate of intake of OM) * (heat of combustion of OM). Of this potential energy, some is lost as OM in the faeces, urine and combustible gases (the latter being more relevant to ruminants. The energy lost in combustible gases in poultry is negligible, and is therefore ignored (Emmans and Fisher, 1986)).

Armsby in 1903 saw the rate of supply of metabolizable energy (ME) as the difference between the GE ingested and that lost in excretions.

$$ME_C \text{ (kJ/d)} = GE - (FE + UE + MTHE)$$

where : ME_C = classical ME
 GE = gross energy
 FE = faecal energy
 UE = urinary energy
 MTHE = methane energy

This ME value is 'apparent' (AME), but is usually adjusted to a 'true' (TME) value by a correction factor that accounts for endogenous energy losses (EEL) that occur regardless of the level of feeding.

$$TME \text{ (kJ/d)} = GE - (FE + UE - EEL)$$

ME_C is also corrected to a value that would have been expected to be observed had the rate of nitrogen retention been zero.

$$ME_N \text{ (kJ/d)} = ME_C - a(6.25*NR)$$

where : $a = 34.4 * 0.16 = 5.5 \text{ kJ/g}$

(Emmans and Fisher, 1986)

Apparently digested protein is either retained or catabolized and appears as nitrogen in various urinary compounds. The protein catabolized yields less energy than that burnt in a bomb calorimeter. Therefore one subtracts from the diet and the protein retained, the UE that would have resulted if all the digested protein had been catabolized.

$$ME = ME - x(\text{digestible CP retained})$$

where $x = (34.4 \times 0.16) \text{kJ/g}$

(Emmans and Fisher, 1986)

The main factors influencing the ME of food are those that affect its digestibility. The ME varies according to whether the amino acids supplied are retained or deaminated and the nitrogen excreted. Figure 8 illustrates this partitioning of the gross energy in organic matter in the body.

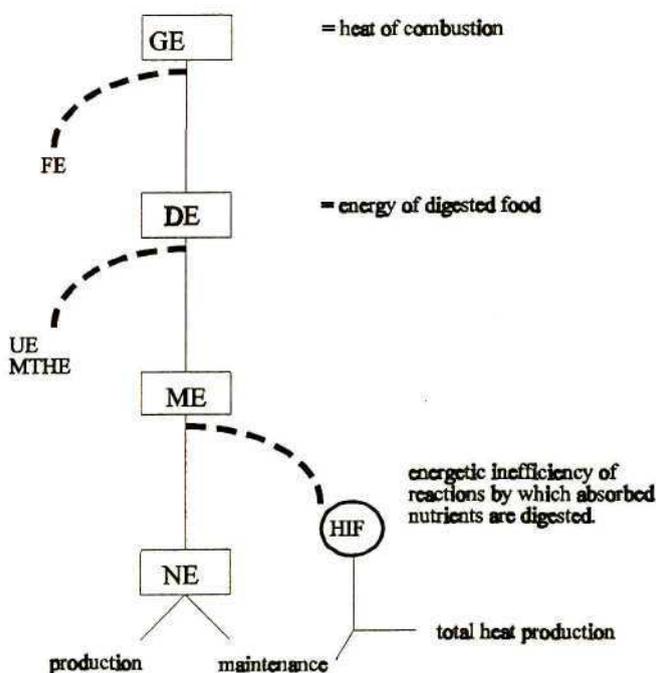


Figure 8 Partition of food energy in the body (MacDonald, 1995).

$NE_{\text{maintenance}}$ = to perform work within the body, leaving the body as heat.

$NE_{\text{growth, fattening, eggs}}$ = stored in the body or leaves the body as chemical energy.

Of the heat lost by the animal, the heat increment (HI) is truly waste energy and constitutes a direct tax on food energy. It is involved with the process of digestion ("specific dynamic action") (Scott in Deaton, 1983), the digestion and propulsion through the tract, where chemical energy is converted to heat energy. Movement across concentration gradients also requires energy expenditure of high energy phosphate bonds.

The efficiency of utilization of ME for maintenance is greater than for fattening. The efficiency of utilization of ME for productive purposes depends on the energetic efficiency of metabolic pathways involved in the synthesis of fat and protein from absorbed nutrients. (As a result, the heat increment of nutrients/feeds below maintenance does not represent the true inefficiency of energy conversion, but rather an inefficiency relative to that of the utilization of body reserves (body fat)). As FI increases, ME above the maintenance requirement has to bear the full cost of nutrient metabolism, leading to the lower value for the efficiency of utilization.

The organic matter ingested by the animal (Figure 9) yields by its oxidation, chemical energy which the animal uses to support the various activities of life (Armsby in Emmans, 1994). The OM ingested and the GE subsequently yielded follows a path within the body, where it is either catabolized, given off as heat production or retained in body tissue.

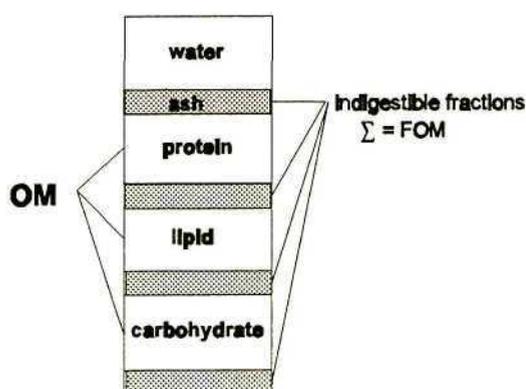


Figure 9 Gross chemical composition of food (MacDonald, 1995).

The contribution of carbohydrate to the overall energy balance of the bird is negligible and can therefore be ignored (Emmans and Fisher, 1986; Emmans, 1994).

Flow of OM in the monogastric above maintenance (Figure 10) elucidates several areas where heat is produced, contributing to a term, the heat increment (HI), a concept that will prove central to our discussion of the response of layers to environmental temperature.

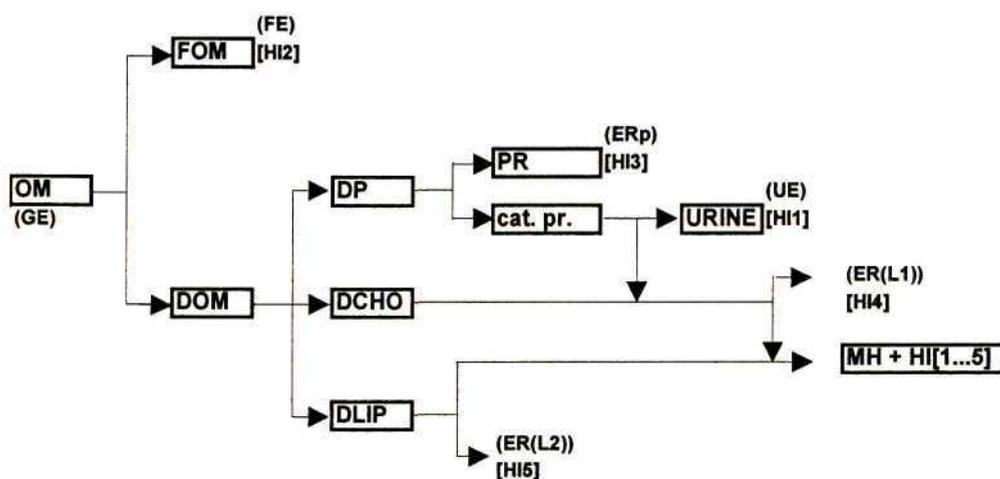


Figure 10 Flow of organic matter in the monogastric above maintenance (Emmans, 1994)

OM ingested is either digestible or it is not. That which is indigestible is excreted as faecal organic matter (FOM), with a concomitant production of heat in the formation of the faecal product. Of the OM digested (approximately 0.9 efficiency), the digested OM provided as protein, lipid and CHO, is partitioned to meet the various body requirements. Protein is either retained or catabolized, where nitrogen products appear in the urine, or deamination products of protein catabolism are used as precursors in the synthesis of body lipid. Digestible CHO generally contributes to the energy retained as lipid. The retention of body lipid follows either the direct path of lipid retention (i.e. lipid digested is deposited as fat), or it is broken down and re-synthesised along with precursors from CHO and protein components to form body lipid. The latter pathway is energetically a less efficient route, in that more energy is required in the catabolism and anabolism than

direct lipid retention. Indeed, this assertion is confirmed by the ARC (1981) where a value (kJ/g) for the production of 1kg lipid retention is expected to be lower where components of dietary lipid are directly incorporated into body lipid in monogastrics (Emmans, 1994). These values are 4.4 kJ/g and 16.4kJ/g of positive lipid retention where lipid is retained from lipid and non-lipid feed sources, respectively.

As indicated in Figure 10, heat increments are associated with positive retentions of lipid and protein, and with the production of FOM and urinary products. These heats of production, added to a maintenance heat quantity, reflect total heat produced in the monogastric above maintenance, and since these heats of production reflect energy that is given off and usurped from that supplied in the ME of the diet, it would make energetic sense that these losses be accounted for in an energy system.

Indeed, the effective energy (EE) system proposed by Emmans (1994) considers a heat increment of feeding (HIF) to be linearly related to five measurable quantities - those of UN, FOM and positive protein retention (PR). In ruminants, a value for methane energy is included and for positive lipid retention from dietary sources. In monogastrics, a value for positive lipid retention from dietary and non-dietary sources is important. It is my intention to fully describe the EE system in relation to the laying hen, but this necessitates our first having to examine the functions within the hen in detail in order to understand how this EE system might more closely describe the energy requirements of the hen.

2.4 FUNCTIONS WITHIN THE HEN

2.4.1 MAINTENANCE

In order to grow and produce eggs, birds must exist and continue to exist - this function of continuing to exist unchanged, is maintenance. Armsby and Moulton (1925) describe the concept of maintenance as one of conserving the existing status of the animal while doing no work and producing no products. There should be exact balance between the in- and outflow of ash, nitrogen, heat and energy, implying that there is neither loss nor

gain of protein, fat, carbohydrate or mineral matter. Strictly, there exists no translocation of material within the animal itself (Emmans and Fisher, 1986).

For maintenance purposes, the animal oxidises nutrients absorbed from its food principally to provide energy for work. If it is given no food, it obtains this energy mainly by the oxidation of body fat (Macdonald, 1995). Should food be supplied in quantities insufficient to provide for all maintenance demands, provision of ATP will be partially transferred from the body fatty acids to the nutrients absorbed. If the energy contained in these nutrients can be converted to ATP as efficiently as can those in body fat, no extra heat will be produced by the animal apart from that associated specifically with the consumption, digestion and absorption of food. (This includes the work of digestion, i.e. heat arising from the energy required in ingestion of food, its propulsion through the gut, absorption of nutrients and their transport in the tissues).

A strict definition of maintenance is $PR=LR=0$

where PR = rate of protein retention (g/d), LR = lipid retention (g/d)

such that energy retention, $ER = 0$ (Emmans, 1994).

At maintenance, the animal is fed such that its rates of protein and lipid retention are zero. To maintain this state, the animal requires a given rate of supply of resources, and there exists a general scaling rule for maintenance relating this rate of supply to the animal's characteristics and its state. The equation to predict maintenance heat (MH)=

$$MH = M_E \times P_M^{0.73} \times u \text{ MJ/d}$$

where : P_M = mature protein weight (kg)

$u = \frac{\text{body protein weight}}{\text{mature protein weight}} = \text{degree of maturity.}$

The value of M_E is constant over all values of P_M (genotype) and degree of maturity.

From experiments on several species, Emmans (1994), estimating M_E as $(MH/P_M^{0.73} \cdot u)$ MJ/unit day, found $M_E = 1.63$ MJ/unit d.

Maintenance is preferably defined at some low level of activity and in a thermoneutral environment. Thus activity and cold thermogenesis are considered separate functions and maintenance is independent of environment (Emmans and Fisher, 1986).

Since the metabolism of food ingested on a maintenance ration will not be metabolised as efficiently as would body fat due to the nature of the food ingredients, the animal fed at maintenance will be producing heat (HM, kJ/d), at a rate greater than the maintenance heat (MH, kJ/d). The heat increment of the maintenance diet, relative to MH, is

$$HIM \text{ (kJ/d)} = HM - MH$$

In broilers to market age, maintenance is a negligibly small proportion of the total requirement for nutrients, and is a relatively small proportion of the requirements of energy (Emmans and Fisher, 1986). Conversely in hens, even those producing at a high rate, maintenance energy is a major part of the total energy requirement and maintenance represents an appreciable proportion of the total requirement for protein and energy. The importance of estimating maintenance accurately is therefore more important in layers than it is in broilers.

Stewart and Hinkle (1959) in Payne (1967) showed that heat production (HP) can be broken into three parts :

- HP under basal conditions
- heat increment (HI) due to feeding
- an activity increment.

Armsby in 1903 defined these as a fasting heat production (FHP), a rate of HP with no food, and a heat increment of feeding (HIF), a rate of HP with food. The former depends only on the animal, being a function of the animal and its current state where the environment is thermally neutral and where activity is adjusted to some constant level.

HP in a fasting animal is a result of the catabolism of protein and lipid once the small stock of carbohydrate is depleted. The heat produced by the catabolism of lipid equals the heat of combustion of that lipid. Protein catabolism causes energy to appear in the urine as nitrogen-containing compounds such that the HP of protein catabolism is less than the heat of combustion of protein, therefore reducing the potential energy supplied by protein to the animal by the amount $(a \times PR)$. This excludes the potential energy that appears in the urine.

$$a = 5.5 \text{ kJ/g} = 34.4\text{kJ/g} * 0.16$$

where : 34.4kJ/g is the energy of N-compounds in the urine
 0.16 = amount of N in protein.

$$\text{FHP (kJ/d)} = (h_p - a) \cdot \text{PR} + h_l \cdot \text{LR}$$

where : PR and LR (g/d) are rates of loss of protein and lipid during the fast as positive quantities.

Some part of the FHP results from the synthesis and excretion of N-containing compounds in the urine. This heat of excretion (HEX, kJ/d) is at a rate of w_u (kJ/g N) in the urine.

$$\text{HEX (kJ/d)} = w_u \cdot \text{FUN}$$

(FUN = fasting urinary nitrogen)

and of the fasting heat production, that not due to HEX, is the MH.

$$\text{MH} = \text{FHP} - \text{HEX}$$

Fed a maintenance diet, there exists an excretion of urinary N (UN, g/d) which can be calculated from the digestible crude protein (DCP) in the organic matter.

$$0.16 \cdot \text{DCP} = \text{UN (g/d)}$$

Since at maintenance, $\text{PR} = 0$, all the protein ingested must be excreted. (This may also lead to the production of methane, which is negligible in poultry and is therefore ignored (Emmans and Fisher, 1986)). This leads us to conclude that the heat increment over maintenance heat (as a result of the animal eating a maintenance diet) is related to three

activities : consumption of organic matter, excretion of nitrogen, and the production of methane in ruminants (Emmans, 1974).

Therefore :

$$\text{HIM (kJ/d)} = k \cdot \text{OMM} + w_u \cdot \text{UN} + w_m \cdot \text{MTHE}$$

where : k = digestibility of organic matter

OMM = organic matter at maintenance

w_u = rate of production of heat associated with N-excretion

w_m = heat associated with the production of methane.

k varies with the digestibility (D , g/g) of the organic matter, such that digestibility, D , assumes a value between 0 and 1, so that k assumes a value between 0 and w_d kJ/g, varying linearly with D .

$$k = w_d \cdot (1-D)$$

$$k \cdot \text{OMM} = w_d \cdot (1-D) \cdot \text{OMM}$$

$$k \cdot \text{OMM} = w_d \cdot \text{FOM}$$

Therefore :

$$\text{HIM (kJ/d)} = w_d \cdot \text{FOM} + w_u \cdot \text{UN} + w_m \cdot \text{MTHE}$$

The amount of metabolizable energy (ME) required at maintenance = MH + HIM (kJ/d). HI of maintenance diets differ with digestible CP, increasing as the digestible CP increases, and also increasing as the digestibility of the diet decreases.

Positive retentions of protein and lipid can be considered in relation to the HI of their retention. The growth in BW of hens after laying the first egg is usually small, and in relation to the resources required for maintenance and egg production, can probably be ignored (Emmans and Fisher, 1986). However, in seeking to fully comprehend the processes within the hen and their contributions to a heat increment, a brief discussion on protein retention is included. It will be invaluable later when the EE system of Emmans (1994) is discussed and which includes this positive protein retention.

2.4.2 GROWTH AND FATTENING

A diet leading to positive retentions of protein and lipid at the rate PR and LR (g/d) will be associated with the production of FOM, UN and methane.

The HIF (kJ/d) relative to MH on a diet leading to positive retentions =
 $w_d \cdot \text{FOM} + w_u \cdot \text{UN} + w_m \cdot \text{MTHE} + w_p \cdot \text{PR} + w_l \cdot \text{LR}$

It is assumed that the latter two quantities are the only additional heats of production associated with diets leading to positive retentions of protein and lipid, those heats of production being proportional to the rates of protein and lipid retentions, with the constant of proportionality being w_p and w_l , respectively.

Armsby (1903) proposed HP to be the sum of the FHP and the HIF (kJ/d), such that :
 $\text{HP (kJ/d)} = \text{FHP} + \text{HI}$.

The theory of the conservation of energy states that energy cannot be created or destroyed, but is rather transferred from one form to another, such that energy intake must either be retained in the body or lost as heat.

$$\text{ME (kJ/d)} = \text{ER} + \text{H}$$

substituting :

$$\text{ME (kJ/d)} = \text{FHP} + \text{H} + w_p \cdot \text{PR} + w_l \cdot \text{LR}$$

$$\text{ME} = \text{ER} + \text{MH} + \text{HIF}$$

$$(\text{MH} = \text{FHP} + \text{HEX})$$

ER is a consequence of performance, MH depends on the kind of animal and state, which leads us to conclude that the ME required by a given animal in a given state to achieve a particular level of performance depends on the HIF.

2.4.3 EGG PRODUCTION

At thermoneutrality,

$$H \text{ (MJ/d)} = MH + HI(\text{excr.}) + HI(\text{def}) + HI(\text{fattening}) + HI(\text{eggs}) .$$

Hoffman *et al.* (1973) computes the heat of combustion of eggs (h_E) as 0.48kJ/kJ where the average energy content of eggs is 251kJ (Emmans, 1994).

$$HI(\text{egg production}) = 0.48 \times 251 = 120.48\text{kJ/d}$$

In hens, Armsby's equation becomes :

$$ME \text{ (MJ/d)} = FHP + h_p \cdot PR + h_i \cdot LR + h_E \cdot (EW \cdot ROL) + HI ,$$

(the energy in eggs is conventionally accepted as energy retained).

To this point, we have been considering functions of the laying hen, in isolation, from fasting, maintenance, growth and fattening to egg production, where the heat increments of each of these processes relies on the fact that the animal is being fed above maintenance, and there exists a concomitant increase in heat production of the bird as a result of feeding allowing the deposition of protein and lipid in the tissues, and leading to the excretion of UN and FOM. The increase in heat production in layers fed above maintenance is also due to the formation of eggs. (As previously noted, the retention of protein in layers after first egg is negligible, and therefore disregarded).

Thus :

$$H \text{ (MJ/d)} = MH + HI(\text{excretion}) + HI(\text{defecation}) + HI(\text{fattening}) + HI(\text{egg production})$$

In the formation of, for example, FOM, the amount of the FOM incurs an energy cost in its formation, w_d . As will be described more fully in a following section, w_d is a work function defined and quantified by Emmans (1994) to be constant across all species and diets, and having the value of 3.8MJ/kg FOM. It is the energy required in the performance of the work function.

Therefore the production of 17.09g of FOM will incur a HI of $17.09\text{g/d} \times 3.8\text{kJ/g} = 64.942\text{kJ/d}$

In the same way we seek to quantify a heat increment for egg production.

Sykes (1972) estimated the size of a component equated to the metabolic cost of egg formation from a regression equation from Byerly's equations predicting ME intake for layers. Many equations developed to describe energy requirements of layers and the energetic efficiency of laying hens include a factor for energy output in the form of eggs (Grinbergen in Sibbald, 1979). Sykes' estimate suggests a net efficiency of 50%, implying an inefficiency of 50%. Hoffman *et al.* (1973) in Emmans (notes) estimating the heat of egg production as 0.48kJ/kJ implies that 0.52kJ/kJ is lost as heat, supporting the notion that the metabolic cost of egg formation might be in the order of 52%.

Sibbald (1979) formulated a regression equation to predict the gross energy (GE) of avian eggs. While a more comprehensive equation would be preferred in terms of allometric relationships between egg components, yielding a more accurate GE prediction, Sibbald (1979) reported egg weight (EW, grams) as the most important independent variable in the equation :

$$\text{GE/egg (kcal)} = -19.70 + 1.810\text{EW(g)} \quad r^2=0.89$$

Sibbald does concede that this equation when applied, consistently under-estimates the reported values in other data sets by about 10% (mean difference = 8.3kcal/egg). Emmans (notes) notes that h_E - the heat of combustion of eggs - is not a constant value, presumably due to this variation between egg component proportions. Until we have accurately determined h_E , we will have to accept this inaccuracy.

Egg weight is a function of the yolk, albumen and shell weight, each of these being subject to change. The egg as a whole can be influenced by the albumen's disproportionate increases with age (Emmans, 1997, pers. comm.), or the yolk's being increased with the feeding of high levels of linoleic acid (March *et al.*, 1990). Effects of

calcium on the thickness of the shell (de Andrade *et al.*, 1976) might also account for divergent proportions in egg components. Thus without even really thinking, we can attribute changes in EW to nutrition, age, and undoubtedly to environment as it interacts with these factors. That these many influences were not considered in Sibbald's equation might well account for the discrepancies. This area of allometry between egg components is one which should receive more attention to arrive at an accurate predictor of egg energy.

However for the purposes of discussion, the equation will suffice.

$$GE/\text{egg (kcal)} = -19.70 + 1.810 \times EW(\text{g})$$

With the equation :

$$H = MH + HI(\text{excretion}) + HI(\text{defecation}) + HI(\text{fattening}) + HI(\text{egg production}) \text{ MJ/d}$$

This value is best illustrated through the calculation of it, which will also elucidate where in the calculation the above discrepancies can be highlighted and elucidated through subsequent research. Emmans (1994, notes) uses the data of Hoffman *et al.* (1973) where the following mean values were found across three experiments.

$$H = 779 \text{ kJ/d}$$

$$UN = 1.33 \text{ g/d}$$

$$FE = 393 \text{ kJ/d} \Rightarrow 393/23 \text{ kJ/g} = 17.09 \text{ g FOM}$$

$$HI(\text{excretion}) = 1.33 \times 29.2 = 38.836 \text{ kJ}$$

$$HI(\text{defecation}) = 17.09 \times 3.8 = 64.94 \text{ kJ}$$

$$HI(\text{fattening}) = 0.38 \text{ g/d LR} \times 16.4 \text{ kJ/g} = \underline{6.232 \text{ kJ}}$$

$$110.008 \text{ kJ}$$

$$MH = 1630 \cdot P_M^{0.73} \cdot u \text{ kJ/d}$$

assuming 1.48kg hen, BP= 0.15*BW

(Emmans and Fisher, 1986)

$$MH = 1630(0.15 \times 1.48)^{0.73}$$

$$= 543.28 \text{ kJ/d}$$

$$H = MH + HI(\text{excretion}) + HI(\text{defecation}) + HI(\text{fattening}) + HI(\text{egg production}) \text{ MJ/d}$$

$$HI(\text{eggs}) = 779 - 543.28 - 38.836 - 64.94 - 6.232 \text{ kJ/d}$$

$$HI(\text{eggs}) = 125.71 \text{ kJ}$$

$$GE(\text{kcal/d}) = -82.42 + 7.57 * EW(\text{g})$$

Assuming an EW = 44g, GE (kcal) = 250.79kJ of egg.

Assuming 50kJ/kJ as an energy cost of egg formation,

$$250.79 \text{ kJ of egg} * 0.5 = 125.4 \text{ kJ}$$

Half of the energy in the egg consists of heat produced in the formation of the egg. This value of 125.4kJ agrees conveniently with the 125.7kJ estimated from the top equation as the HI of egg production.

Thus it is possible to quantify the HI of egg production, and to view it as an important (16% contribution to total heat produced) component of heat increment in the bird. The relevance and importance of this hypothetical situation/bird is elucidated in the section to follow - that of the Effective Energy system.

This HI in egg production allows us to define more accurately the energy requirement of the laying hen, to be able to feed her more closely to that requirement in order that we might prevent her energy intake from becoming a limiting factor in egg production at high environmental temperatures. Sykes (1972) identified also that under voluntary *ad lib.* feeding, layers consume more energy than required for BW maintenance and egg production. Excess energy is partitioned to fat, increasing BW and thereby increasing the maintenance requirement. This represents an inefficiency in the utilization of energy which could be avoided if intake could be regulated to meet economic requirements for energy more precisely.

An important leap in logic to make now is to relate what we have gathered about the mechanisms within the hen, to the practical situation of feeding the hen. As Emmans and

Fisher (1986) would put it - "I am going to feed a group of birds of a given genotype in a given environment in a this way : what will happen?". The aim of the science of nutrition is to provide an answer to this question.

Energy balance in relation to egg production - Figure 11 illustrates the contributions to heat production made by the feed (Sykes, 1977).

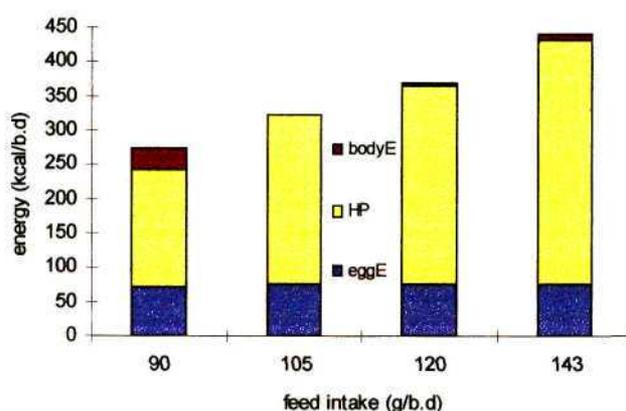


Figure 11 Energy balance at different feeding levels (Sykes, 1972).

Previously the statement was made that the ME required by a given animal in a given state to attain a particular standard of performance is determined by the HIF. Figure 11 demonstrates the decline in HP as the FI is decreased (*ceteris paribus*). Egg energy is constant, and body energy changes very little, but HP decreases substantially. This is a direct reflection on the amount of food consumed.

A variety of sources indicate that feed costs constitute 60-70% of overheads incurred in the production of eggs (Luiting, 1991; Emmans, 1977). It would be advantageous therefore if the extent to which the ME supplied in the diet is wasted, is reduced by any means possible. Sykes (1972) identified the inefficiency of utilization of energy. He considered mechanisms whereby intake could be regulated to meet economic requirements for energy more precisely. Quantitative feed restrictions have not been successful in laying stock (Sykes, 1972), and energy restrictions have therefore been investigated.

Consider, however, a new energy system altogether. Emmans (1994) has introduced a concept of energy utilization applied across species - the Effective Energy (EE) system. It is through this system that we hope to approximate more effectively the properties of the animal and feed that define its requirements for energy. This will lead to better application of energy in feeding systems.

2.5 NUTRITION : FEEDING THE HEN

"I am going to feed a group of birds in a given environment in this way - what will happen?"

Similar to the old dilemma of the chicken and the egg - does the animal grow because it eats, or eat because it grows? This is solved by assuming that it seeks to eat because it seeks to grow!

A desired feed intake (DFI) = $\frac{\text{requirement for the first limiting resource in the feed}}{\text{concentration of this first limiting resource in the feed}}$.

(Emmans and Fisher, 1986)

By definition then, if the feed intake (FI) is sufficient to meet the demand for its first-limiting nutrient, all others will be provided in excess of requirement. The DFI = highest intake that will be found by a given bird in a given state on a defined feed. However, constraints exist in the form of the environment or gut capacity, and the bird may not physiologically be able to maintain intake at the level of the DFI. The difference between the DFI and the constrained FI (CFI) is the actual FI (AFI), this being a function of the animal, its feed and the environmental interaction. These concepts can be illustrated in Figure 12.

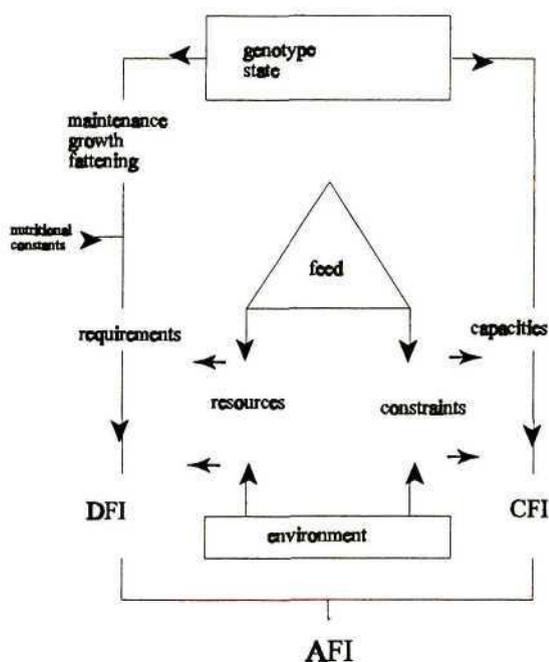


Figure 12 A scheme for predicting FI (after Emmans and Oldham, 1988).

The nutritional value of a feeding stuff to a given animal is defined by the quantity of energy and other nutrients that it yields. There exist non-nutritional properties that are important when using particular feeding ingredients, supporting the notion that there is more to feeding than nutrition!

It is this assertion that precedes our discussion on EE - the properties of feed ingredients affecting their inclusion in rations.

2.6 THE EFFECTIVE ENERGY SYSTEM

It is the opinion of the author that any feeding strategy proposed should not compromise on conventional wisdom in the sense that the hundreds of years in the nutrition of farm livestock has left some well-embedded doctrine. While this should not cloud our judgement as we plough forwards in the quest for more knowledge and the improvement of our feeding systems, there are still 'pearls' that should complement and augment our current and improving knowledge of feeding systems. In the formulation of diets, practice and animal responses have taught that an upper level of inclusion of, for example, 12% oil in a practical chicken diet, and 10% for fishmeal should be effected. Therefore, we should seek to preserve knowledge where it is practically, economically and physiologically possible.

The EE system of Emmans is based on the assumption that work done above maintenance in the animal can be defined by five functions : excretion, defecation, fattening, growth and fermentation (Emmans, 1994). The heat increment of feeding is considered to be linearly related to five measurable quantities - with their heat increments in parentheses.

- UN (w_u kJ/g)
- FOM (w_d kJ/g)
- positive PR (w_p kJ/g)
- methane (w_m kJ/kJ)
- positive LR (w_l kJ/g)

In ruminants the methane contribution is important, though not in poultry as mentioned previously. The positive retentions of lipid in monogastrics have to be distinguished between lipid from non-lipid and lipid sources, their respective heat increments being w_l and w_{ll} kJ/g.

Emmans has quantified these values of heat increment through extensive research, and the result is six work functions that quantify the amount of ME required per unit of each

function, these values being constant across all animals and diets.

- $w_u = 29.2 \text{ kJ/g}$
- $w_d = 3.8 \text{ kJ/g}$
- $w_p = 36.5 \text{ kJ/g}$
- $w_m = 0.616 \text{ kJ/kJ}$
- $w_l = 16.4 \text{ kJ/g}$
- $w_{ll} = 4.4 \text{ kJ/g}$

These work functions with the values for the heat of combustion of protein and lipid at 23.8 and 39.6 kJ/g respectively, allow an EE scale to be defined.

The EE scale is defined where the HIF is subtracted off the ME supplied by the diet.

As defined before, $ME \text{ (kJ/d)} = ER + MH + HIF$ [conservation of energy]

HIF can further be broken down as :

$$HIM \text{ (kJ/d)} = w_u \cdot UN + w_d \cdot FOM + w_m \cdot MTHE$$

$$HIF2 \text{ (kJ/d)} = w_p \cdot PR + w_l \cdot LR$$

$$UN = 0.16(DCP - PR)$$

$$HIM \text{ (kJ/d)} = w_u \cdot 0.16(DCP - PR) + w_d \cdot FOM + w_m \cdot MTHE$$

At maintenance, $PR=0$,

$$HIM \text{ (kJ/d)} = w_u \cdot 0.16DCP + w_d \cdot FOM + w_m \cdot MTHE$$

subtracting this HIM from the ME in the diet leaves the energy supply scale :
EFFECTIVE ENERGY (EE; kJ/d):

$$EE \text{ (kJ/d)} = ME - [w_u \cdot 0.16DCP + w_d \cdot FOM + w_m \cdot MTHE].$$

The requirement for EE (EERQ; kJ/d) is the sum of the MH, and the HI of the positive protein and lipid retentions :

$$\text{EERQ (kJ/d)} = \text{MH} + \text{PR}((h_p - a) + (w_p - 0.16.w_u)) + \text{LR}(h_1 + w_1)$$

giving

$$\text{EERQ (kJ/d)} = \text{MH} + 50\text{PR} + 56\text{LR}$$

EERQ defines the effective energy requirement of the animal, i.e. that energy that needs to be supplied to the animal in order that it achieves a particular performance. In the hen, we have already noted that the growth of the bird is not a major consideration, which is why we have another equation for egg production. Emmans (1994) noted that the system could be extended to deal with pregnancy, lactation and egg production where the heat increments of these components are quantified. He later set out in his notes, the equation for the ME of laying hens:

$$\text{EERQ (kJ/d) HENS} = \text{MH} + 8.8\text{EO}$$

where EO = egg output (g/d) and 8.8kJ/g is the effective energy required/g egg .

Another facet of this EE system, is the tabulation of the EE values of feed ingredients through the use of equations set out by Emmans (1994). This enables the EE supplied by any diet to be calculated to allow comparisons between diets of the amount of net energy available for production that can be supplied by the diet.

The University of Natal's feed formulation package, Winfeed1.1 (developed by Gous and Goedeke, 1996), uses the equation that follows to describe the EE of a feed by the additive property of the EE values for each of the feed ingredients used.

$$\text{EE (kJ/g)} = \text{ME} - w_d \cdot \text{FOM} - 0.16.w_u \cdot \text{DCP} + 3.6 \cdot \text{DCL}$$

where : ME = metabolizable energy content of the feed

DCP = digestible crude protein

DCL = digestible crude lipid

This also allows us to be selective in choosing ingredients. From the equation it is evident that a high proportion of oil in the diet will increase the EE of the diet by virtue of its low HI, in that it is a highly combustible energy source. This relates to the

"conventional wisdom" discussed earlier, since the temptation would be to include high levels of fat to reduce the EE and therefore the HIF. This would obviously mean a diet that is unrepresentable to the birds.

However, it should be evident that this EE system is a more sensitive measure of the energy required and supplied by the diet. Both perspectives alter the ME somewhat, merely by accounting for functions that are occurring in the body. It would therefore be wise to attempt to implement this practically as far as possible in that it might see due reward. From the concept of the energy system, it would assume to be true that more closely approximating the bird's requirements and energy supply would see an appreciable decline in superfluous heat production, if only by virtue of a more accurate energy assessment of the animal. This would be advantageous at high temperature, where the likes of Sykes (1972) have already considered energy restrictions in maintaining performance.

This brings us to another important ramification of the system, that being that it assumes thermal neutrality. Emmans (1994) has assumed that the environment is thermally neutral in his EE scale. In a cold environment, the animal is seeking to increase its heat load where the ME supply and the heat production within the body are inadequate to meet the external heat demand of the bird. A wasteful system, as one would consider the ME system in comparison, would provide the benefit of superfluous heat production which would be to the advantage of birds in a cold environment.

This system will be the subject of the following discussion, which reviews the effects of environmental temperature on egg production and energy balance in the laying bird. The EE system will elucidate some useful energy saving ideas in our quest to remove the constraints to production at high environmental temperatures.

CHAPTER THREE

EFFECTS OF ENVIRONMENTAL TEMPERATURE ON EGG PRODUCTION
AND ENERGY BALANCE

3.1 INTRODUCTION

A review of Marsden and Morris (1987) has been very instructive in the construction of a database from which it is possible to evaluate the effects of environmental temperature on the food intake (FI), egg output (EO) and energy balance in laying pullets. The data sets used by Marsden and Morris have been reviewed and adapted to suit the purposes of the present discussion, with the conclusions set out in this review being augmented by other suitable data sets. Those papers deemed suitable provided information as to the nature of the dietary treatments in each of the temperature treatments, and were restricted to White Leghorns, brown birds having a lower maintenance energy requirement per kg or per $\text{kg}^{0.75}$ (Emmans, 1974). The most exciting part of the investigation involved the re-formulation of the diets in an endeavour to map the trends as affected by T_E , and to test a proposition that this response to temperature might somehow relate to the EE of the diet.

All of the figures presented below are extracted from the spreadsheet (Appendix I), where the data sets are noted. Where necessary, the regression equations of Marsden and Morris are used to illustrate the trend. It is not the purpose to embark on a complicated statistical evaluation of all the data used, assuming that the data were mainly those of Marsden and Morris, and that they had done this adequately. The intention is to postulate the involvement of EE in the response to temperature and therefore trends are indicated, the compound evaluation of which is bound to be the subject of much further, more profound investigation.

3.2 GENERAL

General trends of the effects of an increase in the T_E on the performance of laying hens on which the literature concur, are the following :

- reduction in FI (Mueller in Deaton, 1983; Njoya, 1995; Davis, 1973; Schnepel in Deaton, 1983; Marsden *et al.*, 1973)
- reduction in EW (Mueller in Deaton, 1983; Njoya 1995)
- decreased shell quality (Mueller in Deaton, 1983)
- reduced egg production (Mueller in Deaton, 1983; Njoya, 1995)
- increase in mortality (Mueller in Deaton, 1983)
- decrease in BW gain (Njoya, 1995).

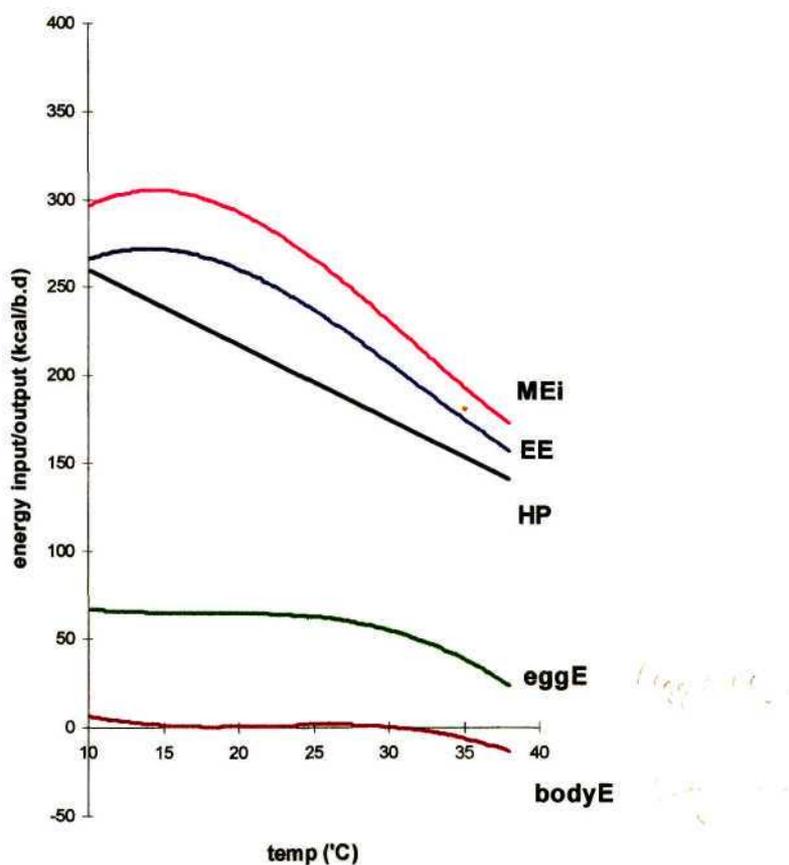


Figure 13 Energy balance in layers at different T_E (after Marsden and Morris, 1987, appendix data).

Figure 13 depicts graphically the response of the hen to rising T_E . The trends that are apparent in this figure, have been constructed from the data, and are explained more fully in subsequent sections.

3.3 FEED INTAKE and ME INTAKE

Many of the responses to T_E can be attributed to their effects through the limitation of FI (Marsden, 1987; Njoya, 1995). FI experiences a curvilinear decline as the T_E increases (Marsden, 1987; Peguri and Coon, 1992; Davis, 1973; Njoya, 1995; Marsden *et al.*, 1973) (Figure 14).

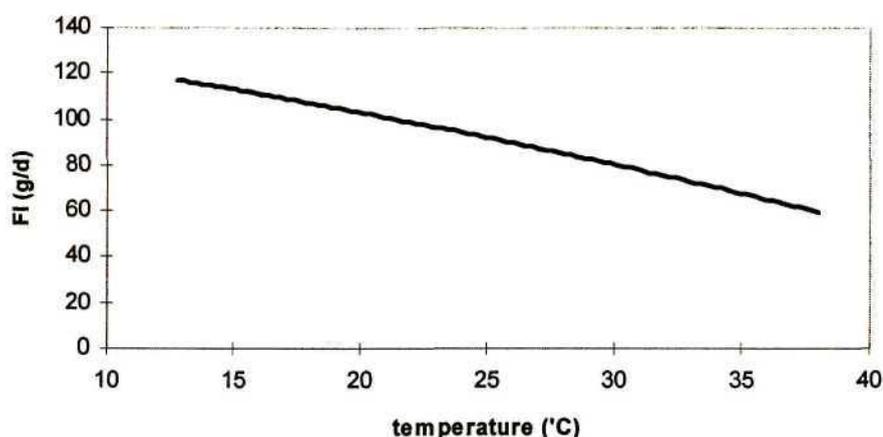


Figure 14 FI as a function of T_E (appendix data)

A primary response of the birds therefore is to stop eating when the T_E approaches body temperature. As a consequence, all concentrations of nutrients ought to be adjusted to this new FI, in order that the actual intake of these nutrients equal the desired intake of the nutrients, as we noted previously (Emmans and Oldham, 1988; Njoya, 1995; Marsden *et al.*, 1973; Payne, 1966; Payne, 1967). An important corollary to this is the balance of the nutriment supplied, in that increases in feed intake are apparent where diets are inadequate in respect of nutrient/s (Bolton, 1959; Morris and Blackburn, 1982). Emmans (1981) calls "animals eating for energy" a myth, because an animal will be

eating for the first limiting nutrient. In attempting to mediate a temperature-related decline in feed intake, the situation of heat stress can be exacerbated where the feed prompts the bird for a higher intake and the environment denies that.

Efficient diet formulation will depend on the accurate prediction of energy intake over a wide temperature range (Marsden and Morris, 1987). The desired FI is defined by the requirement for the first-limiting nutrient over its concentration in the diet. By definition therefore, if FI is sufficient to meet the demand for the first limiting nutrient, then all others are provided in excess of requirement. Working on this assumption, it would assume to be true that the first-limiting nutrient at high environmental temperature would be energy. The constraints in temperature rely on the ability to lose the energy consumed either through the formation of product or loss to the environment.

Many equations exist to predict the ME intake of layers at T_E , and limitations in their application exist where curvilinear effects and interaction are ignored, as in earlier prediction equations (Pesti *et al.*, 1992). The description of ME intake is significantly improved by the addition of a cubic term (Marsden and Morris, 1987), indicating that as T_E increases much above 25°C, there is a more rapid decrease in the rate of decrease in ME intake. Thus energy intake will become restrictive to production above this temperature. 'Comfort' ranges for optimal layer performance are suggested, and 23°C to 24°C seems to be optimum in promoting sustained performance (Marsden and Morris, 1987). This temperature would be within the thermoneutral zone of the bird, where the intake would still be sustainable through adequate heat loss.

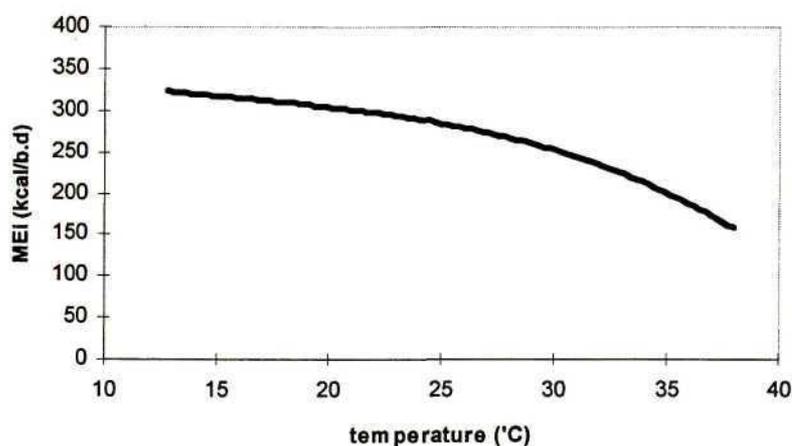


Figure 15 ME intake as a function of T_E (appendix data)

The trend is for a lower ME requirement with increasing T_E (Sykes, 1972; Davis *et al.*, 1973) (Figure 15). Davis *et al.* (1973) quantifies this as 2.7kcal ME/b.d or 1.2kcal/kg^{0.75}/d for each °C rise in temperature. The conventional explanation of the fall in ME intake with T_E is that the energy requirement for maintenance is reduced, since there is no reason to expect that the efficiency of egg formation is altered by T_E . Less energy is required to keep the body warm and physical activities are reduced to a minimum, except panting (Scot in Deaton, 1983). Measurements of maintenance ME intake should be parallel to total ME intake, but lower by the additional energy cost of egg production (Sykes, 1977). The total energy requirement therefore decreases linearly with rising T_E and FI is adjusted accordingly to maintain energy balance. Ingestion of the food causes heat production in the animal due to 'specific dynamic action' of the food, and nutritionally unbalanced diets will cause production of internal heat that is intolerable. Diets unbalanced in protein, amino acids, or vitamins produce a larger HI than do perfectly balanced diets (Scot in Deaton, 1983). If T_E continued to rise, the bird would become hyperthermal and HP would increase, but acclimatization means that this T_E must be greater than 35°C (Davis *et al.*, 1973).

Layers housed at high T_E have been shown to expend less of their ME for the maintenance of constant body temperature and appear to have the option of shifting the energy savings to production or improved feed efficiency (NRC in Peguri & Coon, 1992). At 31.1°C, layers have a significantly improved feed conversion and lower maintenance requirements than layers housed at cooler temperatures, whereas hens at 12.8 and 23.9°C need a higher % of dietary energy for maintenance. Dietary ME efficiency expressed as grams of egg mass per kcal ME intake is significantly improved with higher temperatures (Peguri and Coon, 1992) (Figure 16).

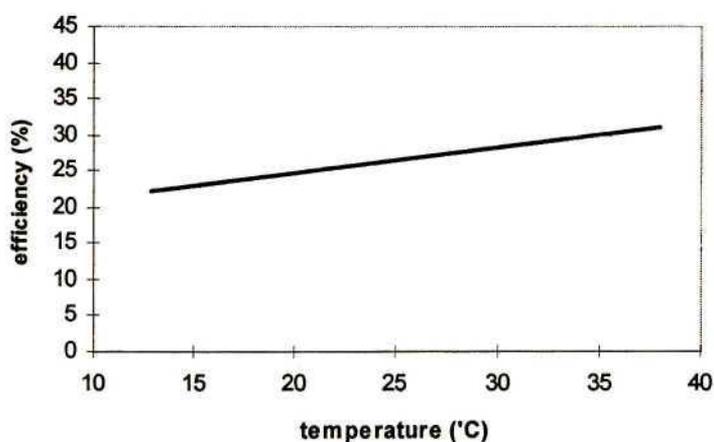


Figure 16 ME efficiency in relation to T_E (appendix data)

Davis (1973) made the assertion that the T_E above which the birds would become hyperthermic (the upper T_C), could be adjusted by acclimatization. The literature conflicts in relation to this period of acclimatization. Jones (in Deaton, 1983) noted that when hens were first exposed to heat stress, feed consumption declined immediately but only one day was required to re-establish FI when the birds were acclimated to 21°C before being exposed to 35°C. Reece (in Deaton, 1983) considered it to take a period of three days, though the process of dietary adaptation could take 3 to 4 weeks (Sykes, 1977). Production responses during lay are affected by the T_E experienced during growth and lay (Kyarisiima *et al.*, 1996), casting some doubt as to the persistency of an acclimatization response acquired in a previous period of growth.

This information becomes important in the design of experiments. One should hesitate to base conclusions on a short period of study during which responses have not stabilised - this stability being indicative of acclimatization. This sentiment is echoed by Gous (1986). Experiments such as those of Romijn and Lokhorst (1966) earn validity through the use of a single animal over a period of months. In terms of experimental design, accuracy is not compromised though the use of very few animals since the experimental material is harvested on a single animal over a long period of time, and repeated extensively. Experiments should include a period during which acclimatization can occur, such that responses can stabilize before data are reported to elucidate these responses.

3.4 HEAT PRODUCTION

The data have been used to calculate a heat production (HP) as the balancing term in the equation

$$ME_1 = HP + ER \quad [\text{theory of conservation of energy}]$$

such that

$$HP = ME_1 - \text{eggE} - \Delta BE$$

where : HP = heat production (kJ/b.d)

$$\text{eggE} = \text{egg energy (kJ/b.d)} = \text{ROL}(7.57304 * \text{EW} - 82.4248)$$

$$\Delta BE = \text{body energy increase (kJ/b.d)} = 14.941 \Delta BW$$

As the only variable that could not be significantly improved through the addition of a cubic term, the linear relationship has to indicate the primary importance of this variable to the bird (Marsden and Morris, 1987). The function describes a linear decrease in heat production as the T_E increases. As noted previously, most responses to T_E can be related to FI, and where HP is a function of MH and HIF and MH remains constant/kg BW^{0.75}, HIF must be getting marginally diminished. In fact, this decrease in the HIF can be explained through the decrease in the amount of food that provides this heat increment. One of the primary tools that the bird has available within a very narrow range, is to reduce food consumption to reduce this heat increment.

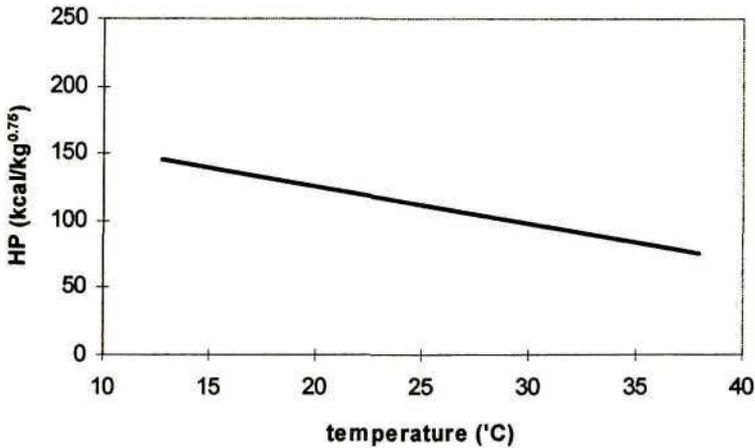


Figure 17 Heat production per kg metabolic BW as a function of T_E (appendix data).

HP follows a linear decline with increasing T_E (Davis *et al.*, 1973) (Figure 17). The classical pattern of TNZ with upper and lower T_C is obtained only under basal or standard conditions, whereas under more normal conditions (existence metabolism), HP falls linearly as T_E rises until it reaches a single T_C which marks the onset of hyperthermal rise in metabolism (Kendeigh in Davis *et al.*, 1973). HP on active, normally fed birds has also shown a linear response with T_A reaching a minimum at a new and higher critical temperature (higher $T_C = 32.5^\circ\text{C}$) above which the bird is in the hyperthermal zone and metabolism rises (Sykes, 1977).

Rate of HP decreased by $0.2\text{kJ/kg}^{0.75}$ on a daily basis. This is $4.8\text{kJ/kg}^{0.75}/^\circ\text{C}$. The decrease in HP with T_E results in a decrease in energy requirements for maintenance (Sykes in Li *et al.*, 1992). HP in turn may be affected by either net energy requirement for maintenance or HP associated with FI or both. In mammals, it is known that the lower T_C decreases as the FI increases, because HP associated with FI contributes to thermoregulation at low temperatures (Blaxter in Li *et al.*, 1992). Li *et al.* (1992) propose however that the rate of HP decreases continuously with increasing T_E at any

FI. This suggests that the HP associated with FI is not directly linked with thermoregulation. When the T_E rose to 32°C, the abdominal temperature of the hens on 90g of food increases, and for hens receiving no food, their body temperature only rose when the T_E reached 36°C. Therefore, FI affected abdominal temperature only when the T_E was high (Li *et al.*, 1992). An increase in HP with FI amounted to 16% of the ME intake (Li *et al.*, 1992).

Metabolic HP of layers changes with FI, muscular activity and T_E (Li *et al.*, 1992). Abdominal temperature varies very little with either T_E or FI below 28°C. Above 28°C, the abdominal temperature increased significantly with increasing FI. HP varies with both T_E and FI (Figure 18).

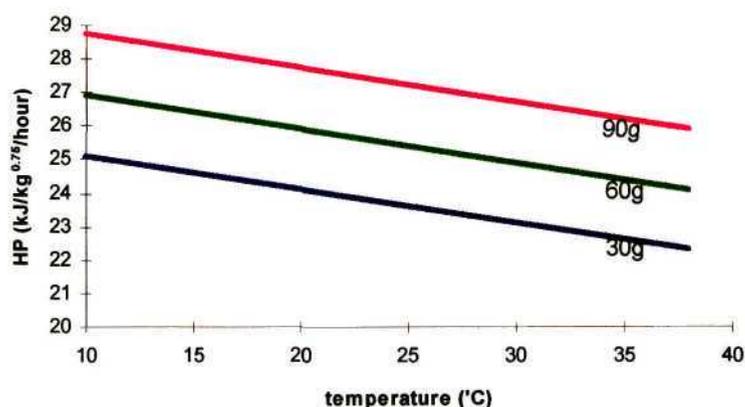


Figure 18 FI and HP at different T_E (after Li *et al.*, 1992).

The post-absorptive state related to a heat increment in feeding can last for 20 hours in meal-eating hens at high levels of intake (Li *et al.*, 1992). However, relief exists in the provision of cool drinking water, where intake alleviates heat stress for 5 to 7 hours after drinking (Degen *et al.*, 1992).

3.5 EGG PRODUCTION

Egg energy output has been identified as a significant contributor to the variability in heat production which decreases with increasing egg energy output (Pesti *et al.*, 1992) (Figure 19).

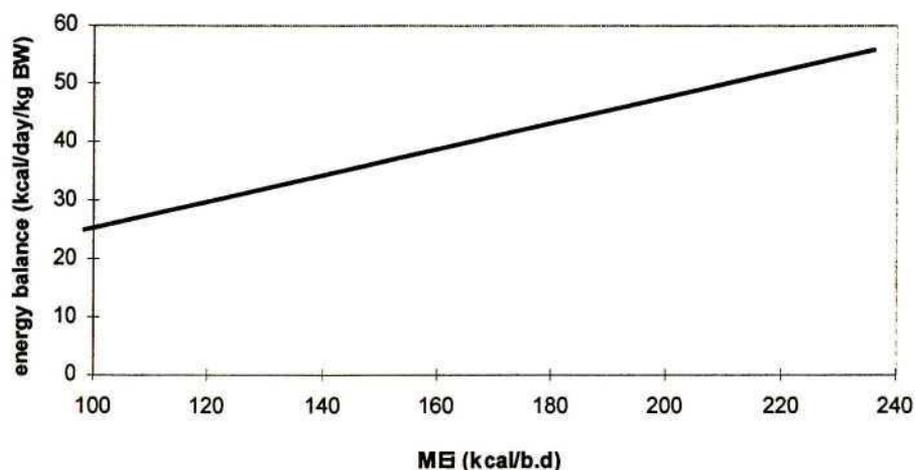


Figure 19 Energy balance as a function of ME intake (after Pesti *et al.*, 1992)

$$(\text{Energy balance (Pesti } et al.) = \frac{(\text{ME intake} - \text{HP})}{\text{BW}} \text{ vs. ME intake/kg BW})$$

This relationship suggests an increase in the retention of the ME ingested, in body and egg energy. There is a decrease in the heat production as the egg energy increases, the corollary to this being that as egg energy output decreases, there is an increase in the heat produced. This decrease in egg energy output is a function of temperature because insufficient energy is ingested at high T_E , and the loss in the capacity to lose heat through eggs means that there has to be an even greater compromise in body energy and ME intake, and this is why total change in body energy becomes negative after the egg energy output starts decreasing (refer figure 13). As mentioned previously, this rate of change in body energy cannot be sustained for any length of time due to the deleterious nature of the change. The negative impact of this change will be exacerbated if the diet cannot

supply sufficient nutrients to the hen to direct the change only to the depletion of fat reserves. Relatively small protein deficiencies are more likely to reduce production than more appreciable energy deficiencies (Emmans and Fisher, 1986).

Egg energy remains fairly constant over the range until 25°C when it begins dropping rapidly, and is significantly depressed at 30°C (Marsden *et al.*, 1973) (Figure 20).

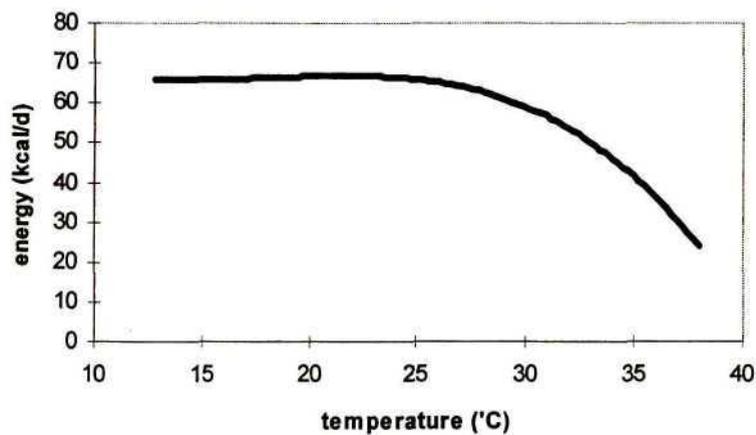


Figure 20 Egg energy as a function of T_E (appendix data).

This is a function of the fall in rate of lay, rather than EW, which is preserved as far as possible (Figure 21), on the romantic notion that the eggs are for the hatching of a healthy chick, and a hen would rather lay fewer, quality eggs that will provide for the embryo (Morris and Gous, 1988).

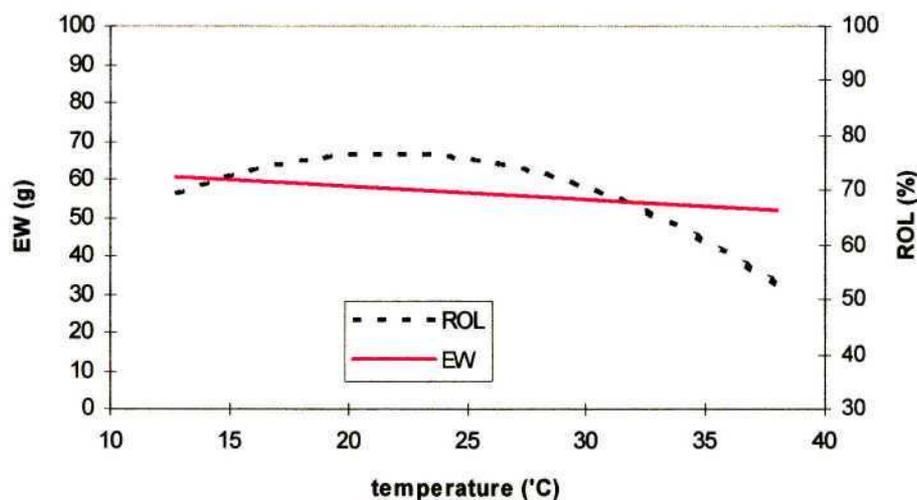


Figure 21 Decline in ROL relative to EW as T_E increases (appendix data).

At 23.9°C, egg mass production is optimised compared with hotter and colder environments (Peguri and Coon, 1992). Above 25°C, energy intake falls more rapidly than heat loss, leading to the reduction in the energy retained in eggs and body tissue (refer figure 13, page 39).

The effects on eggs due to an increase in T_E can be summarised as follows :

- decrease in EW (Deaton, 1983; Peguri and Coon, 1992)
- reduced ROL (Deaton, 1983)
- shell thickness is decreased (Miller, 1975; Schnepel in Deaton, 1983), though bone mineralization is not affected by a change in T_E and there is no net change in skeletal calcium. Low T_E tends to promote shell rigidity in relation to the time of oviposition (Miller, 1975).
- shell quality is reduced and not improved through dietary adjustment (Huston and Carmon in Deaton, 1983)
- albumen quality as measured by Haugh units remains the same (Huston and Carmon in Deaton, 1983)
- there are fewer blood spots (Wilson, 1972).

Dietary adjustment can overcome most of the detrimental effects of elevated T_E on % egg production with some improvement in EW (de Andrade in Deaton, 1983). At lower T_E , mean EW per egg is greater (Peguri and Coon, 1992; Davis *et al.*, 1973).

Bolton in 1959 identified the constraints related earlier by Emmans and Fisher (1986) - as long as the laying bird can consume sufficient food, the FI is governed by the amount of digestible food eaten; beyond this point, FI is governed by anatomical considerations. Under the first set of conditions, FI is controlled by egg production, and under the second, egg production is controlled by FI. Indeed, feeding a more concentrated feed does reduce the decline in egg production at higher T_E (Marsden *et al.*, 1973), mainly through enhancing EW with the increase in ME (Leclercq, 1986), 40 to 50 % of the effects of heat on EW and ROL being attributable to a reduced FI (Peguri and Coon, 1992; Degen, 1995; Smith and Oliver in Njoya, 1995). Bray and Gesell (in Sykes, 1977) noted that egg production can be maintained at 30°C provided a daily protein intake of 15g is ensured by appropriate dietary formulation. T_A does not increase or decrease the requirement for protein, (but it must be considered that as maintenance metabolism falls with T_A , protein requirements might also fall).

Because the egg output remains constant over a wide range of T_E while the ME intake is falling (refer figure 13, page 39) it follows that the gross energetic efficiency of egg production must be increasing, i.e. the egg energy per kJ ME intake. This trend is apparent in the gross energetic efficiency mentioned in the previous section, where the feed is utilized more efficiently in the production of eggs. There would seem therefore to be an advantage in birds housed at high T_E , since they appear to make more efficient use of the resources available to them at these temperatures. It would make sense then to concentrate on these attributes in the practical feeding of the hens, since the financial return from this may well justify the increase in feeding costs.

3.6 BODY ENERGY

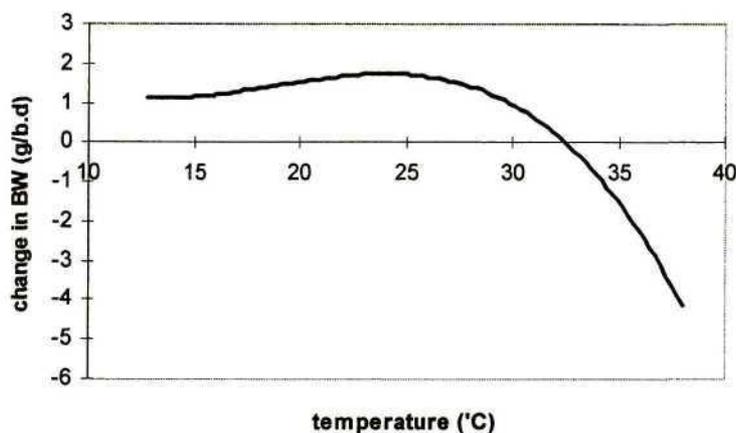


Figure 22 Body energy change associated with increasing T_E (appendix data).

Body energy (BE) is reduced subsequent to the more rapid fall in energy intake relative to heat loss as the T_E increases (Figure 22). At high T_E , this change in BE is a function of the food intake in that the bird is no longer eating enough to sustain it, and body reserves need to be utilized to provide for maintenance. The 'capture' of heat in the formation of energy in the tissues constitutes a manner of heat loss, and ridding the body of excess heat is a concern at these temperatures. Over 25°C , the loss in body energy concomitant with lower FI cannot be sustained. The reduction in BE can support egg production only until a stable weight is reached. This rate of loss is unstable unless the birds are acclimatised and cannot be expected to sustain birds over any length of time. A feature of the response both to an increase and decrease in T_A is the use of body reserves to help meet an immediate negative energy balance (Sykes, 1977). The tendency exists to increase carcass energy at the lowest T_E and to decrease it at the warmest T_E (Davis *et al.*, 1973) to meet the differences between intake of nutrients and the output of eggs (Balnave in Njoya, 1992).

When FI is constrained or controlled, the bird is short of one or more resources and has the problem of having to allocate the scarce resource between its functions using a set

of allocation rules. It would appear that hens will be prepared to lose body lipid to support egg production. For hens of normal composition, relatively small protein deficiencies are more likely to reduce production than appreciable energy deficiencies. The importance of reserves in influencing responses depends not only on the size of the reserve relative to the potential rate of production, but also on the extent to which the rules of allocation used by the hen lead it to use its reserves to support production, and on the rate of loss, and also the duration of the response (Emmans and Fisher, 1986). Under conditions of energy restriction (at high temperatures), there is likely to be competition for the available supply, and it appears that the immediate demand for egg production will be met at the expense of reserves previously accumulated (Sykes, 1972).

3.7 MEANS OF ALLEVIATING HEAT STRESS

Heat stressed chickens increase water consumption, panting rate and body temperature, but decrease FI, produce fewer eggs and have a higher mortality. Water temperature is important in that it will decrease body temperature, HP and respiration rate, increase FI and egg production and decrease mortality (Degen *et al.*, 1995). Wilson (in Deaton, 1983) found water consumption of hens at 35°C was double that for hens at 21°C. Fox (in Deaton, 1983) demonstrated that when exposed to 42°C, a longer survival time was associated with the persistency with which a bird continued to drink. When water is not available to a bird held at 30°C death follows from heat prostration rather than desiccation (Jones and Huston in Deaton, 1983). Food consumption can be limited by water intake and water deficit leads to a reduction in the metabolic rate (Sykes, 1977).

The absence of mortality due to heat stress is due to the availability of water which was more than adequately cooled, water also being effective if the waterer allowed them to immerse their heads, even if only the wattles could be immersed (Boone in Deaton, 1983). Finding large quantities of cool water in the crops of birds exposed to high T_E , Fox (in Miller, 1975) hypothesised that the volume of cool water in close proximity to the main arteries and veins supplying the head region should have a cooling effect on blood circulating the brain. The cooling effect would prevent what Randall theorised

would be the cause of death - paralysis of the respiratory centre due to high blood temperature (Miller, 1975).

Feather coverage is also an important means of alleviating heat stress, such that regions of the world in which temperatures are high for long periods of time would experience a benefit in breeding hens with less feather coverage or that lack feathers (Peguri and Coon, 1992). ME intake and HP are about 50% higher with feathering (O'Neill *et al.* in Sykes, 1977, Emmans, 1987). Activity and therefore HP of hens can be depressed by decreasing the light intensity (Li *et al.*, 1992). Njoya (1992) mentioned pelleted diets, which would perhaps enhance intake of poorer quality or low energy or difficult diets. Promoting uptake would hold similar benefits to the stimulation of uptake by other means, and this would reduce the deficit of nutrients where they are restricted.

Five generalised means of alleviating heat stress are: poultry house ventilation and insulation, evaporation cooling, FI and nutrition and acclimatization, the least understood of which Deaton (1983) considered to be role of nutrition under heat stress conditions. This is however our most inciteful means of alleviation of heat stress. An important section follows in energy restriction.

Sykes (1972) found that normal egg production could be maintained on the lowest energy intakes in the range 1004-1841kJ/d, with attention being paid to the rate of inclusion of other nutrients other than energy to ensure that they would not be limiting. Food restriction of up to 10% of the voluntary feed intake (VFI) can be imposed without any loss in production (Temperaton *et al.* in Sykes, 1977), but most reports with layers indicate that production invariably suffers when food restrictions are imposed (numerous reports in Sykes, 1977). Sykes (1977) found that egg production was not reduced even when the energy intake was as low as 837kJ/d, but this was associated with considerable loss in BW. Egg production can be maintained under conditions which cause a substantial loss of BW and it is suggested that for light and medium weight strains the *physiological* requirements for dietary energy, which is satisfied by *ad lib.* consumption, are appreciably greater than the *economic* requirement. Intakes of about 1130kJ/d (for

birds with an average body weight of 2.3kg) were optimal in Sykes's study (1977).

Temporary return to *ad lib.* feeding might build up reserves and enable restricted conditions to be resumed subsequently. Periodic rehabilitation might provide a margin of safety in a population which would naturally show variation in initial BW and energy reserves. Carcass analysis after a period of energy restriction (Jalaludin in Sykes, 1977) showed a smaller proportion of fat and a larger proportion of protein and water, some of the fat having been replaced by protein.

If the laying bird's energy requirement can be reduced from 1464kJ/d to 1130kJ/d without any reduction in EO, two questions arise :

- how is this brought about?
- how can these findings be put into practice?

Under conditions of energy restriction, there is likely to be competition for the available supply and it appears that the immediate demand of egg production is met at the expense of reserves previously accumulated in response to endocrine stimuli. Thus BW falls particularly during the first three weeks of restriction, and this itself would lead to a reduction in metabolic rate. There would probably be a smaller loss of energy from the specific dynamic action because of the lower food consumption and part of the reduction in metabolism is probably accounted for by diminished muscular activity (Sykes, 1977).

Practically, energy intake can be reduced through ration dilution, restriction of feeding time, or a system of restriction followed by periodic rehabilitation. Towards the end of lay it would be desirable to maintain egg production at the maximum expense of BW (Sykes, 1977). It is the opinion of Leclercq (1986) that restriction reduces EO even if the degree of restriction is slight, the egg number being the most frequently affected variable. BE gain is invariably reduced, but it is impossible to eliminate it completely without adversely affecting egg production. Feed efficiency is enhanced if the restriction is slight, but is reduced if the restriction is too severe. There is an improvement in EO and BW gain with hens on low energy diets at high T_A compared with those on high

energy diets (Scott and Balnave in Njoya, 1992), feeding high energy diets not being a sure solution to counteract the adverse effects of high T_A on laying performance under fluctuating natural tropical climates.

This concept of energy restriction leads into our investigation of the data presented by Marsden and Morris (1987) and others. While it would be intensely satisfying to obtain a direct effect of EE in the diet to the responses at high T_E , the graphs show no such direct response. The response is more likely to be a function of FI, as we have noted the effects of ME to be. Thus we can elucidate the involvement of EE in that manner.

Sykes and Salih (1986) wrote a very interesting exposition on energy intake and heat tolerance in the fowl, in which they clearly attributed the response in heat stress to nutrition. Food restriction favoured survival in their opinion, but increasing the energy intake could bring about a prompt and extensive loss of heat tolerance. Using an index of heat tolerance as the rise in rectal temperature (T_R) over a period of heat exposure (RIT_R) expressed as $^{\circ}\text{C}/\text{h}$, they were able to quantify the loss in tolerance in relation to ME intake. The promptness of the response was shown by the rise in RIT_R (above an acclimatised level ≤ 1.0) on the first day of feeding a high energy diet (maize oil 70g) at the time of test, when only a portion of the FI had been consumed. The loss in heat tolerance was comparable to that of unacclimatised hens, and was similar to a level that would cause mortality in the field. Heat tolerance depended on the ME intake, such that as ME intake increased, heat tolerance decreased. Therefore it follows that in an endeavour to promote heat tolerance, that is, to alleviate the detrimental effects of high T_A , to sustain production at high T_E , we need to reduce the ME intake, which requires that we provide more available sources of energy and lower the energy intake. This involves feeding closer to requirement, a concept encompassed in the Effective Energy system. If we were to use EE as an objective function in feed formulations, at any ME content we would see an improvement in energy intake such that egg production might be maintained.

This proposition is further strengthened by the following graphs :

It must be stressed that the following figures only indicate trends; conclusions can only be drawn after severe statistical analysis reveals the significance of any trend relative to another. They can still be instructive in illustrating the information to provide a tangible grasp of the importance of further exploration and investigation.

The graph of ME intake vs EE intake (Figure 23) obviously depicts the trend of declining FI as the T_E rises. It appears from the figure that the ME intake is greater than the EE intake. (This is to be expected since EE values in any feed are invariably smaller than the corresponding ME values). We have discussed the beneficial effects of reducing the energy intake at high T_E . An important consideration with the energy restrictions, mentioned earlier, is the loss in BW. The concept of EE is that all functions within the bird are considered in the calculation of an energy requirement. Energy intake is restrictive to production above 25°C. Therefore there exists benefit in attempting to provide a more targeted energy supply to the hen. It would assume to be true that the EE ingested over these periods of restriction is more likely to meet the needs of the bird, rather than compromising production requirements due to an excessive heat load and reduced nutrient intake.

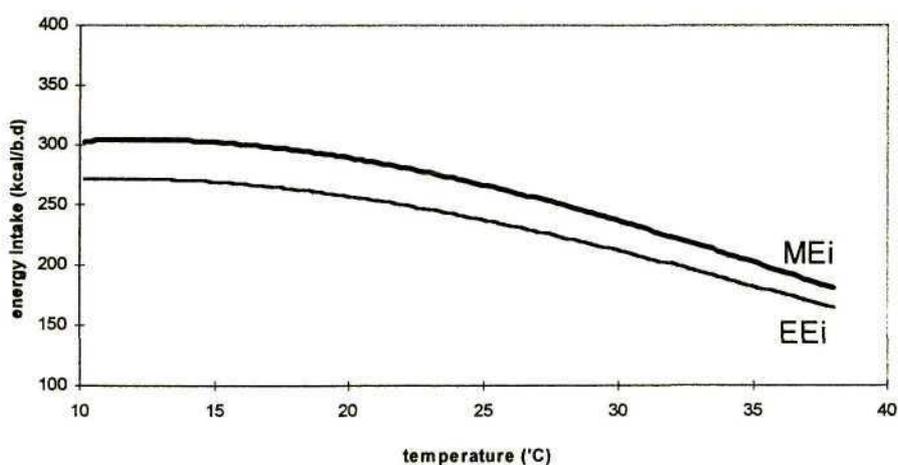


Figure 23 Relative changes in EE and ME intake as a function of temperature (appendix data).

Figure 24, depicting the energy intake against the EO, shows that the EO more closely follows that of the EE intake, rather than that of the ME intake.

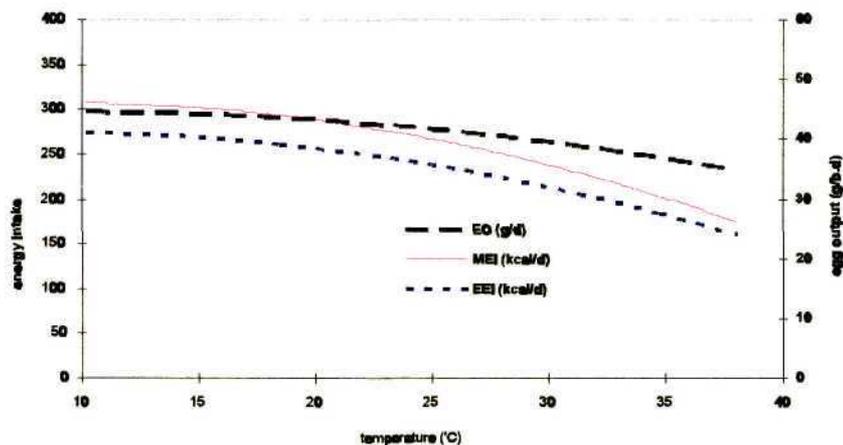


Figure 24 Energy intake and its relation to EO at T_E (appendix data).

The HP associated with EE intake is lower than that associated with ME intake by virtue of levels of intake. This superfluous HP contributes to heat stress at high T_E and it is therefore important if a saving can be effected in this way. Our primary concern at high T_E is the heat load and subsequent reduction in performance. If we consider any minor savings, in the smaller range of opportunity that exists at high T_E , then it is quite probable that these might accrue favourably and present an interesting response in the birds.

Postulation :

Noting the arguments presented above, we should attempt a calculation with an effective energy perspective. Sykes (1972) did a number of experiments with energy restrictions (where other nutrients were not first limiting), and found an intake of 270kcal (1130kJ/d) to promote high egg productions without sacrificing EW and body weight too drastically. If we follow a calculation using the specifications of Sykes' hens, we note the following:

assuming : BW = 2.31kg
 EO = 45g/d
 EERQ (kJ/d) = MH + 8.8EO

$$\begin{aligned}
&= 1630(0.15 \cdot 2.31)^{0.73} + 8.8(45) \\
&= 751.919 + 396 \\
&= 1147.919 \text{kJ/d} \\
&= 274.36 \text{ kcal/d}
\end{aligned}$$

It is very interesting to note that this value is equivalent to the 1130kJ/d presented as necessary for Sykes' hens - what he was in effect doing was meeting more precisely the needs of his hens, and reducing the supply of superfluous energy.

Assuming an intake of 120g/d,

$$\begin{aligned}
\text{Dietary EE concentration} &= \frac{\text{EE requirement}}{\text{DFI}_{\text{EE}}} \\
&= \frac{1147.919 \text{kJ/d}}{120 \text{g/d}} \\
&= 9.57 \text{MJ/kg}
\end{aligned}$$

Analysing the results in terms of EE is not the same as formulating and then feeding feeds based on EE. The heat increment would be lower and the amino acid supply might be more closely matched to the hen's requirements in the latter scenario. What this example of Sykes' (1972) data does illustrate is that savings in production in laying hens start with economies in energy supply. In our feed formulation package we could now exclude ME and set our parameters to achieve an energetically efficient feed, where all the feed ingredients are qualified in terms of their EE yield. Being aware of the curvilinear response of FI to T_E , we would ordinarily expect a similar trend in the decline of ME intake, but it would appear that the decline in EE intake is far less pronounced. This would be a function of the multiplicity of feed ingredients that were used in the formulation of the experimental diets included in the spreadsheet. Not being acutely aware of the EE nature of the feed ingredients did well to provide an unbiased and interesting array of dietary compilations, but the EE values appear to be less variant in nature. Perhaps being aware of the nature of EE in feed ingredients will serve to narrow this variation even further as we endeavour to lift restrictions to layer performance at high T_E .

3.8 CONCLUSIONS :



Plate I *Inputs and Outputs within constraints determine performance of the laying hen.*

Conclusions in chapter one might be summarised by Plate I.

The following have been reviewed :

- heat productions and losses in the hen
- flow of organic matter in the hen with energy partitioning
- interaction of feed and environment in providing resources as well as constraints to the potential production
- Effective Energy and the potential of this energy system to address the implications of high environmental temperatures.

All the aspects discussed above have been taken into account in the formulation of two trial protocols which test the nature of a heat increment in feeding, and which provide a test of the validity of the Effective Energy system, both under conditions of controlled environment. With such information, there is a real test of the effects of environmental

temperature, but more importantly, interrogation of the data encourage the understanding of the responses of the hen to temperature under the effect of specially designed dietary treatments.

CHAPTER FOUR

RESPONSE OF LAYERS TO HEAT INCREMENT COMPONENTS IN THE
DIET AT TWO ENVIRONMENTAL TEMPERATURES

4.1 INTRODUCTION

The introduction of the concept of heat increment by Armsby in 1903 has been invaluable in the construction of the Effective Energy system by Emmans (1994), and provides the platform for this experimental procedure. Work done in the immature animal above maintenance is directed towards only five functions - those of excretion, defecation, fermentation, growth and fattening, where the metabolizable energy (ME) required per unit of each function remains the same for all animals and diets (Emmans, 1994). The energy required in the performance of these work functions is noted in Table 1.

TABLE 1
Work Functions (after Emmans, 1994)

work function	energy value (MJ)	units
W_u	29.2	MJ/kg UN
W_m	0.616	MJ/MJ CH_4
W_d	3.80	MJ/kg FOM
W_p	36.5	MJ/kg PR
W_l	16.4	MJ/kg LR (non-lipid sources)
W_{ll}	4.4	MJ/kg LR (lipid sources)

where :

UN = urinary nitrogen

FOM = faecal organic matter

PR = protein retention

LR = lipid retention

In a mature animal, energy consumed is directed to functions other than growth and fattening. As an adult, the bird fulfils its production capabilities, and energy supplied is utilized in the formation of product. Retentions of lipid and protein are redirected in that these are incorporated as components of product. The energy required in the

performance of these work functions is supplied by the diet. The maximum quantity of chemical energy which any substance can furnish for vital activity by its oxidation is measured by its heat of combustion. While the animal would endeavour to utilize all the chemical energy supplied, inefficiencies render part of the gross energy (GE) unavailable, with chemical energy being lost in excretion or the production of gases, or being lost as superfluous heat. However, this metabolizable energy (ME) still does not represent the total amount of energy available to the animal. The available energy, AVE, is defined by the following expression :

$$\text{AVE (MJ/d)} = \text{ME} - w_m \cdot \text{MTHE} - w_d \cdot \text{FOM}.$$

The metabolisable energy in monogastrics is not reduced by the amount of methane, but in producing FOM, there exists a loss in that energy ingested is not available for productive purposes. The energy available for productive purposes is further diminished by energies required in the digestion, absorption and excretion of feed ingredients. The HIF is a function of five quantities - UN, FOM, positive retentions of protein and lipid (and methane production in the ruminant). The kilojoules (kJ) supplied in the diet are usurped in these processes, producing heat, and detract from energies available for productive purposes.

$$\text{HIF (kJ/d)} = w_d \cdot \text{FOM} + w_u \cdot \text{UN} + w_m \cdot \text{MTHE} + w_p \cdot \text{PR} + w_l \cdot \text{LR}$$

The ME requirement, MERQ (kJ/d), is a function of ER, MH and HIF. The ER (energy retention) is a consequence of the performance of the animal in terms of its rates of protein and lipid retentions, and MH (maintenance heat) depends on the kind of animal and its state. Thus, the ME requirement of a given animal in a given state to attain a given level of performance, depends on its heat increment in feeding. A fundamental principle of the EE system is that the energy ingested and actually available for retentions in the animal is diminished by the energies that are usurped in dealing with the factors in heat increment. Where environmental conditions are conducive to the release of heat generated, the heat increment can be constructive in meeting maintenance heat demands. The case where the environment produces constraints to this heat loss is the focus of the experimental procedure.

A heat production can now be defined as the difference between the ME and EE intakes of any diet. In essence, this relates the properties of the feeds to their intakes. Where the EE system has accounted for such characteristics as the digestion and accretion and excretion of the protein, lipid and indigestible portions of the diet and the ME system accounts for that metabolizable, the difference will reflect the superfluous heat that is produced, and that needs to be disposed of. By comparing this heat production across different diets, one can evaluate the intrinsic properties of the EE system, and interpolate the effects in a heat constrained environment. Diets have therefore been formulated to test the proposition that heats of production will be different across diets that promote heat increments according to the EE system. Not only this, but that these increases in heat will either promote or detriment laying performance at cool and hot environmental temperatures. The fact that brown and white layers respond differently to temperature constraints (Emmans, 1974; Marsden and Morris, 1987) with the brown birds having a lower maintenance energy requirement per kilogram or kilogram^{0.75}, was used to exacerbate the response of the birds to the diets. The diets were designed to test the extent to which the theoretical heat increment produced by each diet would influence feed intake, particularly at high temperatures. The nutrients supplied within the constraints of the environment define a level of performance and it should be possible to predict levels of performance from the data available by applying the knowledge that the data impart. A full description of the system and the diets available will define the characteristics of the heat production that make the EE system at least as good as the ME system previously used.

The objectives of this experiment were therefore three-fold :

- to formulate diets of different effective energies by manipulating the heat increment components,
- to test the sensitivity of the individual responses of brown and white birds to these diets
- under high and low environmental temperatures.

4.2 MATERIALS AND METHOD

4.2.1 FACILITIES

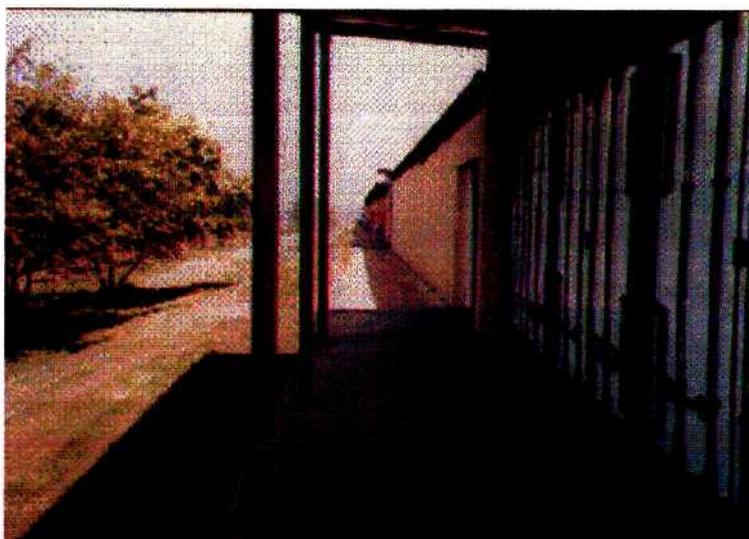


Plate II *Controlled environment chambers at the University of Natal Research Farm.*

It is useful to consider first the construction and design of the chambers in which the birds were housed (Plate II). Completed in 1994, the controlled environment research unit (CERU) consists of five insulated marine shipping containers (the sixth chamber installed 1998). Each container is individually and independently controlled with respect to temperature, humidity, lighting and internal air exchange and each has its own water supply.

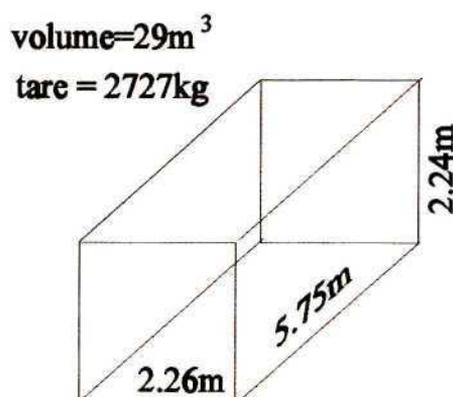


Figure 25 *Internal dimensions of the controlled environment chambers (after Paton, 1994).*

Modified layer cages run the length of the chamber. As observed in the Plate III, there are three tiers of 16 cages, making 48 individual cages per chamber.

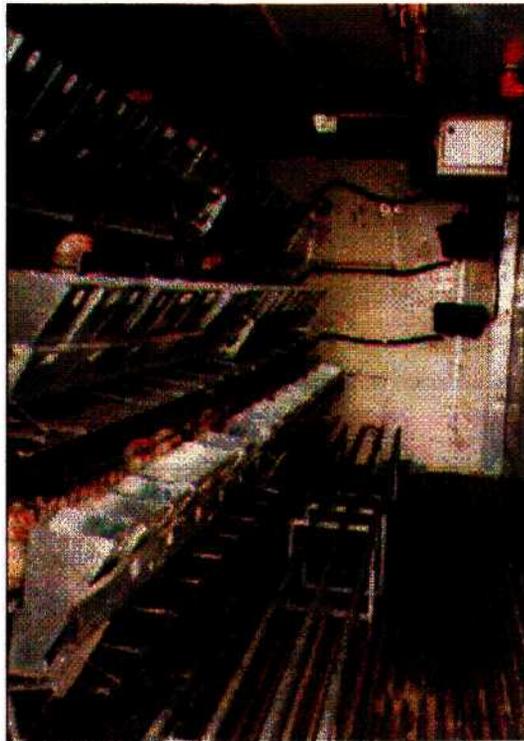


Plate III *A longitudinal view of layer cages from the door of the chamber.*

A cistern and water tank supply each tier with water. Each bird has a floor area of about 1m^2 . The bird has its own nipple drinker and drip cup overhead, and the trough that runs the length of the cage holds individual feeders, such that each bird has *ad lib.* access to its own feed (Plate IV). The design is such that thieving is prevented, since the sides of the large 22cm feeders are flush with the sides of the cages, and the hen is not able to put her head through to the adjacent feeder.



Plate IV *Food and water supply to the hens within the chambers.*

Full operating details of the CERU were the subject of another study (Paton, 1994). A brief description allows us to evaluate the capacity of the chambers in providing a safe, controlled environment for the hens. Integral to this current study was the accurate assessment of temperature control in the chambers prior to the installation of new software to regulate and control temperature and humidity settings within the chambers. A TinyTalk™ instrument was used in conjunction with the Orion Tiny Logger Manager (OTLM™) software to log the temperature in the chambers every 10 minutes, and this information was regularly downloaded and printed in graphic form to evaluate the temperature control. They indicate that control for the period of the data presented was within 0.5°C of the desired temperature. It is true that the one chamber was less well controlled than the other, and care was taken to evaluate the results in terms of this. Blocking structures in the analysis of variance do indicate that although there might be slight differences, as anticipated by the author, these were in fact non-significant, and one can conclude that the two chambers did not produce significantly different responses when set at the same temperature for replicated observations. It is the intention of the Poultry Section at the Ukulinga Research Farm to upgrade the software and control mechanisms of the chambers, and this augurs well for subsequent trial work in these very efficient facilities.

The chambers use Hot Bypass Gas refrigeration. Two Recoil (NST 1300) blower units exist for refrigeration, with two 34 watt fans in each unit. Two Black Heat heating elements are mounted inside the blower unit. Behind the blower unit in line with the two fans are two Eintal™ pulsating mist jets which operate on the pressure of the incoming water.

External lighting is effected by means of florescent tubes, internally there are two 9watt florescent tubes in waterproof bulkheads. These are operated automatically by an electronic controller, and are situated equidistant from the centre of the chamber roof. The light obtained in this manner is bright, while the florescent tubes emit little heat.

Air exchange is effected by means of fans blowing air through the portholes of the marine container. The top porthole receives air for the chamber with a conventional blower fan motor, which is single speed and air movement is controlled by the intervals at which this fan is operated. The bottom porthole emits exhaust air. The incoming air is controlled by the electronic control unit. Air exchange occurs at a maximum rate of 6.5m³ per minute.

The electronic controller (Plate V) situated at the back of the chambers is responsible for the:

- control of temperature within the chamber
- number of daylight hours
- alternation of day/night temperature regimes
- controlling humidity of the environment
- the amount of air exchange between the chamber and environment

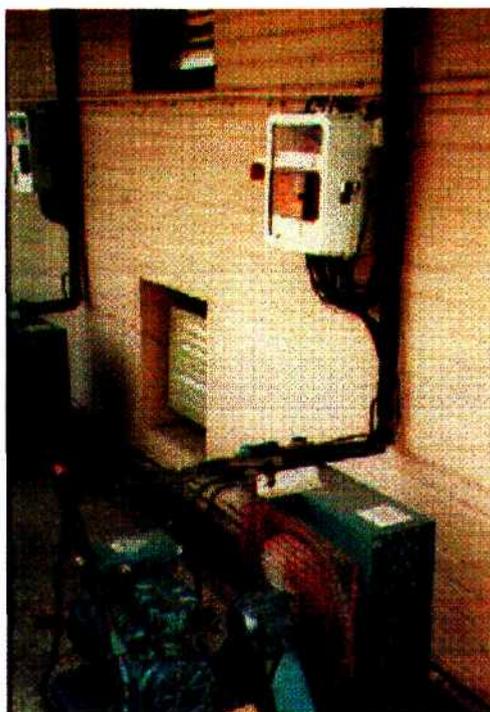


Plate V *The electronic controller at the rear of the chambers.*

4.2.2 BIRDS

Forty eight Hyline Brown and 48 Amberlink hens of 26 weeks of age were obtained from a standard cage layer flock during the Spring (November 1996). The hens were receiving *ad libitum* access to a standard summer ration (Layer 111- 15% protein, 11.85MJ/kg) and continued to receive this for a further two weeks inside the experimental facility. Equal numbers of brown and white birds were randomly allocated to 96 pens in two chambers. The acclimation period served to settle the birds to the routines for the following weeks and also provided a baseline "potential" performance estimate for each bird. Feed was available *ad libitum* in individual feeders. A temperature of 25°C was chosen as comparable to the ambient temperature of the region at that time, which also corresponds to a comfort temperature for the hens (Marsden and Morris, 1987).

4.2.3 TEMPERATURES

The experimental period was divided into two segments of six weeks each. After the two week pre-trial, the two chambers were separately differentiated by 7°C to give 18°C and 32°C constant temperature. These temperatures represent a sufficiently low and high temperature under which the effectiveness of heat increment theories were tested. After six weeks, the temperatures in the two chambers were exchanged, such that the birds were subjected to 24 hours per day of the alternate temperature for a further six weeks. The birds received 16L:8D; on at 04h00 and off at 20h00.

4.2.4 FEEDS

Winfeed 1.1 (1996) was used to formulate a basal ration (Tables 2 and 3) containing 0.08 more energy, amino acids, vitamins and minerals than a Layer 100 ration (formulated to satisfy requirement at 100g FI per day).

TABLE 2
Specifications (g/kg) for the formulation of the basal diet

nutrient	specification
AME _n (MJ/kg)	12.20
crude protein	108 - 324
lysine	9.00
methionine	4.10
methionine and cystine	8.20
threonine	5.50
tryptophan	2.10
arginine	7.60
histidine	2.60
isoleucine	7.60
phe and tyrosine	9.50
valine	8.40
calcium	35.1-37.8
phosphorous	3.80
sodium	1.90-2.40
chloride	4.30
fat	21.6-108.0

TABLE 3

Formulated composition (g/kg) of the basal diet

INGREDIENT	g/kg
maize	533.0
sunflower 37	147.2
soya bean meal 48	49.0
fish meal 65	100.0
sunflower oil	48.0
wheat bran	30.0
DL-methionine	1.4
vit/min premix	2.5
limestone	82.0
monocalcium phosphate	4.3
salt	2.0

The 0.08 increment in nutrient density in the basal diet was designed to compensate for an equivalent dilution of the basal ration with the test diluent. The choice of the diluent was correlated to the heat production it would induce. Diluents were:

- soy protein isolate
- sunflower husks
- sugar and starch (50:50)
- sunflower oil
- fishmeal

Table 4 summarises the dietary treatments and their anticipated effects.

TABLE 4

Summary of the six dietary treatments and motivation for inclusion.

DIET	Treatment Code	Description
basal	BSL	three protein sources, wheat bran and maize with a standard vitamin and mineral premix to serve as a concentrated layer ration
oil	OIL	an increase in the ME supplied without the heat increment associated with its consumption
filler	FIL	milled sunflower husks contribute bulk only, imposing volume constraints in consumption and the 3.8kJ/g of FOM produced.
sugar/starch	S/S	readily available carbohydrate as a 50:50 mixture obviates the internal synthesis of energy, while still involving metabolism to release the nutrients.
soy protein isolate	SPI	a concentrated protein source containing 70-80% protein and amino acids in a concentrated form, incurs energy costs in the metabolism of the protein (23.9kJ/g) and the amino acid excretion (30.6kJ/g). Imbalanced amino acids leave the body at an exaggerated energy cost.
fishmeal	FIS	increases the protein and energy of the basal ration in a more balanced fashion, in combining many of the attributes of the above diluents.

Table 5 documents the formulated composition of the six diets, followed by the laboratory analyses of the same diets.

TABLE 5

Formulated nutrient composition (g/kg) of the six test feeds

DIET	basal	oil	filler	protein	sug/stch	fishmeal
AME _n (MJ/kg)	12.2	14.3	11.2	12.7	12.5	12.3
EE (MJ/kg)	10.7	13.2	9.5	11.1	11.0	10.6
CP	201.5	184.6	185.3	249.0	185.5	241.9
lysine	9.5	8.7	8.8	13.3	8.8	12.9
methionine	5.5	5.0	5.0	6.1	5.1	6.6
calcium	35.0	32.1	32.3	31.0	32.2	35.4
phosph av.	3.8	3.5	3.5	4.3	3.4	5.4
DM	896.2	904.1	903.7	898.9	903.7	897.4
FAT	80.0	156.4	73.5	75.4	73.6	80.6
CF	42.5	38.9	39.1	45.8	39.1	38.7

TABLE 6

Analysed composition (g/kg) of diets

DIET	basal	oil	filler	protein	sug/stch	fishmeal
AME _n (MJ/kg)	11.7	14.1	11.5	13.3	13.4	11.8
crude protein	188.6	176.7	188.0	240.6	176.1	225.3
lysine	10.6	9.6	9.7	14.4	10.3	10.6
methionine	5.9	4.6	4.5	5.6	5.7	5.2
calcium	36.2	34.8	36.0	34.4	33.6	38.5
phosph av.	5.8	5.2	5.6	5.9	5.5	6.4
dry matter	885.0	908.0	878.0	900.5	903.0	884.5
crude lipid	54.4	138.8	61.3	68.7	67.4	67.4
crude fibre	48.4	36.7	79.7	35.4	33.7	29.6

4.2.5 MEASUREMENTS

Measurements were taken of body weight, feed intake, rate of lay and egg weight. Egg component data (not reported here) were also taken. Body weights were established at the start of the pre-trial and the two subsequent periods, and also in the middle of the second period and at the end of the trial. From these measurements, changes in body weight could be calculated. Feed troughs were filled on the Monday and weighed, and

subtracting the weight left the following Monday gave the feed intake for the week. Eggs were weighed on three consecutive days to give an average egg weight for each hen, and rates of lay were determined daily. Tables 7 to 11 report the average performance of the hens in the two chambers.

4.3 RESULTS

TABLE 7

Data collected for Amberlink and Hyline Brown hens during the two week pre-trial period

VARIABLE	STRAIN		mean	S.E.	CV%
	Amberlink	Hyline Brown			
body weight (kg)			1.919	0.037	9.5
BWchange (g/bird.d)	chamber4				
	chamber5				
average			-7.43	1.136	
feed intake (g/bird.d)	chamber4				
	chamber5				
average			103.1	3.15	10.6
rate of lay (%)			92.32	1.610	8.5
egg weight (g)			56.5	0.971	8.4
egg output (g/bird.d)			52.21	1.292	12.1
% in lay			96.87		

(means with a different superscript differ at $\alpha=0.05$)

TABLE 8

Chamber L-H : Mean responses of Amberlink and Hyline Brown birds subjected to 18°C for six weeks, followed by six weeks at 32°C on six test feeds.

	DIET	body weight (kg)		change in BW (g/bird.d)		egg weight (g)		rate of lay (%)		egg output (g/bird.d)		feed intake (g/bird.d)	
		18°C	32°C	18°C	32°C	18°C	32°C	18°C	32°C	18°C	32°C	18°C	32°C
Amberlink	basal	2.025	1.803	-0.04	-15.21	59.48	47.99	78.5	50.0	46.9	27.8	97.4	67.5
	oil	2.013	1.760	1.74	-12.58	58.50	53.00	76.2	44.6	44.7	24.2	89.0	59.6
	filler	1.766	1.667	-1.83	- 8.29	55.50	54.19	86.1	28.6	47.7	16.0	93.7	62.0
	protein	1.776	1.657	-1.09	-10.72	54.78	52.87	80.3	38.9	44.0	26.6	95.9	66.0
	sug/stch	1.810	1.611	-2.64	-10.24	52.78	49.35	76.8	36.3	41.1	18.9	88.3	61.8
	fish	1.967	1.754	-1.11	-12.00	53.13	51.37	69.6	51.2	37.3	29.4	88.3	70.0
mean		1.893	1.709	-0.83	-11.51	55.69	51.46	77.9	41.6	43.6	23.8	92.1	64.5
Hyline Brown	basal	1.860	1.748	0.28	-13.02	53.28	50.93	58.0	50.0	36.2	28.3	88.2	66.4
	oil	1.704	1.590	0.31	-8.64	58.42	53.20	70.5	28.6	43.6	16.2	75.9	56.9
	filler	1.801	1.623	0.54	-9.44	53.17	53.47	78.6	31.8	41.7	18.5	98.0	58.9
	protein	1.731	1.586	-0.23	-7.71	58.40	54.73	56.8	34.9	36.2	22.3	71.9	59.5
	sug/stch	1.924	1.743	0.11	-11.41	58.80	56.60	73.2	48.0	56.2	27.7	97.1	69.4
	fish	1.751	1.634	-1.78	-5.70	59.63	57.55	56.3	56.5	34.4	32.9	87.0	69.9
mean		1.795	1.654	-0.13	-9.32	56.95	54.41	65.6	41.6	39.6	24.3	86.3	63.5
overall mean		1.844	1.681	-0.48	-10.41	56.32	52.94	71.8	41.6	41.6	24.1	89.2	64.0
s.e.		0.180	0.146	2.44	5.13	4.45	4.66	18.04	12.56	10.53	7.92	13.04	8.83
%cv		9.7	8.7			7.9	8.8	25.1	30.2	25.3	32.9	14.6	13.8

TABLE 9

Chamber H-L : Mean responses of Amberlink and Hyline Bown birds subjected to six weeks at 32°C, followed by six weeks at 18°C on six test feeds.

	DIET	body weight (kg)		change in BW (g/bird.d)		egg weight (g)		rate of lay (%)		egg output (g/bird.d)		feed intake (g/bird.d)	
		18°C	32°C	18°C	32°C	18°C	32°C	18°C	32°C	18°C	32°C	18°C	32°C
Amberlink	basal	1.770	1.761	-5.74	7.99	52.65	57.53	70.5	47.9	37.4	40.7	78.7	91.8
	oil	1.869	1.767	-5.00	0.20	50.07	51.30	46.8	52.8	25.8	29.7	62.7	81.0
	filler	1.739	1.817	-5.46	3.18	54.73	55.90	59.5	47.0	32.5	28.3	70.1	80.2
	protein	1.894	1.836	-7.73	8.09	53.05	56.30	62.5	54.8	33.2	31.7	69.1	96.2
	sug/stch	1.817	1.773	-3.81	2.57	50.10	52.37	60.7	55.6	30.3	29.7	74.0	88.8
	fish	1.712	1.680	-5.07	5.34	49.70	56.23	65.5	52.4	33.3	32.6	73.8	88.6
mean		1.800	1.756	-5.47	4.56	51.72	54.94	60.9	51.7	32.1	32.1	71.4	87.8
Hyline Brown	basal	1.820	1.754	-9.41	7.40	56.20	59.10	48.8	60.7	31.3	36.0	62.7	85.3
	oil	1.741	1.960	-7.74	12.01	56.89	57.57	50.0	52.1	28.3	33.2	61.0	85.3
	filler	1.685	1.525	-6.79	10.49	51.37	55.13	59.9	48.8	32.4	29.4	68.9	93.6
	protein	1.642	1.584	-8.95	9.28	53.30	54.78	51.8	51.8	30.7	33.4	61.4	83.8
	sug/stch	1.571	1.541	-5.33	5.83	54.88	57.40	61.6	61.0	36.3	39.7	68.5	83.6
	fish	1.873	1.847	-7.12	8.84	54.70	61.80	56.3	63.7	32.3	39.6	70.3	100.0
mean		1.722	1.675	-7.56	8.97	54.56	57.63	54.7	56.3	31.9	35.2	65.5	88.6
overall mean		1.761	1.715	-6.51	6.77	53.14	56.29	57.8	54.0	32.0	33.7	68.4	88.2
s.e.		0.160	0.168	2.61	4.38	3.84	4.07	18.60	14.80	8.40	10.67	10.17	12.63
%cv		9.1	9.8			7.2	7.2	32.2	27.4	26.3	31.7	14.9	14.3

TABLE 10

Chamber L-H : Mean responses of Amberlink and Hyline Brown birds subjected to a constant 18°C for six weeks, followed by six weeks at a constant 32°C on six test feeds.

STRAIN	DIET	heat (kJ/bird.d)		ME intake (kJ/bird.d)		EE intake (kJ/bird.d)		volume (kg ²⁶)	
		18°C	32°C	18°C	32°C	18°C	32°C	18°C	32°C
Amberlink	BSL	130.4	93.9	1139	812	1008	718	13.82	10.90
	OIL	79.4	53.1	1250	837	1171	784	12.05	10.33
	FIL	124.8	82.6	1079	714	954	632	10.41	9.29
	SPI	126.4	87.0	1271	874	1145	787	10.56	9.15
	S/S	88.0	61.6	1180	827	1093	765	11.09	8.75
	FIS	106.7	84.5	1043	827	937	743	12.89	10.25
mean		109.3	77.1	1160	815	1051	738	11.80	9.78
Hyline Brown	BSL	118.1	89.0	1031	777	913	688	11.68	10.32
	OIL	67.7	50.8	1066	800	998	749	9.73	8.50
	FIL	130.4	78.4	1128	678	997	599	10.90	8.79
	SPI	94.8	78.4	953	788	858	710	10.04	8.44
	S/S	96.8	68.8	1299	924	1202	855	12.40	10.21
	FIS	105.1	84.4	1028	826	923	742	10.29	8.91
mean		102.1	75.0	1084	799	982	724	10.84	9.20
overall mean		105.7	76.0	1122	807	1017	731	11.32	9.49
s.e.		16.3	10.4	162.1	110.9	146.2	100.8	2.11	1.59
%CV		15.4	13.7	14.5	13.8	14.4	13.8	18.6	16.8

TABLE 11

Chamber H-L : Mean responses of Amberlink and Hyline Brown birds subjected to a constant 18°C for six weeks, followed by six weeks at 32°C on six test feeds.

STRAIN	DIET	heat (kJ/bird.d)		ME intake (kJ/bird.d)		EE intake (kJ/bird.d)		volume (kg ²⁶)	
		18°C	32°C	18°C	32°C	18°C	32°C	18°C	32°C
Amberlink	BSL	105.4	122.9	1073	920	950	815	10.48	10.41
	OIL	55.9	82.2	1138	881	1066	825	11.76	10.55
	FIL	93.3	106.8	924	807	817	714	10.12	9.92
	SPI	91.0	126.8	1274	915	1148	824	12.02	11.29
	S/S	73.7	88.4	1187	989	1098	915	11.02	10.48
	FIS	89.2	107.0	1047	872	940	783	9.87	9.49
	mean		84.7	104.0	1107	897	1003	813	10.88
Hyline Brown	BSL	83.9	114.2	997	733	883	649	11.08	10.35
	OIL	54.4	76.1	1199	857	1123	803	10.14	10.79
	FIL	91.7	124.5	1077	793	953	702	9.51	7.79
	SPI	80.9	110.5	1110	814	1000	733	9.01	8.38
	S/S	68.2	83.2	1117	916	1034	847	8.34	8.02
	FIS	84.9	120.8	1181	830	1061	846	11.76	11.45
	mean		77.4	104.9	1114	824	1009	746	9.97
overall mean		81.1	104.5	1110	861	1066	780	10.43	9.91
s.e.		12.7	15.5	157.8	123.5	142.7	111	1.90	1.93
%CV		15.7	14.8	14.2	14.4	14.2	14.2	18.2	19.5

4.4 DISCUSSION

The Reading Model provides coefficients of response for a range of amino acids (Table 12) from which it is possible to evaluate the motivation for feed intake in this trial. The coefficients of response enable the calculation of a theoretical requirement for each amino acid, which can be compared with the concentration of that amino acid in the feed, so that a desired feed intake can be calculated. Emmans (1986) explains the relationship between the desired feed intake and the manner in which the environment and volume capacity seek to constrain it. By observing the responses of the birds at each temperature, and by calculating the first limiting nutrient, it may be possible to attribute the changes in production and in the performance of the bird to the constraints that the environment is placing on or lifting from the birds. The focus of this trial was the calculation and explanation of heats of production as defined by the difference between the ME and EE intakes. This was done by the dilution of a basal diet with ingredients postulated to promote different heat increments. The manner in which the environment accommodates the losses in heat required to achieve desired nutrient intakes to maintain a "potential" production, as revealed by pre-trial data, would indeed test the extent to which the theoretical heat increment produced by each diet will influence feed intake, particularly at high temperatures. The nutrient supply that exists within the constraints of the environment will define a level of performance and it should be possible to predict levels of performance from the data available by applying the knowledge that the data impart. A full description of the system and the diets available will define the characteristics of the heat production that make the EE system at least as good as the ME system previously used.

TABLE 12

Coefficients of response of laying hens to dietary amino acids (mg/d) and well-balanced protein mixtures (g/d). (After Gous, 1981).

amino acid	mg amino acid/g egg	mg amino acid/ kg BW
	a	b
lysine	10	73
methionine	4.77	31
isoleucine	7.97	67
valine	8.9	76
arginine	8.9	53
histidine	3.3	16
leucine	12.5	32
phenylalanine and tyrosine	13.5	32
threonine	6.9	32
tryptophan	2.62	11
methionine and cystine	8.3	80

Using the analysed amino acid contents of the diets (Table 13), desired feed intakes of each bird for the pre-trial and first and second six week periods have been calculated.

TABLE 13

Analysed amino acid compositions (g/kg) of diets used in the pre-trial and test periods.

amino acid	DIETARY AMINO ACID CONTENT						
	LAY111	BSL	OIL	FIL	SPI	S/S	FIS
lysine	8.51	10.60	9.57	9.70	14.37	10.29	10.61
methionine	2.48	5.90	4.59	4.43	5.61	5.67	5.21
isoleucine	6.17	9.05	7.73	8.21	12.00	8.35	8.66
valine	7.48	11.19	9.52	10.20	14.00	10.43	10.97
arginine	10.86	13.36	10.86	12.41	17.46	11.96	12.44
histidine	4.01	5.80	5.05	5.34	7.05	5.43	15.56
leucine	11.64	16.20	13.99	14.85	20.34	14.81	15.37
threonine	5.64	7.48	6.67	7.22	9.55	7.08	7.43
phenylalanine and tyrosine	10.92	14.77	12.24	12.82	19.31	13.70	13.47

The desired (calculated) and the actual feed intakes were compared to determine whether an amino acid was first limiting, and if so, which amino acid was limiting. Table 14 describes the number of hens incapacitated in this way and attributes the deficiency to a particular amino acid.

TABLE 14

First limiting amino acids in the pre-trial and test periods and the number of birds affected.

chamber	pre-trial		period one		period two	
L-H	methionine	48/48	methionine	1/48	lysine	1/48
			isoleucine	2/48	methionine	4/48
					isoleucine	17/48
H-L	methionine	41/48	lysine	2/48	isoleucine	2/48
			methionine	6/48		
			isoleucine	7/48		

Peterson (1983) and Etches (1996) note that methionine is normally the first limiting amino acid in the diet. Considering that they are from the USA and Canada where soya is the only protein source fed, it is natural that this should be so. The desired feed intakes of the LAY 111 diet were 21.48 ± 1.80 g higher ($\alpha=0.01$) than the actual feed intakes in the pre-trial period, causing methionine to be first limiting in all but seven of the pre-trial birds. This contributes to the 7.43 ± 1.14 g/bird.d body weight loss in that the birds were on average 53mg short, which had to be provided by the catabolism of body tissue. Peterson (1983) was able to drop methionine intakes to 255mg/bird.d without affecting egg production. Birds in this study were consuming a little more than this, at an average of 256mg, and it follows that this need not be affecting the egg production of the hens. In addition, ME intakes were greater than the requirement for energy at this temperature.

One would anticipate that the environment be conducive to heat loss in the cool periods such that feed intake would not be limited to the extent that amino acids become limiting. In L-H, three hens were in this position, losing weight in order to sustain a low egg output. In H-L, two birds exhibited a general deficiency in amino acid intakes in the oil and the fish diets. During the hot periods, desired feed intakes were often not satisfied for a spectrum of amino acids, indicating that feed intake as a whole was depressed. Diets predominantly affected by this were the oil and filler diets in L-H and after a period of cool, OIL, S/S, FIS and FIL produced restricted amino acid intakes, where lysine and methionine and isoleucine became first limiting in the diets. The same trend was apparent with metabolizable energy intake. Using pre-trial energy intakes as characteristic values for the birds, both the cool periods allowed some birds to consume at least as much energy as during the pre-trial period. During hot periods, energy intakes were significantly lower.

Having confirmed that a major consequence of the high environmental temperatures was depressed nutrient intake, and a change in the first limiting amino acid, a study of the heats of production should elucidate to what extent the restriction in heat loss was responsible for the limitation in nutrient intake. Of major concern to nutritionists is the economic optimization of nutrient supply to sustain potential production. The Effective Energy system seeks to provide at least as good a response to this objective as the ME

system that precedes it. Focus remains on the ability of the EE diets to reduce heat constraints in production at high temperatures. The diets in this trial have combined many facets of heat production as indicated by the concepts of the EE system, and heat production remains the focus in this discussion.

Macleod (1997) endeavours to persuade that in attempting to promote a heat increment by increasing the energy concentration, decreasing the protein concentration, or providing an imbalanced amino acid mixture, none can be produced. While much of his work disclaims a heat increment in the provision of excess amino acids (A discussion of which is included later), the lack in heat increment he observes can justifiably be explained by the concept of '*ceilings in heat production*'. The concept of there being an upper limit to the bird's capacity to lose heat is supported by Mount (1974) and Emmans (1989). No response in heat production can be observed where a maximum amount of heat is being lost. The chicken as a spherical body has heat loss capabilities defined by the surface area of exchange surfaces. Total heat loss is the sum of the evaporative and sensible heat losses, both of which have a limit, which defines a zone within which the bird can exist comfortably. For this reason, heat production cannot extend beyond a certain threshold, at maximum heat loss, and behavioural and physiological adaptations are brought into consequence to reduce the debilitating effect of high heats of production.

Heat production by definition is the difference between the ME intake and the energy retained. By definition also, the EE ingested accounts for all metabolic processes and the immediate energy requirements of the bird, so that the difference between the ME intake and the EE intake is truly heat production - superfluous heat that needs to be removed. Without making many assumptions, this simple calculation portrays the integral difference between what the bird really needs and that which is superfluous. As such, an analysis of heat production calculated like this, will demonstrate characteristics of the birds and feed. Moreover, an investigation of the variate, heat production (HP), and the surface area of the bird available to lose it, will be valuable. Kleiber (1969) expressed surface area as $10.W^{2/3}dm^3$. Heat production per dm^3 should be a valuable indicator of

whether the capacity of the bird to lose heat in any manner ameliorates the production of it.

A thermally neutral environment is one in which the heat loss in that environment (H_{TN}) is enough to keep the bird warm. In a cold environment, the environmental heat demand (EHD) is greater than the H_{TN} , and the ME intake needs to increase in order to meet the extra heat demand. In a hot environment, H_{TN} cannot be lost and feed intake must be reduced. A constraint is the upper limit to the capacity to lose heat. These trial diets test the capacity of the bird to lose the heat produced under cold and hot environments.

Given a balanced feed, a bird would seek to meet its effective energy requirement (EERQ) (Emmans, 1994), such that the desired feed intake (DFI) would be defined as the quotient of the EERQ and the EE content of the feed.

$$DFI_{EE} = \frac{EERQ}{EEC} \text{ kg/d}$$

This is equivalent to saying that, on a balanced feed, it seeks to meet any other nutrient requirement. On an imbalanced feed, the DFI for protein would be greater than that for EE, and the animal would seek to meet the protein requirement by consuming excess energy. This excess energy as ME must either be retained as lipid (with the heat production associated with its deposition), or be lost as heat. This set of diets is intentionally imbalanced, and the response of the birds under the particular set of circumstances will address several of the above-mentioned issues.

During the pre-trial period, Amberlinks produced 7.0 ± 2.81 kJ/bird.d more heat than Hyline Browns ($\alpha=0.05$). Higher heats of production were apparent in the one chamber during the pre-trial using the same rations. To obtain an indication of heat production at 25°C, values were averaged from both chambers to produce a value on a standard ration of 128kJ/bird.d. In the chamber that changes from 32°C to 18°C (HL), heat production was significantly reduced in the first period (51.5 ± 2.89 kJ/bird.d lower) as a result of the increase in temperature. At 32 °C, the heats of production achieved on the oil and sugar/starch diets were 27.0 ± 7.09 kJ/bird.d lower than the basal, filler, protein and fishmeal diets. As the temperature changed to 18°C, a significant increase in heat

production was experienced (23.4 ± 2.89 kJ/bird.d), while diets followed the same trend with S/S and OIL giving heats of production 36.68 ± 7.09 kJ/bird.d lower than the average of the other diets. Over all weeks of the trial, Amberlinks appeared to produce more heat than the Hyline Browns. HP decreased as the temperature decreased from 25°C to 18°C , and then again by 29.7 ± 2.83 kJ/bird.d as the temperature increased again. The response in heat production to diet over the periods of trial was not constant. At 18°C , the BSL and FIL diets elicited higher heats of production than the SPI, S/S, and FIS, which were higher than the OIL diet. HP of BSL and FIL diets were not significantly different from results during the pre-trial period, while a reduction was evident for SPI, S/S, and FIS at 18°C . As the temperature increased to 32°C , HP was decreased to 76.0 ± 2.83 kJ/bird.d, but the lowest HP values were achieved by the S/S and OIL diets, which were 26.2 ± 6.93 kJ/bird.d lower than the average of the other diets during this period.

From a dietary point of view, the effects of the dilution of the basal diet with the specific diluents is explained by Emmans (1994). The dilution of a dense highly digestible feed with starch means that the protein content will decrease while the EE increases, such that the feed is imbalanced. This will cause the increase in feed intake to meet the DFI (protein), causing an increase in the ME intake which must increase heat production, except where ME is directed to lipid retention, instead of being given off as heat. At the other end of the spectrum, dilution with fibre (sunflower husks) with no nutritive value means that the EEC falls faster than the protein content, such that energy is the first limiting resource, and FOM will increase, as will organic matter intake and volume to meet this need. With the EE/ME ratio falling, heat production will have to increase. Only the 32°C period data of chamber HL are reported in Table 15 in order to illustrate the above concepts that can then be extrapolated in the interpretation of the other data sets. It is apparent that the response in heat production is not consistent across the diets. In fact, it has been possible to delineate the response in terms of the diluent, with the higher effective energy diets (OIL and S/S) having lower heats of production. A calculation of this nature (Table 15) would promote an understanding of the areas of nutrition that the EE system addresses, and it may then be possible to use the information in predictive modelling.

TABLE 15
Dietary characteristics affecting heat productions and performance at 32°C in chamber HL.

Diet	BSL basal	S/S sugar/ starch	FIL filler	OIL oil	SPI protein isolate	FIS fishmeal
ME (MJ/kg)	11.7	13.4	11.5	14.1	13.3	11.8
CP (g/kg)	188.6	176.1	188.0	176.7	240.6	225.3
CL (g/kg)	64.4	67.4	61.3	138.8	68.7	67.4
calc FOM (g/kg)	183.3	110.0	185.9	168.0	116.8	172.4
calc EEC (MJ/kg)	10.4	12.4	10.2	13.2	11.9	10.6
FI (g/bird.d)	70.7	71.3	69.5	61.9	62.3	72.1
DFI _{EE} (g/bird.d)	116.9	97.8	118.8	91.9	101.4	114.0
DFI _{FLaa} (g/bird.d)	60.8	64.3	71.1	72.1	56.1	62.4
FOM intake (g/bird.d)	13.0	7.8	12.9	10.4	7.6	12.4
ME intake (kJ/bird.d)	826.4	852.3	800.0	869.1	864.4	851.5
EE intake (kJ/bird.d)	731.7	881.4	707.5	813.9	778.4	764.5
heat (kJ/bird.d)	94.7	71.0	92.5	55.2	86.0	87.0
change BW (g/bird.d)	-7.6	-4.6	-6.1	-6.4	-8.3	-6.1
EO (g/bird.d)	34.4	33.3	32.5	27.1	32.0	32.8
ROL (%)	59.7	61.2	59.7	48.4	57.2	60.9

The following conclusions can be drawn from the data in Tables 7 to 11 and Table 15. In chamber HL, where the temperature was kept at 32°C for six weeks before being dropped to 18°C for the final six weeks, each period of the trial produced a significantly different result, with the imposition of the environmental constraint to heat loss followed by the lifting of this restriction. Body weights were 175±34.1g lighter than the pre-trial weights at 32°C, but periods one and two were not significantly different. No effect on BW of the birds being on different diets could be found. The Hyline Browns lost more weight at 32°C and were able to gain more at 18°C than Amberlinks, so that strain body

weights were not different, although Amberlinks were slightly heavier birds. Hyline Browns were able to lay eggs 2.54 ± 0.70 g heavier consistently over the weeks of trial, although both types of bird had reduced egg weights at the higher temperature. At 18°C , the eggs of both strains were 3.42 ± 0.86 g heavier, although no dietary influence on EW could be inferred. Rates of lay were unaffected by diet but the high temperature decreased rates substantially ($\alpha=0.01$) which the birds were able to maintain in the subsequent cool period. The same was true for the egg outputs.

The change in performance characteristics must be a function of the nutrient intake and the heats of production at the two temperatures. Heats of production in chamber HL decreased to 81.1 ± 2.89 kJ/bird.d from a pre-trial value of 132.2 kJ/bird.d. When it was cool once more, they were able to produce 104.5kJ/bird.d. This must mean that the environment constrained the amount of heat they could lose to a value in the order of 132kJ/bird.d. Sykes in Li *et al.* (1992) quoted a value of $4.8\text{kJ/kg}^{0.75}/^{\circ}\text{C}$ as a decrease in energy requirements for maintenance as the environmental temperature increased, and conversely, if we assume a maintenance energy requirement to increase by the same value when the temperature decreases, then the 7°C increase that the birds were subject to would involve the alteration of the heat produced by 22.0kJ. Emmans (1974) has also shown that the energy required for maintenance decreases by $8.4\text{kJ/kg.d.}^{\circ}\text{C}$ at temperatures greater than 25°C). The addition of this value to the heat produced at 18°C would give a value of 126.5kJ which is not significantly different from the pre-trial value. This heat then has been produced, but is used for the maintenance of body temperature at the cool 18°C . Also apparent from the data is that the sugar/starch and oil diets produced 27.0 ± 7.09 kJ/bird.d less heat at 32°C and 36.68 ± 7.09 kJ/bird.d at 18°C than the other diets. These two diets had the highest effective energy contents and their desired feed intakes to meet the requirement for EE were more closely met than on the other diets. The non-significant difference between diets in the feed intakes within any period translated to strain differences ($\alpha=0.05$) in ME and EE intakes, with the Amberlinks able to consume more energy. A slight difference in EE intake across diets at 32°C could be inferred ($\alpha=0.056$) with the sugar/starch diet giving higher EE intakes. At 18°C , the dietary difference in ME intakes was lost, but this caused a greater disparity in the amount of EE the birds consumed. The oil and filler diets were the two extremes on

offer to the birds, but the environment was not hampering any amount of heat loss from the birds, and these disparities did not influence the performance of the birds. Data from non-laying hens can be used to provide a measure of the heat increment associated with laying.

TABLE 16

Energy intakes and exchanges in non laying hens in both chambers at 32°C.

hen	diet	strain	ME intake (kJ/bird.d)	EE intake (kJ/bird.d)	HP (kJ/bird.d)	BW change (g/bird.d)
#66	filler	HB	414.7	366.8	47.9	-6.4
#67	filler	AL	609.3	538.8	70.5	-6.7
#80	oil	HB	488.7	457.7	31.0	-6.9
#3	oil	AL	877.3	821.6	55.7	-4.5
#29	fish	AL	580.6	521.3	59.3	-10.0

A comparison of heats of production across the two chambers at the same temperature indicated that the data were not different ($\alpha=0.01$), and a mean response in heat production of 78.05 ± 17.03 kJ/bird.d and 104.67 ± 23.68 kJ/bird.d was achieved at 32°C and 18°C, respectively. This meant that the average HP for the above hens (Table 16) could be pooled. If non laying hens were producing heat at a rate of 52.88kJ/bird.d, (the average of the above data) then that meant that the difference between this value and the actual heats of production equalled the heat increment of laying. Strong evidence exists of a linear trend between heat production and egg output (Figure 26). The regression sum of squares is not improved by fitting a quadratic model.

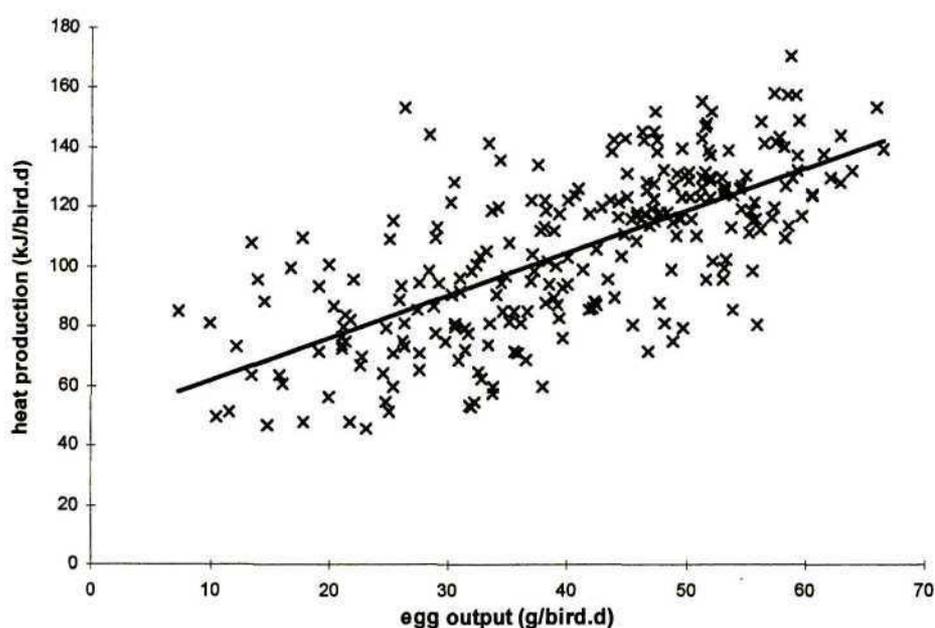


Figure 26 *The relationship between heat production and egg output over 14 weeks of trial.* $HP(kJ/b.d)=47.73+1.433 EO$

The model predicts that for zero egg output, heat production has a value of 47.73 ± 4.04 kJ/bird.d. The average value obtained from the non-laying birds falls within the confidence interval of this parameter estimate ($\alpha=0.01$), validating the value obtained. Without extrapolating outside the range of the data, maximum egg outputs will give a maximum in heat production. The alternate temperature regime (L-H) produced similar results. Once again, the addition of a maintenance heat demand to the heat production at 18°C negates the decrease in heat production apparent as the temperature drops to 18°C in the first period in this chamber. The heat production is curbed again as the temperature is increased to 32°C . The response in heat production to diet over the periods of trial was not constant, in that the basal and filler diets promoted more heat than the protein, fish or sugar/starch diet, followed by the oil diet at 18°C . At 32°C , the highest effective energy diets, sugar/starch and oil, were lower than the rest by 26.2 ± 6.93 kJ/bird.d. These results correlated significantly with the effect of diet on the EE intake of the birds. In the first period, the disparity between the sugar/starch and fishmeal diets was noted ($\alpha=0.01$), which did not have any effect on egg output though. At the higher temperature, the higher EE intakes of sugar/starch and oil ($\alpha=0.01$) compared to filler translated into heats of production ($\alpha=0.01$) and egg output ($\alpha=0.05$),

such that egg outputs on the filler diet were significantly lower than the rest. Since feed intakes and ME intakes showed no response after temperature to diet or strain, the response in heat and egg output could be attributed to the EE intake. While the high temperatures appeared to severely compromise rates of lay, a significant regression ($\alpha=0.01$) accounting for 44% of the variation related egg output to the effective energy consumed.

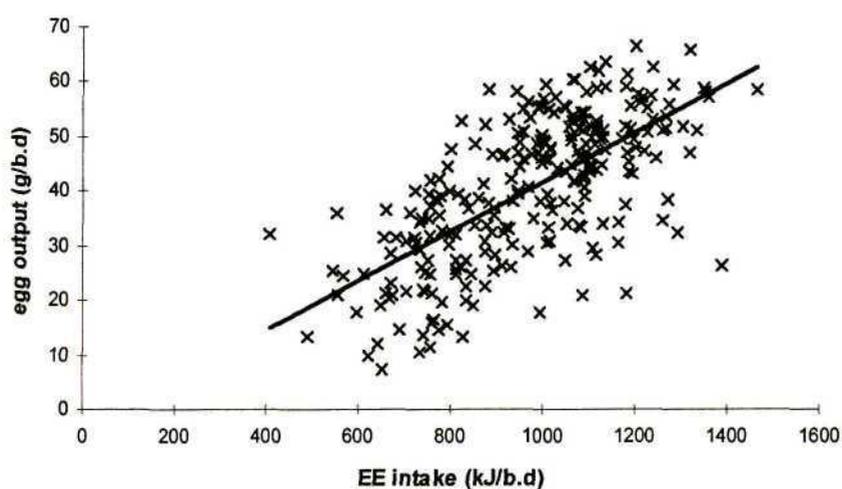


Figure 27 *The relationship between egg output and effective energy intake.*

$$EO(g/b.d) = -3.50 + 0.04526 \text{ EE intake}$$

[As an aside, the inverse of this graphic, with egg output as the independent variate and EE intake as the dependent variate permits two calculations : the regression equation produced is $EE \text{ intake (kJ/bird.d)} = 572.42 + 9.8201EO$

This means that 9.82kJ of EE are required per gram of egg output, in contrast with the calculated value of 8.8kJ of EE required per gram of egg of Emmans (1994). It can also be inferred that maintenance EE requirements are 572.42kJ, which is $1630 \cdot (0.133 \cdot 1.7985)^{0.73}$ kJ, the only assumption being the protein percentage of the adult hen. Emmans and Fisher (1986) make the assumption of 15% protein in the mature hen].

The birds were able to maintain weight through the first period, but lost weight in the second period. Highest BW losses were experienced on the BSL, OIL and S/S diets. Filler resulted in the lowest BW loss, and implied a severe reduction in egg output and

the reduction of BW loss rather than the maintenance of lay. The depletion of reserves was reflected in the inability to maintain egg weight in the second period. Egg weights dropped by 2.89 ± 0.99 g. It became apparent that the Hyline Browns were laying heavier eggs ($\alpha=0.05$) at 32°C . The response in rate of lay over the weeks of trial was not constant, such that the significantly higher rate of lay on the filler diet (82.3%) that placed it above the oil and sugar/starch diets at 18°C was the lowest rate of lay at 32°C . The significant decrease in laying performance at 32°C could be attributed to the influence of the four diets oil, filler, protein and sugar/starch at the higher temperature. While rates of lay were similar between strains in the pre-trial period, the Amberlinks laid $12.3 \pm 5.21\%$ more eggs, all be they smaller, at the cool temperature. Both strains had a similar rate of lay at 32°C .

From the above, it would appear that the factors affecting heat production can be summarised as the egg output, the effective energy intake and perhaps the surface area of the body. The latter is calculated as $10 \cdot (\text{BW})^{0.75}$ (Kleiber, 1969), and its inclusion in a multiple regression model might explain some variation in heat output. The multiple regression model including effective energy intake, egg output and the volume of the radiating sphere accounts for 62.7% of the variation in heat production, which is significant at the 1% level. All the data points over the period of trial have been included in the estimation of heat production. Table 17 summarises the regression analysis, and explains the significance of the included terms.

TABLE 17

Estimates of multivariate regression coefficients for trial data relating heat production to effective energy intake, egg output and volume of the bird.

	estimate	standard error	t probability
egg output (g/bird.d)	0.694	0.109	<0.001
EE intake (kJ/bird.d)	0.06472	0.00768	<0.001
volume ($\text{kg}^{0.75}$)	1.399	0.511	0.007

This regression accounts significantly for the variation occurring in heat production, although graphic evaluation indicates the necessity of some grouping structure to account more effectively for the variation. The residual mean square can be reduced to 9.15kJ/bird.d when diet is introduced as a grouping structure. As such, it serves to segregate the multivariate regression into responses with different intercepts and regression coefficients. An accumulated analysis validates the interaction of the variates with Diet ($\alpha < 0.01$), and the resulting regression equations (Table 18) support collectively the conclusions made previously in this thesis.

TABLE 18

Estimates of multivariate regression coefficients for trial data relating heat production to effective energy intake, egg output and volume of the bird, grouped by dietary treatment.

DIET	constant	EO g/bird.d	EE intake kJ/bird.d	volume kg ^{3/4}
BSL	16.61	+0.5196	+0.08701	-0.224
OIL	-58.09	+0.5196	+0.08701	+3.419
FIL	28.91	+0.5196	+0.08701	-1.474
SPI	-2.69	+0.5196	+0.08701	+0.686
S/S	-30.39	+0.5196	+0.08701	+1.564
FIS	1.11	+0.5196	+0.08701	+0.368

Different intercepts and slopes in the multivariate regression model increase the variation accounted for to 84.0% and reduce the residual mean square to 11.02, both of which are significant improvements on the previous models, except that including Diet makes it experiment specific. Examination of the regression coefficients in Table 18 reveals that heat production can be manipulated by consideration of the factors mentioned here. The constant term in itself explains that basal heat productions on the higher effective energy diets, OIL and S/S are lower than when the basal diet is diluted with a non-nutritive filler. Egg output cannot sensibly be diet-specific, and neither can the EE intake, so that heat production will increment consistently with egg output and EE intake across levels of

diet in the regression model. The only significant interaction exists with volume, where the coefficients indicate that heat production is a function of the body volume. The higher effective energy diets demonstrate the greater capacity of the birds on these diets to increase live weight. The importance of EE intake in the prediction of a heat production lies in the reduction of the increase, ie. the FIL diet would be contributing more to heat per kilojoule of energy consumed than the OIL diet. This underlines the concepts of effective energy, by quantifying the effect of the EE:ME ratio. The lowering of this ratio implies that the EE is lower per kilojoule of energy consumed. Collectively the model is more informative, and builds on the theories formulated earlier.

The information reported has shown the validity of the assumptions made by Emmans in his formulation of the Effective Energy system (1994). The Effective Energy system realistically accounts for partitioning of energy consumed beyond a metabolizable level, and responses in the bird are achieved where diets are formulated to test an hypothesis that the factors in heat increment should have no effect at all on performance in laying hens. The objectives expressed earlier have been achieved. Diets of different effective energies have been formulated through the dilution of a basal diet with diluents motivated in choice by their contribution to a heat increment as defined by Emmans (1994). Individual responses of white and brown birds have been established. Strain differences are apparent in the performance criteria such as egg weight and rate of lay, although these remain non-significant as an egg output, and no difference between strains in response to effective energy can be inferred. Emmans (1994) was very careful to note that the Effective Energy concepts depend on there being a nutritional restriction, such that at cool temperatures, little benefit would be realised in the application of the system, because nutritional inadequacies could be compensated for by an increase in nutrient intake with the environment placing no restriction on the amount of heat the birds could lose. At high environmental temperatures, it becomes critical that the nutrient density be maximised, or rather that the supply of effective energy be maximised in order to maintain egg production.

It is important to include some opposition to the theories expounded on in this trial. In defending the system, one is able to establish integrity of the system. Macleod (1997)

was unable to elicit a reaction in heat production across a number of diets considered to elevate metabolic rates, *viz.* high energy concentration, low protein concentration and an imbalanced amino acid mixture. *Inter alia*, he concluded that there was "no indication of a stimulation of heat production by excess amino acids". Because this statement directly contravenes an integral part of the Effective Energy system, and indeed, results of this trial, it is important to disclose why he might have reached this conclusion. There are two means of doing this. One would be assessing the theoretical validity of the heat increment that eludes him, and the second would be to investigate what in his data led him to that conclusion. The former is rather laboriously expressed by a simulation of energy metabolism in which complete stoichiometric relationships are established in energy metabolism (Schultz, 1978). Schultz uses a computer-based calculation of the amount of ATP formed (mol) during oxidative metabolism, and calculation of the utilization of ATP for maintenance and biosynthesis, based upon the representation of the animal as a quasi-steady state system. Requirements for energy exist in the :

- absorption and transport of nutrients into the blood stream against a concentration gradient
- the synthesis of triacylglycerols from free fatty acids and for the formation of the protein coat of chylomicra
- passage of metabolite through the cell membranes and into the blood stream
- absorption and membrane transport of nutrients required for maintenance is the one component of a maintenance requirement, but the energy cost of these processes for nutrients in excess of requirement must be accounted for in an explicit manner
- excretion of urea by the kidneys

Thereby, each mol of metabolite involved in the biosynthesis of body substances is transported across biomembranes with the expenditure of energy as ATP. The biosynthesis of body substances involves the expenditure of energy for processes other than transport, for example synthesis of nucleic acids. Available energy (ATP) is the ATP (mol) formed upon complete oxidation of CHO and fat to CO₂ and H₂O, and protein to urea, CO₂, H₂O and SO₄²⁻. 77.3kJ is available per mol of ATP from any nutrient.

Schultz gives the following calculated parameters of energy balance :

$$\text{HP} = (\text{dietary available energy} + \text{energy available in body substances oxidised-} \\ \text{available energy in body substances synthesised})$$

In terms of the foundations laid for the EE system, this can be equated to :

$$\text{HP} = \text{ME} - \text{ER}$$

Schultz describes heat increment as the difference between the HP and maintenance energy and consisting of two components :

1. HI (energy retention) - the sum of ATP required for membrane transport of metabolites involved in net synthesis of body substances, ATP required for the synthesis of AA to direct protein synthesis, ATP required for the synthesis of covalent bonds and the ATP required for all other reactions associated with the synthesis of body substances.
2. HI (metabolic processes) - in processes , for example gluconeogenesis, lowering the yield of ATP during metabolism, but processes which are not related uniquely to the net synthesis of body substances.

It is precisely these heat increments in feeding that Emmans (1994) captures in the Effective Energy system. The EE system recognises the following work functions as incurring energy costs in their excretion (Table 1). It is important to mention that these are not mutually exclusive events in respect of their demand on energy. Not even maintenance can be said to have an absolute demand for ingested energy. Figure 10 indicates where heat increments and energy retentions exist. The organic matter oxidised represents the gross energy ingested by the animal, which, if it is digestible, is partitioned in protein, lipid and CHO fractions.

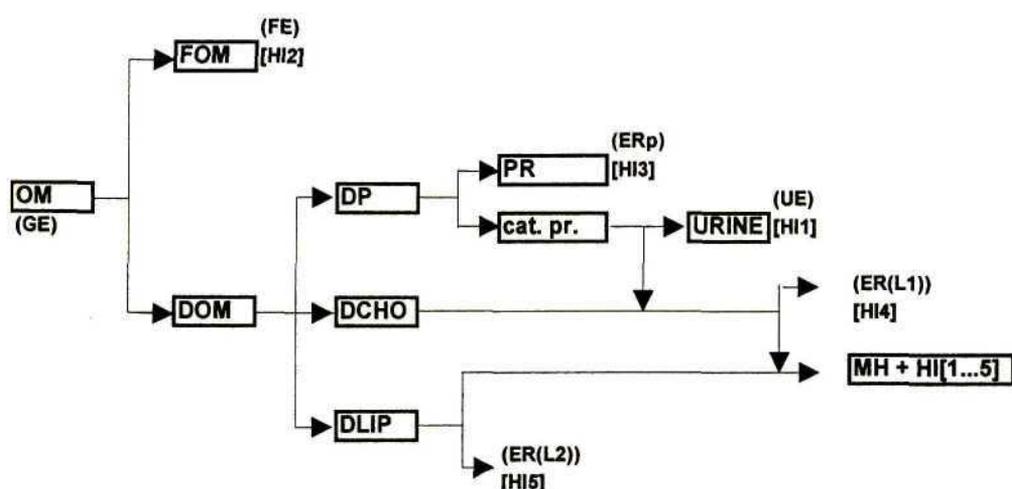


Figure 10 Flow of organic matter in the monogastric above maintenance (after Emmans, 1994).

Specific dynamic action (exothermic reactions associated with metabolism of absorbed nutrients) accounts for most of the observed increases in heat production (Farrel, 1976). Protein *per se* is not the only factor thought to influence SDA. Fat in poultry diets is incorporated directly into tissue lipid at low energy cost (Annison (1974) in Farrel (1976), Emmans, 1994), whereas lipogenesis from dietary CHO induces a substantial increase in heat production which is higher than when CHO is oxidised for maintenance (Bulacu *et al* 1969, in Farrel, 1976). Protein turnover is energetically an expensive biochemical process (Buttery and Annison 1973, in Farrel 1976). Poultry are inefficient in converting food to animal protein (Deschepper and de Groote, 1995). Reduction in nitrogen excretion and improvement in the efficiency of nitrogen deposition is achieved by matching the amino acid composition of the diet with the amino acid composition of the broiler for maintenance and meat production. Keshavars (1991) in Deschepper and de Groote (1995) postulated that low protein diets increase the tolerance of birds to elevated temperatures because heat productions associated with the utilization of protein are greater than with utilization of CHO and fat.

Substitution of protein for CHO would tend to reduce net energy yields of the diet because of the poorer net efficiency of protein as a dietary energy source. It is possible that poor quality protein, fuelling catabolism of unwanted excesses of amino acids, would exaggerate thermogenesis and further reduce a net energy yield from protein (Boorman and Ellis 1996). HP adjusted for BW ($/\text{kg BW}^{0.67}$) in broiler chicks at 21 days old was independent of AME concentration but increased by about 8% on the higher CP diets, associated with a decrease in the net efficiency of energy utilization for growth. Protein synthesis has a higher energy cost than fat deposition (Macleod, 1991). Poorer feed utilization is really due to heat increment (Guillaume and Summers, 1970). Data on pigs indicate the high energy cost of apparent synthesis of protein in growing animals - the cost is definitely higher than theoretical estimates from metabolic pathways (van Es, 1971 in Charlet-Lery, 1976). Dietary protein content increases the level of gaseous exchange and heat production. Higher energy expenses are incurred in energy utilization for higher protein turnovers on high nitrogen meals (Charlet-Lery, 1976).

Macleod (1997) reports an experiment wherein he concludes that "there is no indication of a stimulation of heat production by excess amino acids". He is of the opinion that because more protein is being excreted, less is being retained. The ratio of ATP yield to utilization is 68:32, and in this fashion, the ATP contributed from oxidized amino acids is potentially available to spare the oxidation of other substrates. Macleod has segregated the issue of protein in energy metabolism in saying that the net yield of ATP in oxidation of amino acids over the synthesis of uric acid for their excretion is sufficient to prevent the oxidation of other substances and therefore need not lead to heat productions additional to that from oxidation of CHO and fat.

It is true that amino acids cannot be stored, and as such, provision by the diet in excess of that required for the synthesis of body protein must be excreted. It is also true that "the cost of uric acid synthesis is more than offset by the energy resulting from the oxidation of amino acid molecules" (Macleod, 1997), if protein metabolism were an isolated event. But, truth also exists in the relative efficiencies of the processes further explained by Schultz (1978). The partial efficiency of maintenance energy is approximately 0.925, and for retention is 0.72 (Macleod, 1997). This anticipates the

release of heat energy as an inescapable product of energy utilization. Provision of amino acids in excess of requirement provides energy in oxidation, but also sacrifices energy as heat as a function of energetic inefficiency. Heat energy is also lost in the utilization of ATP in the formation of excretory products. The amplification of this effect over 20 amino acids is more significant than the energy savings in initial oxidation, and the conclusion is made that there are theoretical grounds for the stimulation of heat production by excess amino acids.

A thorough review of the papers of Macleod (1990-1997) has produced a theory as to why there would be no indication of an increase in heat production related to the supply of excess of amino acids in the diet (Macleod 1997). Macleod (1990) concluded that growing female fowl responded to large differences in voluntary energy intake and dietary protein concentration by changes in the quantity and chemical form of retained energy but not in the rate of energy dissipation as heat. Variation in HP did not have an important regulatory role in energy deposition and body composition. A pervading theory apparent in his work then is the expectation that diet-induced thermogenesis be accounted for in an increase in heat production, or that there is a role in heat production in modifying dietary effects on body composition. He offers that diet induced thermogenesis would instead be apparent in a change in body composition. It is indeed this change in body composition that would allow the "absorption" of heat produced by the diet.

Macleod (1997) calculated that the ATP energy obtained through oxidation of protein offset the energy cost in synthesis of uric acid, so that the oxidation of excess amino acids need not lead to heat productions additional to those of CHO and fat, and one could potentially spare the oxidation of other substrate. In Macleod (1990) he concedes that as the proportion of non-protein energy decreases, amino acids are left to function increasingly as substrate through either oxidation, gluconeogenesis or lipogenesis. He also notes that the catabolism of amino acids as an energy source is indicated by the high nitrogen maintenance requirement and the low gross and partial efficiencies of nitrogen retention as observed when the CP:TME ratio increased. Unfortunately, the connection between the low efficiencies and the protracted metabolism of protein as an energy

source have eluded him as a probable cause for heat increments. Direct calorimetry measures the heat production as a function of oxygen and carbon dioxide concentrations. While this should demonstrate an increase where more metabolic reactions are occurring, Pullar *et al.* (1969) found that the estimate of total heat loss by direct physical measurement in the calorimeter were found to be 3-12% lower than those by indirect method involving body analysis at the beginning and end of an experimental period. That this means that higher heat productions could be expected from calorimetry results is speculative, but the truth of the matter exists in the concept of there being an upper limit to the bird's capacity to lose heat (Mount, 1974; Emmans, 1989). No response in heat production can be observed where a maximum amount of heat is being lost. The chicken as a spherical body has heat loss capabilities defined by the surface area of exchange surfaces. Total heat loss is the sum of the evaporative and sensible heat losses, both of which have a limit, which defines a zone within which the bird can exist comfortably. For this reason, heat production cannot extend beyond a certain threshold, at maximum heat loss, and behavioural and physiological adaptations are brought into consequence to reduce the debilitating effect of high heats of production.

Using broiler males over the period 14 to 21 days of age, Macleod (1997) uses calorimetry to measure responses to diets intended to elevate metabolic rates and thereby induce heat production. The broiler characteristically optimises protein retention (PR) in growth, and 14-21 days of age in the reported trial represents a region of exponential growth. Priorities of protein for growth in PR will be curbed by the first limiting amino acid in the diet. Macleod has purposefully ensured that lysine remains first limiting such that growth will be restricted to the level of lysine intake (Gous and Morris, 1985; Morris *et al.*, 1987). Lysine required (g/kg diet) for optimum growth or maximum efficiency is directly proportional to the protein content of the diet, with a single essential amino acid deficiency having no effect on the ability of chicks to extract ME from the diet (Okumira and Mori, 1979).

Macleod has many responses consistent with those reported in the literature, for example, Harper *et al.* (1970) in Boorman and Ellis, (1996) stressed that the body's response to amino acid imbalance could be viewed as a homeostatic system for the defence of a

normal plasma amino acid pattern. One part of this system is the compensation for diet induced relative plasma deficit of one essential amino acid by the release of that amino acid from muscle through the normal process of protein turnover. Protein resynthesis will be constrained in the protein turnover cycle and this might be enough of a constraint to register as a curtailment of maximum response. This explains why it is necessary to maintain ideal amino acid ratios in the diet even when protein and amino acids are no longer limiting (Morris *et al.*, 1987). It also explains many of the responses of the low lysine diets used by Macleod (1997). Many of the responses of Macleod (1997) can be explained in terms of a decrease in feed intake. Fisher *et al.* (1960) in Boorman and Ellis (1996) (also Farrel 1976) asserts that the imbalance of amino acids manifests itself in a reduced feed intake. There is no evidence of a decrease in the efficiency of lysine utilization for weight or nitrogen gain as protein quality decreases. HI in lysine deficiency was extremely low. Basal metabolic rate (BMR) per unit metabolic BW was increased by deficiencies of lys, thr, ile, leu. (Farrel 1976). That Macleod did not perceive these as explanations rather than discounting the heat production in amino acid excesses can be regarded with intrigue. Calculations on the data of Macleod (1997) clearly indicate the presence of a heat increment. Using the data of diets A and E which provided 4g/kg lysine from an imbalanced protein source and additional synthetic amino acid respectively, heat production can be calculated as the difference between the EE and ME intakes. The diets have effective energies of 9.09 and 10.55MJ/kg and the superfluous heats of production are 77.2 and 40.50kJ/bird.d, respectively. A low lysine diet with a high effective energy produces 32.5kJ/bird.d of heat. Diets providing 8g/kg lysine using a lysine supplement and an imbalanced plant protein produce 129.91 and 110.92kJ/bird.d of heat. The disparity in heats of production between the last two diets is reduced, but the birds were housed at 20°C and no upper threshold limits exist to the production of heat. These observations are similar in a number of respects to the heat increment trial reported by the author. Superfluous heats of production can be promoted through an imbalanced amino acid mixture, and where the environment allows the production of heat in a manner that feed intake satisfies the requirement for a first limiting nutrient, performance is a matter of the intake of the first limiting resource. While no difference in HP was apparent between Macleod's diets, they clearly possess different characteristics, as the EE component and heat production indicate, and this

would not be apparent from a unilateral comparison of gaseous exchange.

Macleod (1991) asserts that there is no indication that a regulatory increase in HP was used as a sink for "excess" energy either on a low protein or a high energy diet. This is for all intents and purposes true, along with his assertions that birds will respond by changes in the quantity and chemical form of retained energy but not in the rate of energy dissipation as heat. The nature of energy balance is such that the metabolizable energy intake be partitioned among the energy retentions, but apart from the heat production being a balance in the equation : $ME_i = ER + HP$, there are inalienable consequences of the ingestion and partition of the ME which exist as heat production. We have sufficient evidence to disregard his assertions that the supply of excess amino acids does not bear with it a heat increment, and his own data support this. We have been fortunate in pursuing the trail of information following from Macleod's (1997) work, in that the EE system accounts for many of the responses to which Macleod sought an explanation. Trial work by the author demonstrates also the effects of a heat increment in one form or another, including the inhibition of performance where CP levels are increased and provide an unbalanced mixture of amino acids.

Because the Effective Energy system incorporates factors that have been proven to cause differences in heats of production, it has to be at least as good as the ME system in the formulation of feeds for hens, especially at high temperatures. The next experimental procedure is designed to specifically evaluate this context of the Effective Energy system, in that EE diets are considered relative to a commercial standard and are tested against the notion of simply increasing the nutrient density at high temperatures. Valuable information now exists about the definition of Effective Energy and its intrinsic properties in accounting for properties of the feeding of feeds. There is more to feeding than nutrition, and the value of the Effective Energy system lies in its comprehension and appreciation of its facets.

CHAPTER 5

RESPONSE OF LAYING HENS TO EFFECTIVE ENERGY AT HIGH AND LOW ENVIRONMENTAL TEMPERATURES.

5.1 INTRODUCTION

Valuable information has been generated regarding the definition of effective energy as well as the components of the system that are integral in the formulation of feeds for laying hens at high environmental temperatures. The main motivation for the present study was the response in heat production that was achieved when a basal diet was diluted with single ingredients to promote different heat increments in feeding in a previous study. The effective energy contents of the test feeds varied as a result of the dilution, and the performance of the laying hens encouraged the more direct exploration of the effect of the supply of effective energy to hens at high temperatures. Diets were therefore formulated to test the proposition that heats of production could be minimised with effective energy diets. These diets include commercial alternatives that simply alter the nutrient density of the feed.

The objectives of the experiment were therefore to:

- test the response of Amberlink layers at high and low environmental temperatures
- to the high and low effective energy diets, and to
- compare the effective energy diets to the commercial alternative

5.2 MATERIALS AND METHOD

5.2.1 FACILITIES

The controlled environment unit at the University of Natal Research Farm Poultry Section was used in this protocol. The characteristics and capabilities of the chambers were the subject of another study (Paton, 1994), and have been discussed in Section 4.2.1. An important difference between the two procedures was the extent of the

environmental control within the chambers. The previous study conducted there indicated that the chambers operating under the same temperatures produced slightly different results from the birds. Practically, more stringent control was taken of the temperature profiles of the separate chambers. A TinyTalk™ instrument was used in conjunction with the Orion Tiny Logger Manager (OTLM™) software to log the temperature in the chambers every 10 minutes, and this information was regularly downloaded and printed in graphic form to evaluate the temperature control. One such output is included as Appendix II. The output indicates that control for the period of the data presented was within 0.5°C of the desired temperature. It is true that the one chamber was less variable in temperature than the other, and care was taken to evaluate the results in terms of this. Statistical control by replicating observations in both chambers increased the validity of the data by indicating that performances in each chamber were not statistically different.

5.2.2 BIRDS

Ninety six Amberlink layers at 26 weeks of age were removed from a standard cage layer facility at the beginning of spring (September, 1997) and were randomly allocated to 96 individual cages in the two chambers. Conditions were replicated in both chambers. Prior to the experiment they were receiving a standard winter LAY 117 mash (formulated to satisfy intake of all nutrients at an intake of 117g/bird.d). This they continued to receive in individual feeders for a period of three weeks in the chambers set at a constant 25°C. The lighting program of the birds of 16L:8D was not changed throughout the period of trial. Water and feed access were unrestricted and manure was removed frequently to prevent the build up of ammonia and pests.

5.2.3 TEMPERATURE

For the first three weeks of pre-trial, the chambers were set at 25°C. Three seven-week periods followed during which the temperature was increased to 30°C, dropped to 20°C and increased to 30°C constant temperature.

5.2.4 FEEDS

Diets were formulated using Winfeed 1.1 (Windows Feed Formulation software developed at the University of Natal, Pietermaritzburg, Gous, 1995). Much evidence exists of the bird's inherent capability to differentiate between feeds on offer (Emmans, 1979; Gous, 1981), and the bird's nutritional wisdom would be appreciated to understand what choices it would motivate at high temperatures. A commercial Lay 111 diet (formulated to satisfy requirement for all nutrients at an intake of 111g/bird.d) was used as an ingredient in producing a LAY 95 and LAY 125 diet for high and low nutrient density diets, respectively. Both were offered as the 95/125 choice diet. A high (H) and low (L) effective energy diet were formulated, varying as much as possible in EE, given the ingredients available at the time. Specific ingredient choices were used to maximise and minimise effective energy as an objective function. A disparity of only 1.13MJ/kg between the diets proved to be sufficient to induce a response to the diets. To test the extent of the disparity between the high and low EE diets, blends of these diets were offered. That the choice made by the birds would somehow reflect a percentage in this dilution series was considered. These treatments are listed in Table 19. Eight diets were to be randomised over the 48 birds in each chamber, two of which were choice diets.

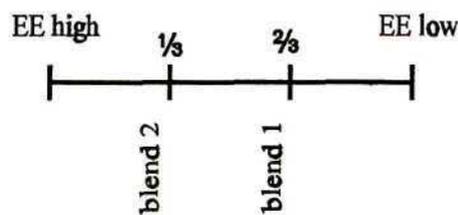


Figure 28 *Scheme of the high and low effective energy diet blends.*

TABLE 19

Dietary treatments and code identification.

DIET	DIET CODE
high effective energy	H
low effective energy	L
high low choice	H/L
$\frac{2}{3}$ Low : $\frac{1}{3}$ High	B1
$\frac{2}{3}$ High : $\frac{1}{3}$ Low	B2
LAY 95	N
LAY 125	O
95/125 choice	N/O

Formulated compositions of the diets and their formulated nutrient specifications are found in Tables 20 and 21, and Table 22 contains the analysed nutrient contents of the diets.

TABLE 20

Formulated composition (g/kg) of the six dietary treatments available to Amberlink hens at 30°C and 20°C.

ingredient	HIGH EE (H)	LOW EE (L)	LAY 95 (N)	LAY 125 (O)
maize	416.45			
wheat bran	222.68			
brewers dried grain	53.59			
lupin	52.80	120.00		
lucerne meal	40.00		20.00	22.10
fish meal	58.91	100.00	41.50	
carcass meal	60.00			
L-lysine HCl	1.96	1.96		0.20
DL methionine	4.16	4.16	1.00	0.50
vitamin/mineral premix	2.50	2.50	0.68	0.53
limestone	83.94	96.35	24.10	
salt	2.65	3.62	1.60	12.90
maize gluten 60		120.00	1.40	0.60
sugar/starch		11.62		
full fat soya		133.89		
monocalcium phosphate		1.28	0.30	
soy protein isolate		120.00		
sunflower husks		220.35	87.70	138.30
sunflower oil		63.92	36.80	36.60
sunflower 37			57.40	
LAY 111			728.20	788.80

TABLE 21

Formulated nutrient composition (g/kg) of the six dietary treatments available to Amberlink hens at 30°C and 20°C.

nutrient	HIGH EE	LOW EE	LAY 95	LAY 125
	(H)	(L)	(N)	(O)
CP	141.50	300.00	161.90	121.00
lysine	9.10	18.20	8.70	6.60
calcium	35.80	38.50	34.20	27.60
phosphorous	3.90	3.90	3.70	2.80
fat	38.00	110.00	80.00	80.00
crude fibre	65.90	33.60	100.00	115.30
dry matter	898.92	943.55	918.50	916.39
ash	55.80	33.00	44.20	38.10
AME _n (MJ/kg)	11.00	11.00	11.30	11.30
EE (MJ/kg)	9.49	8.36	10.18	10.37

TABLE 22

Laboratory analyses (g/kg) of the six diets fed to Amberlink hens at 30°C and 20°C.

nutrient	HIGH EE	LOW EE	Blend 1	Blend 2	LAY 95	LAY 125
	(H)	(L)	(B1)	(B2)	(N)	(O)
AME _n (MJ/kg)	11.79	13.19	12.65	12.24	12.30	12.35
CP (g/kg)	17.92	34.68	29.50	23.97	17.76	13.70
calcium (g/kg)	3.60	4.07	3.96	4.12	3.78	2.63
phosphorous (g/kg)	0.60	0.50	0.54	0.55	0.58	0.45
fat (g/kg)	5.18	13.33	10.72	7.67	11.67	11.46
crude fibre (g/kg)	4.73	13.63	10.59	7.44	10.33	12.77
dry matter (g/kg)	90.70	93.20	92.85	91.50	91.85	91.10

5.2.5 MEASUREMENTS

Measurements were taken of body weight, feed intake, rate of lay and egg weight. Egg component data (not reported here) were also collected. Body weights were established at the start of the pre-trial and the two subsequent periods, and also in the middle of the second period and at the end of the trial. From these measurements, changes in body weight could be calculated. Feed troughs were filled on the Monday and weighed, and subtracting the weight left the following Monday gave the feed intake for the week. Eggs were weighed on three consecutive days each week to give an average egg weight for each hen, and rates of lay were determined daily. Table 23 reports the average performance of the hens in the two chambers. Results presented in the table are average values over the last four weeks in each period, as such constituting a stable and exclusive response to the conditions in that period.

5.3 RESULTS

TABLE 23

Responses of Amberlink layers to eight experimental diets at 30°C and 20°C.

PRE-TRIAL PERIOD									
	body weight kg	feed intake g/bird.d	egg output g/bird.d	rate of lay %	egg weight g	ME intake kJ/bird.d	EE intake kJ/bird.d	heat prod. kJ/bird.d	BW change g/bird.d
mean	1.71	108.40	48.40	92.20	52.09	1285.0	1150.0	134.40	-1.79
se	0.13	14.32	6.67	10.48	3.60	169.70	151.90	17.76	4.87
%cv	7.7	13.2	13.9	11.4	6.9	13.2	13.2	13.2	
TEST PERIODS OF SIX WEEKS EACH									
DIET	body weight (kg)			feed intake (g/bird.d)			egg output (g/bird.d)		
	30°C	20°C	30°C	30°C	20°C	30°C	30°C	20°C	30°C
B1	1.56	1.68	1.56	93.7	114.8	80.2	48.3	47.0	36.1
B2	1.67	1.77	1.64	98.1	119.4	92.6	48.7	49.6	42.6
H	1.60	1.72	1.58	93.0	118.8	99.4	45.7	45.9	40.3
HL	1.65	1.73	1.66	106.4	115.4	108.1	49.9	50.5	43.8
L	1.60	1.63	1.54	86.1	95.5	72.9	43.5	39.7	36.9
95	1.63	1.72	1.65	97.0	117.7	96.2	47.3	42.5	42.6
95/125	1.73	1.85	1.70	103.7	125.4	102.1	47.4	54.9	42.7
125	1.60	1.71	1.58	102.3	123.7	95.5	44.5	44.3	39.4
mean	1.63	1.73	1.61	97.5	116.3	93.4	46.9	46.8	40.5
se	0.15	0.14	0.13	14.1	14.1	14.1	5.3	8.6	7.1
%cv	9.00	8.30	8.20	14.4	12.1	15.1	11.4	18.4	17.5

TABLE 23

Responses of Amberlink layers to eight experimental diets at 30°C and 20°C.

DIET	rate of lay (%)			egg weight (g)			ME intake (kJ/bird.d)		
	30°C	20°C	30°C	30°C	20°C	30°C	30°C	20°C	30°C
B1	89.9	82.0	65.4	53.6	57.2	55.3	1185.0	1452.0	1014.0
B2	90.1	86.6	75.0	54.0	57.2	56.5	1201.0	1462.0	1133.0
H	89.0	83.3	74.9	51.6	54.9	53.7	1096.0	1400.0	1171.0
HL	93.2	89.2	79.2	53.6	56.6	55.4	1282.0	1408.0	1296.0
L	86.1	74.5	70.9	50.6	53.5	52.1	1136.0	1260.0	962.0
95	89.1	74.9	77.0	52.8	56.0	55.1	1193.0	1448.0	1183.0
95/125	89.1	91.4	75.6	53.1	60.1	56.6	1278.0	1545.0	1258.0
125	80.4	73.3	67.8	55.5	60.7	58.3	1262.0	1528.0	1179.0
mean	88.4	81.9	73.2	53.1	57.0	55.4	1204.0	1438.0	1150.0
se	8.8	13.4	11.9	3.2	3.9	3.6	172.9	173.5	175.6
%cv	9.9	16.3	16.3	6.0	6.8	6.4	14.4	12.1	15.3

DIET	EE intake (kJ/bird.d)			heat production (kJ/bird.d)			BW change(g/bird.d)		
	30°C	20°C	30°C	30°C	20°C	30°C	30°C	20°C	30°C
B1	998.0	1223.0	854.0	187.1	229.3	160.3	0.45	2.67	-6.43
B2	1026.0	1249.0	968.0	174.3	212.2	164.6	-0.83	0.93	-7.21
H	960.0	1227.0	1027.0	135.3	172.9	144.6	1.87	1.83	-3.13
HL	1111.0	1212.0	1126.0	171.0	196.3	170.2	0.54	-0.29	-2.90
L	939.0	1042.0	796.0	196.4	217.9	166.6	-0.27	4.85	-4.78
95	1066.0	1294.0	1057.0	127.4	154.6	126.4	-1.74	5.29	-3.80
95/125	1143.0	1382.0	1126.0	134.4	162.6	132.2	-2.00	0.52	-4.26
125	1133.0	1371.0	1058.0	129.5	156.8	121.2	-1.78	2.29	-4.79
mean	1047.0	1250.0	1001.5	156.9	187.8	148.3	-0.61	2.26	-4.66
se	152.3	151.3	152.7	21.2	23.2	23.6			
%cv	14.5	12.1	15.3	13.5	12.3	15.9			

5.4 DISCUSSION

The Reading Model provides coefficients of response for a range of amino acids from which it is possible to evaluate the quality of the diets, and to identify the factors promoting feed intake.

Table 12 contains these coefficients which have been used with the analysed amino acid compositions of the diets to calculate desired feed intakes over the weeks of trial based on the *potential* performance criterion indicated by pre-trial data (Table 24). Where desired feed intakes are lower than actual feed intakes, the birds have been able to meet their calculated requirement for energy and amino acids, and feed intake is able to satisfy energy and production requirements. However, if the actual feed intake does not meet the desired level, then an amino acid or energy will limit performance, and production will be governed by the amount of this nutrient consumed. The desired and constrained feed intakes interact to produce the actual feed intake, so that one might reasonably assume that the environment will be constraining intakes above a certain level. The influence of temperature on the resultant nutrient intake is a function of the heats of production of the diets. The data should be able to demonstrate the decline in performance where the environment constrains the amount of heat the bird can lose, and the associated decline in performance to accommodate this.

The desired feed intake for amino acids that might be first limiting (Table 24) are higher than the actual feed intakes of the 95 and 125 diets. The effective energy diets were formulated with particular attention to the amino acids profiles, whether in minimising total essential amino acids, or ensuring that an excess was present. Only three birds throughout the trial were unable to meet a desired feed intake for any amino acid on any of the effective energy diets, and this during the hot periods only.

TABLE 24

Desired feed intakes for the intake of the first limiting amino acid and effective energy and mean actual feed intakes (g/bird.d)

DIET	DFI _{EE}	DFI _{aa}	actual feed intakes			FL _{aa}
			30°C	20°C	30°C	
high	98.54	83.4	93.0	118.8	99.4	
low	93.44	35.2	86.1	95.5	72.9	
B1	95.47	42.6	93.7	114.8	80.2	
B2	95.99	49.5	98.1	119.4	92.6	
95	93.73	98.5	97.0	117.7	96.2	isoleucine
125	91.66	130.3	102.3	123.7	95.5	methionine
s.e.	8.57	11.9	14.1	14.1	14.1	

Of concern in this department were the 95 and 125 diets. During the hot periods, birds were unable to eat sufficient to meet their requirement for the first limiting amino acid. The 95 diet failed to reflect this in egg output. What is interesting is that the birds on the 95 diet continued to eat beyond a level that satisfied an energy and amino acid intake when it was cool. The extent of this may be controlled by the need to compensate for compromises in the previous hot period. The 125 diet was designed only to meet requirements at 125g/bird.d feed intake, and it is therefore not surprising that the intakes given in Table 24 indicate amino acids as being first limiting.

It needs to be established whether the response to effective energy is simply a response to an increase in nutrient density. The nature of the treatments lends itself to a structured treatment set, and orthogonal contrasts were employed to compare the high and low effective energy diets, the choice and single diets, and the effective energy and commercial choice diets. Temperature was used to affect the nutrient intake to elucidate the response to effective energy. Because the EE diets (B1, B2, H, L and H/L) provide a range of nutrient intake and specifically, EE intake, these will be considered first in a continuous fashion, using regression. The commercial diets offer an alternative of

standard performance achievable by commercial means, and as such, means can be compared finally in an assessment of the two systems of nutrition. Choice feeding relies on the ability of the bird to demonstrate a preference, assuming that the combination is in the best interests of the bird. This comparison should support many of the singular responses of the single diets offered to the hens.

Data from the two chambers were combined. Diet as a treatment structure was significant in affecting properties of lay as well as nutrient intake and heat production. Table 25 indicates the partitioning of the treatment effects in the structured treatment set. The response in feed intake invariably translates to significant differences in nutrient intakes. At 30°C, the choice between two feeds that are opposite in characteristics enables the birds to eat significantly more than the birds that don't have a choice. It is expected that at 20°C when the birds can actually eat to capacity, greater disparities in lay and nutrient intake are evident, so that the birds may be partitioning to body reserves. In fact this very factor may have an influence on subsequent performance in that the reserves built during the cool period increase the insulation and therefore impede heat loss required when the temperature is increased again (Blaxter, 1977). Table 26 (Appendix III) documents the important pairwise comparisons that can be made on the performance of the same bird in successive periods. The information on pairing is used to eliminate a source of extraneous variance, that existing from pair to pair (Steel and Torrie, 1980). The responses in body weight change and in lay have to be a function of the change in nutrient intake across the two temperatures. All of the activities of the birds can be summarised by the response in heat production, which is significantly different between diets, and more importantly so, between high and low diets and between the commercial and effective energy diets.

TABLE 25

Analysis of variance demonstrating significance of dietary treatments and the partitioning of the treatment sum of squares in orthogonal contrasts.

temperature		FI	ROL	EW	EO	BW	MEi	EEi	CPi	HP
30°C	diet	*	*	*				**	**	**
	choice vs single	**						**	**	
	H/L vs 95/125								**	**
	H vs L								**	**
20°C	diet	**	**	**	*	**	**	**	**	**
	choice vs single		**		*	**			**	*
	H/L vs 95/125			*	*			**	**	**
	H vs L	*						**	**	**
30°C	diet	**		**	*		**	**	**	**
	choice vs single	**			**		**	**		
	H/L vs 95/125								**	**
	H vs L	**					**	**	**	*

Where : ** indicates significance at $\alpha=0.01$, and * at $\alpha=0.05$

The data demonstrate a typical response to temperature with nutrient intake and heats of production higher at the cool temperature. An increase in egg weight is evident and only the low EE diet has a lower egg output at 20°C. When the temperature is elevated, nutrient intakes decrease so that heats of production can decrease to cope with the environmental constraint to the heat loss, and egg outputs are lower. This is accompanied by the depletion of the body weight (fat) reserves that accumulated during the cool period to curtail the loss in egg production. What is apparent from the study is that the low EE diet seems to contravene most norms. The investigation begins with the EE series of diets. The diets provide a range of EE intakes, while the environment serves to spread these intakes across a range of variables.

Sykes (1972) noted that heat production must increase with the amount of food consumed. Figure 29 illustrates that there is indeed a strong relationship between the amount of food consumed and the heat that is produced. It is important that the largest portion of the variation is not accounted for by this single relationship, but indeed, by the amount of the particular effective energy diets consumed.

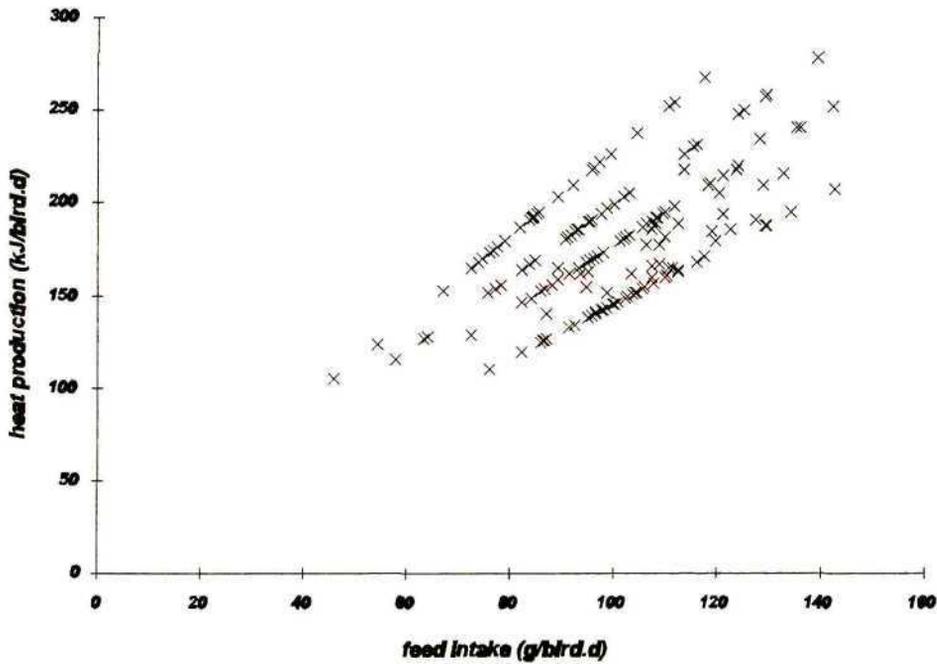


Figure 29 *Response in heat production to feed consumed by Amberlink hens.*

$$HP(kJ/b.d) = 54.8 + 1.239 FI(g/b.d) R^2 = 41.0\%$$

By letting diet account for the variation (96.5%), it is actually attributing the heat production per unit feed intake to the diet, in this case the effective energy of the diet. The rank order of these heats of production with an average feed intake for each diet (Table 27) follows the percentage inclusion of the low EE diet, so that Figure 30 illustrates the highest heat production per unit feed intake for the low EE diet gradually decreasing to the highest EE diet having a low heat production.

TABLE 27

*Predicted heat production using average feed intake values
for each effective energy diet.*

DIET	heat production (kJ/bird.d)	s.e.
LOW	228.77	1.65
B1	200.27	1.13
B2	178.11	1.12
HIGH/LOW choice	163.09	1.41
HIGH	145.92	1.08

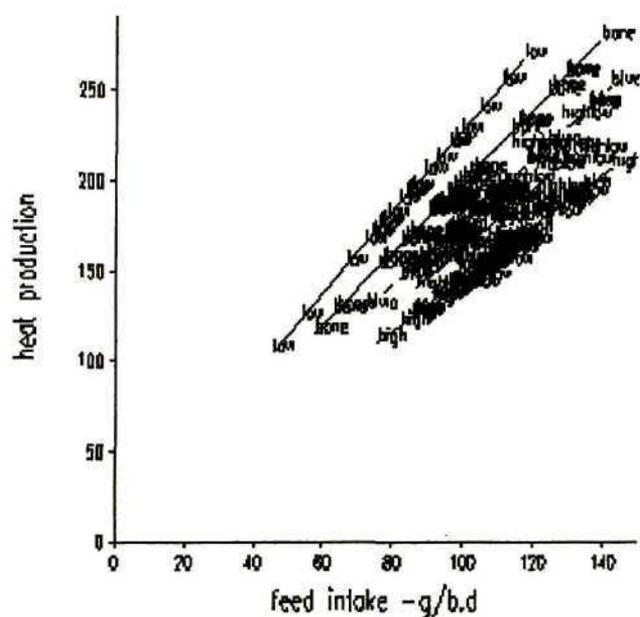


Figure 30 *Response in heat production (kJ/bird.d) to diet and feed intake by Amberlink hens.*

<i>estimate of regression coefficient</i>	<i>estimate</i>	<i>s.e.</i>
<i>feed intake</i>	1.9991	0.0329
<i>FI.diet B₂</i>	-0.2211	0.0153
<i>FI.diet H</i>	-0.5421	0.0150
<i>FI.diet H/L</i>	-0.3689	0.0151
<i>FI.diet L</i>	0.2844	0.0181

The coefficients indicate the significance of the heat production response for each of the effective energy diets. The L and B1 diets represent the only responses to heat production in the second 30°C period. Combining the responses of the two 30°C periods depends on their being not significantly different. While 156.8kJ/bird.d and 148.4kJ/bird.d are not different ($\alpha=0.01$), the pairwise comparisons of the two diets, B1 and L, are. After a period where positive body weight gains have been achieved, it is these diets that have to compromise more to meet a threshold heat loss factor as the temperature is increased. Tests of the mean values for the hot and cold periods indicate that these are significantly different ($\alpha=0.01$). Taking an average for the hot periods as 152.1kJ/bird.d and 187.4kJ/bird.d for the cool period, it may now be possible to quantify the extent of the restriction in nutrient intake and hence explain the compromises in rate of lay and egg output where they occur. Although the regression accounting for the variation is significant, a poor fit of the data is obtained ($R^2=28.9\%$) in relating the egg output to the EE intake. Figure 31 nevertheless indicates that the egg output increased as the EE intake increased. Increasing the EE intake also increases positive weight gains (Figure 32), and reduced the drain on body reserves to sustain lay.

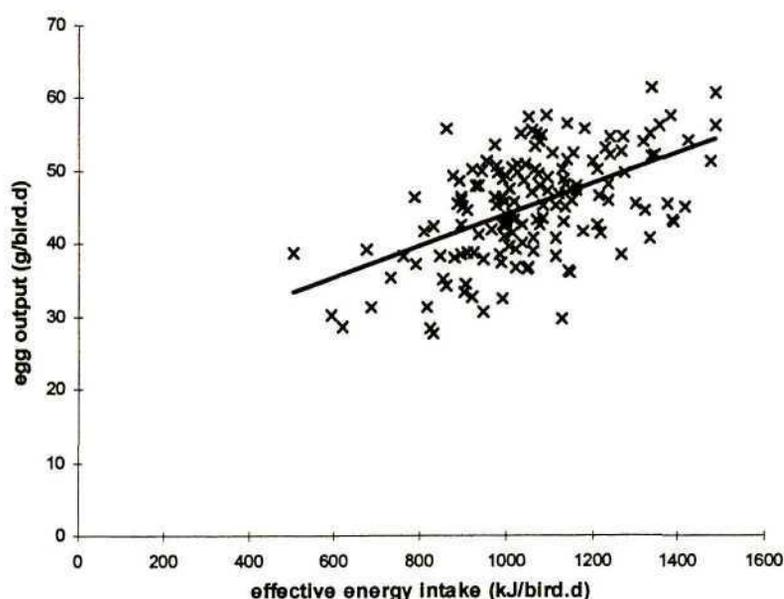


Figure 31 *Response in egg output (g/bird.d) to the effective energy intake (kJ/bird.d) of Amberlink hens at 20°C and 30°C.*

$$EO(g/b.d)=22.40+0.0216(EE\ intake)$$

$$R^2=28.9\%$$

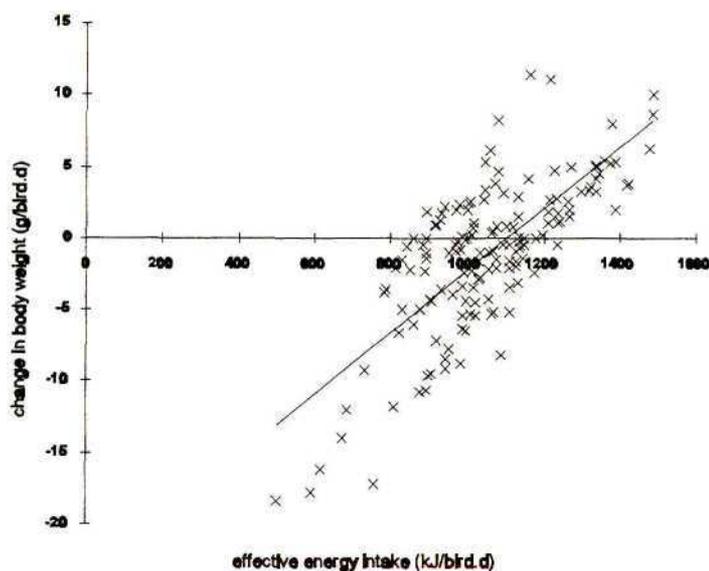


Figure 32 *Response in body weight change (g/bird.d) to the effective energy consumed (kJ/bird.d) by Amberlink hens at 20°C and 30°C.*

$$BWchange \text{ (g/b.d)} = -23.8665 + 0.02159 \text{ EEintake} \quad R^2 = 54.7\%$$

The strong relationships to effective energy in the above regressions suggest the intrinsic nature of this structure, suggested also by effective energy intake being the only variable supported in multiple regression models of heat production (disregarding the effect of volume, egg output, body weights). These diets were designed to support the strength of these suppositions. The regressions also indicate the options available to the bird in the case of heat restriction. Essentially, the hen has to weigh up the heats of production for egg output and for energy retention, both of which act as reservoirs for the loss of energy from the system. The formation of eggs depends on the availability of materials and energy for accretion and production, as does energy retention. The respective heat increments of these processes and the environmental pressures may explain why the low EE birds may have a lower rate of lay, but BW losses are not as exaggerated. Assuming that the hen would use the rule that as much weight gain as possible should take place (as fat), these results could assist in the disproving of such a rule by considering the heat increment components of these respective functions. Emmans (1994, unpublished) compiled an example not unlike Table 15, where the EE in excess was calculated. This

excess energy could be partitioned to $\frac{\text{excess EE kJ}}{56 \text{ kJ/g}}$ g lipid retention, which leads to 1g of extra lipid and 16.4kJ of heat. An effective energy requirement for eggs is 8.8kJ/g EO, which represents an energy requirement as well as the 0.48kJ/kJ heat produced. What is important is that the laying of eggs is an accumulative process, requiring that the whole egg be laid, while energy retentions can occur as excess energy becomes available. Therefore, while the hen can retain energy in part, eggs must be laid to preserve a particular egg weight. The excess effective energy available seems to be partitioned to body weight gain only where the environment will not support heat production in the formation of eggs, as at 30°C.

The commercial diets offer information on the effect of nutrient density. These diets also display a typical temperature response, and the birds fare better at the cooler temperature, where egg outputs do not decrease and body weight can increase as the feed and nutrient intake increase. The faster rate of gain of BW is evident with the higher nutrient density of the 95 diet. It has been mentioned that the intake of the 125 diet, even at 20°C, precludes the intake of sufficient amino acids, and this would account for the lower rate of lay on this diet. From an effective energy point of view, calculated values for this nutrient are similar, as are the ME values so that calculated heats of production would be a function of the feed intake of the respective diets. Heats of production are not different, and the amount of feed that the animal can eat must simply be a volume constraint. Heats of production are in fact a good deal lower than on the EE diets. One might argue that they are then adequate in all respects if heats of production are lower. The balance of nutrients in the diets is what makes the comparison of the EE diets with the commercial diets valid.

The question to answer is : how does the high EE diet compare with the 95 diet, and the 125 with the low EE diet? This would solve the question of whether the EE diets are just emulating a density function of commercial diets to solve the problem of reduced performance at high temperatures. At 20°C, the high and the 95 diets are similar in feed intake, body weight and egg production, and birds on the 95 diet gain more weight. At 30°C, no difference is evident between the two diets. The production characteristics of

Amberlink hens on the high EE diet and the 95 diet are similar. The Amberlinks on the 125 diet lay larger eggs. The hens eating the low EE diet prefer to partition to body weight gains at 20°C. The greatest difference between these two diets is the presentation of the diets. Birds obviously prefer the 125 diet, and will eat more of it at any temperature. The heat production associated with the low EE diet is much higher, which accounts for the lower intakes when it is hot. This also means that ME and EE intakes are very different, though these apparently have no effect on the low egg production from these hens.

From an egg production point of view, using the EE system must have an advantage. Table 28 displays the calculated costs of the high and 95 rations, and the anticipated margins per unit egg output for both diets.

TABLE 28

Cost analysis of the high effective energy and 95 diets.

(Prices valid : September 1998)

<u>cost parameter</u>	<u>HIGH</u>	<u>95</u>
cost/ton feed (R)	1186.22	1267.37
EO (g/bird.d)	43.03	44.94
kg feed/kg eggs - 30°C	2.24	2.15
cost/kg eggs - 30°C	R2.65	R2.72
kg feed/kg eggs - 20°C	2.76	2.62
cost/kg eggs - 20°C	R3.27	R3.32

Cost is a severe determination criterion, and the merit of the high EE diet is a comparative egg production with a potentially more cost effective ration, that supplies all the necessary nutrients in good measure. Although the benefits of effective energy are disguised under cooler temperature when feed intake boosts nutrient intake, perhaps this analysis elucidates a benefit even under cooler conditions of refining the ration to obviate the cost of superfluous nutrient supply especially at higher feed intakes.

Choice feeding in broilers has been very successful in maximising response with the correct formulation of choice feeds. They indicate the ability of the bird to discern the relative merits of two or more feed sources, and as such portray a motivated decision by the bird to meet its physiological requirements. In this vein, the 95/125 and H/L choices have sought to represent the birds in the matter of feeding under stressful (hot) and unstressful (cool) conditions.

TABLE 29

Choices made by Amberlink hens at at 20°C and 30°C when offered a high vs low EE feed and a 95 vs 125 feed.

DIET	30°C	20°C	30°C
high	81.41 ^b	69.75 ^c	85.76 ^a
low	18.59	30.25	14.24
s.e.	12.65	17.84	10.30
95	63.32 ^d	65.55 ^d	62.16 ^d
125	36.68	34.45	37.84
s.e.	14.08	15.25	15.87

(values with different superscripts differ significantly, $\alpha=0.01$)

In Table 29, the ratios of the two diets on choice do differ significantly from 50% of each diet. This must indicate a motivated choice of the birds. The data indicate that the difference in the nutritive value of the high and low EE diets is perceived by the birds, causing them to consume more of the high EE diet. Although the percentages of the high EE diet are slightly different at the two 30°C periods, both are much higher than the 69.75% chosen at 20°C. This supports our hypothesis that the heat of production associated with the low EE diet cannot be supported at high temperatures. The difference in ME intake and heat production between the two diets at 30°C fails to affect egg production, and at 20°C, no difference between the two diets can be detected. Because the EE intakes at the high temperature are similar and egg outputs remain unaffected, one could assume that the proportion of LOW at this temperature is too low to affect the heat production of the birds, although this is only slightly elevated. The

increased intake at cooler temperatures would serve as gut fill, because the HIGH portion of the diet already sees to the needs for production. It would seem to indicate that the birds need to augment their adequate high EE diet at the cooler temperature with something that will increase a heat production to assist in meeting the higher environmental heat demand at the time.

It is interesting to note the consistently high performance of the B2 diet, and its similarity to performance of the birds on the H/L choice diet. The B2 diet contains $\frac{2}{3}$ of the high EE diet and $\frac{1}{3}$ of the low EE diet, and as such is very similar to the choice made by the hens given a choice of high and low EE at 20 °C. The data from the hens on these two treatments are remarkably similar. This evidence supports the notion that the birds have an educated insight into the composition of the feeds, and can justify the intake of a choice in terms of the positive effect it might induce. At 30°C, the choices favour the intake of the high EE diet, which would account for the disparity between the B2 and H/L treatments at the high temperature, particularly with respect to live weight changes, the choice once more reflecting a more suitable dietary composition for the hens at that temperature.

The proportion of the 95/125 choice does not change and the birds consume roughly 64% of the 95 and 36% of the 125, regardless of the temperature of the environment. This would indicate that the disparity between the diets is not as marked as that between the high and low EE diets, and increasing intake of the diets in the same proportion serves to meet demands of the environment and the birds. This relationship is only significant in terms of performance at the cooler temperature where the fact that the 95 birds are gaining more weight and lay a larger number of eggs means that the choice birds don't feel the need to increase the consumption of one particular diet, and adjust production to what they do consume of both. Another consideration is that an intake of 95g/bird.d is supposed to satisfy the requirement for all nutrients of birds on this diet. Average intakes for the 95 diet are at least 95g/bird.d, indicating that the birds are able to support their production requirements, with very little need to change the proportion of the choice in pursuit of missing nutrients.

The H/L and 95/125 choice diets produce similar results, except when feed intakes can be increased, and the higher fat content of the commercial diets increases the egg weights of those birds. A difference in egg output ($\alpha=0.05$) between the two choices can then be reported. What the choice diets do accomplish, is consistently higher rates of egg production, in rates of lay and egg output where egg weights are not dissimilar. This must confirm the ability of the birds to discern best which formulation promoted their potential performance under the given set of circumstances.

Comparisons were made between the intakes of eight amino acids in each period for the eight diets (Table 30). Of particular interest were the comparisons between the choices and the next most similar feed. For example at 20°C, the proportion chosen by the birds emulated the B2 blend, since both offered $\pm 67\%$ of the high EE diet. Intakes of the choice diet are most similar to B2 for all amino acids at 20°C. Intakes of these amino acids are higher on the 95 diet, and the choice is more similar to the higher nutrient density diet. At 30°C, the ratio of high to low EE increases, and the profile of intakes between the high and low diets is linear. This is valuable evidence of an additive effect of EE, i.e. a linear series in intakes and performance is obtained through linear combinations of the diets. Graphically, the data indicate the birds preference for consuming more than 67% ($\frac{2}{3}$) of the high EE diet in their ration for all amino acids. The 95/125 choice reflects the higher proportion of 95 chosen to a limited extent, because the intake of all amino acids on the choice and the single 95 and 125 feeds are very similar. Amino acid intakes of the 95 diet are slightly higher.

The effective energy intakes of the choice diets reflect the higher feed intakes of the choice diets, especially at the higher temperature.

TABLE 30

Comparison of the amino acid intakes (g/bird.d) and EE intakes(kJ/bird.d) of Amberlink hens at 20°C and 30°C on eight dietary treatments.

DIET		amino acid intakes (g/bird.d)									EE
		feed	lys	met	ile	val	arg	his	leu	thr	intake
		intake (g/bird.d)									kJ/bird.d
95	30°C	97.0	0.681	0.288	0.492	0.600	0.820	0.339	0.665	0.441	1066
	20°C	117.7	0.826	0.350	0.597	0.729	0.995	0.411	0.807	0.536	1294
	30°C	96.2	0.675	0.286	0.488	0.595	0.813	0.336	0.660	0.438	1058
125	30°C	102.3	0.670	0.222	0.478	0.578	0.807	0.301	0.902	0.427	1133
	20°C	123.7	0.810	0.268	0.578	0.699	0.976	0.364	1.091	0.516	1370
	30°C	95.5	0.626	0.207	0.446	0.540	0.753	0.281	0.842	0.398	1058
95/125	30°C	103.7	0.710	0.278	0.510	0.621	0.855	0.341	0.785	0.457	1143
	20°C	125.4	0.860	0.337	0.618	0.752	1.035	0.413	0.947	0.554	1382
	30°C	102.1	0.698	0.272	0.502	0.611	0.841	0.335	0.779	0.450	1126
H	30°C	93.0	0.799	0.573	0.545	0.700	0.897	0.398	1.190	0.529	961
	20°C	118.8	1.020	0.732	0.696	0.895	1.145	0.508	1.521	0.676	1227
	30°C	99.4	0.854	0.612	0.582	0.748	0.958	0.425	1.272	0.566	1027
L	30°C	86.1	1.731	0.728	1.282	1.354	1.783	0.753	2.720	1.039	939
	20°C	95.5	1.921	0.807	1.422	1.502	1.978	0.835	3.017	1.153	1042
	30°C	72.9	1.466	0.616	1.085	1.147	1.510	0.637	2.303	0.880	795
B1	30°C	93.7	1.480	0.696	1.096	1.222	1.559	0.669	2.289	0.885	998
	20°C	114.8	1.813	0.853	1.343	1.497	1.910	0.820	2.805	1.084	1223
	30°C	80.2	1.266	0.596	0.938	1.046	1.335	0.573	1.959	0.757	854
B2	30°C	98.1	1.313	0.698	0.932	1.098	1.337	0.602	1.953	0.800	1027
	20°C	119.4	1.598	0.850	1.134	1.336	1.627	0.733	2.377	0.974	1249
	30°C	92.6	1.239	0.659	0.880	1.036	1.262	0.569	1.844	0.756	969
H/L	30°C	106.4	1.140	0.700	0.800	0.962	1.243	0.543	1.730	0.730	1111
	20°C	115.4	1.387	0.789	0.986	1.150	1.492	0.647	2.122	0.875	1211
	30°C	108.1	1.107	0.702	0.773	0.941	1.213	0.532	1.674	0.714	1126

5.5 CONCLUSION

The effective energy diets have again behaved theoretically in that heats of production can be linked to ingredients in the ration that characterise the diet as either having a high or low effective energy. No synergistic effects exist between the two effective energy diets such that blends fall within the range in the proportions blended, i.e. the effective energy content is an additive measure. The low effective energy diet tests the ability of the bird to lose the heat that is associated with its intake, and the hens choose the option of body weight gains rather than augment a heat increment through egg production. The high effective energy diet has high egg production results, and birds maintain rates of lay without undue changes in body weight. The commercial diets prove that a high effective energy diet can be very similar to just increasing the nutrient density at high temperatures, although a rudimentary evaluation of the costs indicates that the concepts of the effective energy system serve more than simply meeting requirements, but meeting the hen's requirements at that level which optimises performance without superfluous supply of nutrients that cost money. The 125 diet is much more effective than a low EE diet in maintaining respectable performances, indicating that a low EE diet has characteristics that exacerbate low nutrient densities, *viz.* heat production and imbalanced nutrient supply. A choice of the H/L and 95/125 diets achieved the highest performances, and results obtained are not dissimilar from those of the high and 95 diets, respectively. The birds were able to motivate choices depending on the environmental temperature and the characteristics of the diets on offer. This provides more evidence of a greater disparity between effective energy and nutrient density in a diet; also of the hen's ability to discern which formulation promotes potential performance under a given set of circumstances.

This trial has greatly supported the credibility of the effective energy system. Its precepts are valid, and can be extrapolated from the theoretical to practical application. Small differences in effective energy have produced remarkably dissimilar results, and their comparison to commercial alternatives would prompt the more serious contemplation of the role that effective energy has to play in poultry nutrition.

CHAPTER SIX

GENERAL DISCUSSION AND CONCLUSIONS

Perhaps nutrition would be a simple matter if variation in individuals, populations, environment, rations, production capabilities and characteristics did not exist. The challenge for the nutritionist lies in accommodating these facets into the realm of nutrition. The data reported indicate strongly that this challenge has been addressed by the Effective Energy system of Emmans (1994).

'The field of research, not the tools, should produce the *'whys'* of the research problem' (Steel and Torrie, 1980). A cumulative review by Marsden and Morris (1987) quantified the effects of environmental temperature on food intake, egg output and energy balance in layers. The same data were used in augmenting this review by the calculation of effective energy contributions to the scheme of response. This field of research certainly provided some *'whys'* to a research problem that had to begin with the hen itself. It was important to define the hen as a thermally active animal. Interactions with the environment define zones of comfort in which performance can be optimised. Heat loss and production are integrally correlated in the situation of this zone. Functions within the hen contribute to losses and productions of heat, and it is important to identify with these how feeding the hen might alleviate or aggravate such exchanges. The general approach of the contribution of functions within the hen to the thermal exchange is refined by the more specific approach of Emmans, who defines a system that explains the contribution of nutrition to the thermal exchanges of the hen and environment. The system introduces a concept of energy utilization applied across species, and considers the heat increment in feeding to be linearly related to five measurable quantities. These in turn permit the evaluation of feed ingredients in terms of effective energy so that the value of a ration can be gauged against the heat that it will produce. This knowledge at high environmental temperatures would reduce the rate of approach of constraints to production, making its pursuit worthy for the sustained egg production that could be generated in hotter climates.

As a means of introducing the concept to scrutiny, the temperature review of Marsden and Morris (1987) was used to illustrate that effective energy could definitely find a place in the explanation of response to temperature. Two trial protocols are described in which the EE system is evaluated. The objective of the first experiment was the formulation of diets of different effective energies by manipulating the heat increment components of the diet. EE values of feed ingredients and therefore rations, can be calculated, and are largely a function of the heat increment that they induce. Using imbalanced amino acid mixtures, increasing faecal organic matter excretion, more carbohydrates and crude lipids and a more balanced increment of protein and energy as diluents of a basal ration, the responses of Amberlink and Hyline Brown hens at high and low environmental temperatures were tested. Controlled environment chambers were used to measure a response in feed intake, body weight change and egg production of 96 hens of the two strains at 18°C and 32°C. An important parameter was heat production, calculated as the difference between the ME and EE intake. As such, this variable indicates superfluous heat production that could incapacitate production at high temperatures.

The major consequence of high environmental temperatures is depressed nutrient intake, with diets becoming first limiting in amino acids and therefore limiting production to the level of ingestion of these nutrients. The depression in egg output can be related to the heat production of the diet, and heat production to EE intake, so that EE intake has a particular role to play in egg production. The response to the diets was not constant, in particular for heat production. Amberlinks had a higher heat production than Hyline Browns. Brown birds have a lower maintenance energy requirement per kilogram or kilogram^{0.75} so they may eat less to meet this. Should Amberlinks have fared worse than the Hyline Browns, this might have been attributed to the higher maintenance heat portion that would have exacerbated any of the dietary effects. Standard effects of temperature indicate that HP will decrease as the feed intake decreases at the higher temperature. At the high temperature, the heats of production of the oil and the sugar/starch diet were lowest, *i.e.*, the diets in which the EE/ME ratio was increased through the addition of readily digestible carbohydrate and lipid energy. Where the EE:ME ratio falls, as in the dilution of the basal diet with sunflower husks, heats of production were higher because of the higher FOM content, and the work function value

associated with its excretion. The significantly lower egg output of the filler diet was a result of the constraint in heat loss from the environment which must reduce the intake of a diet that produces more heat.

Effects of the different heats of production were ameliorated to some extent by the low temperature. Energy is consumed to meet a maintenance heat demand because of the cold temperature, and to meet a demand for egg production. Because the environment was more forgiving in terms of the heat that could be produced (maintenance heat demand absorbs some of the superfluous heat production) egg outputs were not affected by the disparity between the diets. At high temperatures, egg outputs on the filler diet were lower. The compromise between rate of lay and body weight change was apparent between strains and temperatures. The Hyline Browns fluctuated more in gain than the Amberlinks, gaining more when it was cool, and losing more weight when it was hot. Amberlinks laid more eggs when it was cooler, although both strains laid at a similar rate at 32°C.

A multiple regression model quantified the effect of the egg output, EE intake and volume of the radiating surface on the heat production from the birds. As such, it corroborated many of the heat increment and effective energy theories already put forward. The significance of the grouping factor in the multiple regression strongly supported the suggestion that the diets impart different properties to the birds with respect to heat production. The levels of egg output and effective energy intake as well as the volume (which is related to the body weight of the birds) on the different diets did not contribute equally to the heat production. This would be because of the effect of the diet on the respective elements in the regression, having either a negative or positive effect on the ability of the bird to sustain egg output, often at the expense of body reserves, or *vice versa*. The effect might also be related to the characteristics of the diet in providing for the intake of essential nutrients. What the interaction of the diet and effective energy intake demonstrates is the ratio of effective energy to ME. By illustrating that the dilution of a basal diet with a non-nutritive filler contributes to heat production more per unit of energy consumed than an oil dilution, it essentially attributes heat production to a decrease in the EE:ME ratio.

Thus it has been possible to attribute changes in laying performance at high temperatures to heat increment properties of the diet. The response of the strains (it being supposed that the higher energy requirement for maintenance would pressure the white birds into responding more acutely to the diets) has been consistent in relation to the diets on offer. Diluents of a basal have elicited responses in heat production, which has varied the laying performance on the diets at high temperatures. The response at lower temperatures has to a larger extent been ameliorated by the increase in intake possible, an anomaly already considered by Emmans (1994). The fact that heat increment theories can be supported in this way, encouraged the exploration of the direct effect of effective energy in the diets of laying hens.

The objective of the second experiment was the comparison of high and low effective energy diets, when such had been formulated using the heat increment theories already confirmed by the previous protocol. A very small difference in formulated EE values produced significantly difference effective energy intakes, and the response to effective energy could be quantified in this manner. The comparison with the commercial diets, the density of which is varied accordingly in summer and winter rations, permitted the evaluation of a response to effective energy relative to changes in nutrient density. The ability of the hen to prescribe to a stress situation while offered a choice of feeds was presented to corroborate the responses to effective energy and commercial diets.

The experiment was conducted in the controlled environment chambers, both chambers being held at the same temperatures for the same length of time. The diets were tested at high and low temperatures. Typical responses to temperature were apparent, with the high temperature limiting only the commercial diets in the intakes of isoleucine and methionine. The intake of all diets at the respective temperatures served to separate hens in terms of rates of lay and egg weight. An important parameter at the high temperatures was the heat production as calculated by the difference between the ME and effective energy intakes. Diet accounted significantly for the increases in heat production associated with the increase in feed intake of the hens. As such, the low effective energy diet could be identified as producing the most heat per unit feed intake, with the high effective energy diet producing the least. Significant regressions explained the change

in egg output with an increase in effective energy, as well as a positive weight gain when the effective energy intake was increased. The strong relationships to effective energy indicate the value of effective energy in accounting for variation in the data sets at the cool and hot temperatures. As the intake of effective energy is increased, the energy balance of the birds is increased, and the lower heats of production associated with the high effective energy diet permit higher feed intakes and therefore increase nutrient supply.

The birds on a high nutrient density (LAY 95) diet gained more weight, although laying characteristics were not different whether the birds were being fed from a density or an effective energy point of view. What was interesting from an economic point of view, was the higher cost per ton for the 95 diet. The 125 diet promoted higher egg weights than the low effective energy diet, (probably due to the higher formulated linoleic acid content). Rates of lay on the low effective energy diet could be lower, and the higher heat production of this diet certainly reduced the amount of food that the hens could consume, and the low production was the result. The difference between the 125 and low effective energy diets was greater than that between a high effective energy and high density diet. Offering a choice between effective energy and density indicated the greater disparity between the high and low effective energy diets. In fact, the greater disparity between the performance on these diets, as well as the percentage of the choice made by the hens, indicated the greater sensitivity to the composition of the feeds. The 95/125 choice differed from 50:50, but remained static at 64:36, respectively at the hot and cool temperatures. The proportions of the high effective energy diet eaten were significantly higher at 30°C and the hen used the low effective energy diet to provide for the higher maintenance heat demand when it was cool. Since the choice diets represented the highest overall performances of the birds, it could be concluded that the choice diets met the birds needs most effectively, and they were able to manipulate the proportions using the characteristics of the feed to meet their needs under different environmental conditions.

The experiments have explored the applicability of the effective energy system. Highly theoretical though the system may seem to be, real responses have been achieved by

testing the heat increment contributions of the experimental diets, and by testing effective energy contents of feeds. Effective energy started by evaluating the metabolisable energy supply of animals. By following the flow of organic matter in the animal, areas of work could be identified, and heat increments associated with each of them, so that the supply of available energy to the animal could be refined one step further. Not only was the supply of energy curtailed by these works, but heat capacities were challenged if the environment was not conducive to heat loss. A double tax on the energy ingested was identified by Emmans (1994) and by considering that the feed ingredients used in the formulation of rations might each have a quality that could alleviate or exacerbate heats of production in this manner, he has offered another means of seeking to relieve the stress on laying hens housed at high environmental temperatures. The trials reported here have indeed supported the value of these ideas. Further work to improve our understanding of the nature of the effective energy response could include a more substantial cost analysis. While laying performances have been shown to be equal in the commercial and high effective energy diets, marginal revenues and costs will be the arbitrators in its application commercially. The physiological requirement for dietary energy as satisfied by *ad libitum* intake, is greater than the economic requirement (Sykes, 1972). Efficiency can be measured by the amounts of nutrients supplied (not their cost) and the amount of nutrients represented in eggs obtained (not their value). In assessing prospects for improving efficiencies in future, it would be foolish to ignore costs, and economics should be kept in mind when arguing what developments seem likely to prove worthwhile. While the effective energy system is proving effective, economic considerations would eventually motivate its commercial application. Economically also, revenues might be split between the rates of lay and egg weight, and the manipulation of egg weight has been seen to depend on the fat (and linoleic acid) content of the diets. High effective energy diets can be adjusted to accommodate such requirements. In fact the egg component data should provide a study all on their own. Apart from being able to identify the nature of the increase in egg weight between hot and cool periods and diets, the analysis of the egg yolk itself would give valuable evidence of the nature of the heat response. Further to this goal would be the analysis of the critical response in egg output of the hens by means of egg component data, and fatty acid profiles of the yolks and the feed. Whether the effective energy intakes promote a higher efficiency of

absorption into the yolk at high temperatures to preserve egg weights, and to what extent the shell thickness and composition of the egg can be preserved at high temperatures deserves attention. The theoretical knowledge of the effective energy system implores the exploration of pathways of metabolism. Whether or not the fatty acid profiles in the feed and the egg are similar will allow one to deduce whether the bird is affecting an energy conservation at high temperature by using the energetically more efficient pathway of direct assimilation into the yolk, as opposed to degradation and re-assimilation (suggested by Emmans, 1997, pers. comm.). This also depends on the maintenance of the integrity of the egg yolk. Assuming that the hen is providing for an embryo necessitates a constant composition of the yolk. To what extent can this be modified to the end of improved efficiency? This would indicate the sensitivity of the heat response. Is the effect of the superfluous heat production so profound as to elicit biochemical adjustment to alleviate the source of stress? Carcass data would also be useful, although sample size in specialised chamber units makes it difficult to isolate the chemical composition changes to a particular period of the trial without sacrificing all the data providers.

Information about the nutrient contents and digestibilities of the feed ingredients is vital to the calculation of an effective energy value of a feed. The matrix in the feed formulation package is the key to the effective formulation of diets. While hens are very forgiving of commercial diets and some of their inadequacies, the more precise nature of the effective energy diets necessitates that the feed ingredients be properly described in terms of nutrient contents. What the hen is fed and what she does on this feed can be used to predict performances. If the theoretical values of heat increments of production are evaluated, the deliberation of the hen in choosing to partition between body reserves and egg production can be examined, and it would then be more probable that one could predict feed intakes based on what the hen would like to produce, with the materials available, and under the heat and other constraints that her environment impose. Because the effective energy system has endeavoured to encompass all factors that would lead to heat increment, researchers can imagine getting closer to the prediction of feed intake as motivated by the goals that the hen is seeking to fulfill and being constrained by. Emmans and the effective energy system make that prediction seem more likely. The

effective energy system also seeks to embrace the theory of internal machinations in the hen, and factors in the feed that would cooperate in the work that the hen needs to do. As such, it incorporates theory and practice in the most sensible way, allowing researchers and farmers alike to leap from biochemistry and physiology to calculations and predictions.

Energy systems have evolved and are evolving, and the understanding of the infinite permutations in defining an animal's response to its environment and nutrition make it a dynamic field of study. This work provides another perspective on energy systems, in particular the effective energy system of Emmans (1994). It is a journey through, and with, and on behalf of the hen that treads the path to the destination of fulfilling an objective in existence. It considers boundaries that the bird places on itself and external constraints that moderate how it responds to the influences around it. It embraces the dynamic theory of actions and reactions and motivations in this end to reach an individual goal, with sensitivity to these actions. It is the journey to that place where one can reflect: 'I understand you'.

REFERENCES

Ahmad, M.M., Mather, F.B., Gleaves, E.W. (1974) Effect of environmental temperature and dietary energy on dwarf and normal hens and roosters.

Poultry Science 53 : 927-935.

Biometry course work notes (1994, 1995), University of Natal, Pietermaritzburg.

Blaxter, K.L. (1977) Environmental Factors and Their Influence on the Nutrition of Farm Livestock in : Haresign, W., Swan, H and Lewis, D. , *Nutrition and the Climatic Environment*, p.17-29 (London, Butterworths).

Blaxter, K.L., Boyne, A.W. (1978) The estimation of the nutritive value of feeds as energy sources for ruminants and the derivation of feeding systems.

J.agric.Sci., Camb., 90 : 47-68.

Bolton, W. (1959) The efficiency of food utilization for egg production by pullets.

J.agric.Aci., Camb., 52 : 364-368.

Boorman, K.N., Ellis, G.M. (1996) Maximum nutritional response to poor quality protein and amino acid utilization.

British Poultry Science 37: 145-156

Charlet-Lery, G. (1976) Influence of protein feeding pattern on heat production in the growing pig, in M.Vermorel, (Ed) *Proceedings of the 7th EAAP Symposium on the Energy Metabolism of Farm Animals*, Vichy, France, p97-100 (Clermont-Ferrand, Guy de Bussac).

Combs, C.F. (1982) The interrelationships of dietary energy and protein in poultry nutrition in : Morgan, J.T., Lewis, D., (Eds), *Nutrition of Pigs and Poultry : Proceedings of the University of Nottingham 8th Easter School in Agricultural Science*, Butterworths London, pg 127-147

Cowan, P.J., Michie, W. (1978) Environmental temperature and broiler performance : the use of diets containing increased amounts of protein.

British Poultry Science 19 : 601-605

Davis, R.H., Hassan, O.E.M., Sykes, A.H. (1972) The adaptation of energy utilization in the laying hen to warm and cool ambient temperatures.

J.agric.Sci., Camb. 79 : 363 -369.

Davis, R.H., Hassan, E.M., Sykes, A.H. (1973) Energy utilization in the laying hen in relation to ambient temperature.

J.agric.Sci., Camb., 81 : 173-177.

de Andrade, A.N., Rogler, J.C., Featherston, W.R. (1976) Influence of constant elevated temperature and diet on egg production and shell quality.

Poultry Science 55 : 685-693.

de Andrade, A.N., Rogler, W.R., Featherston, W.R., Alliston, C.W. (1977) Interrelationships between diet and elevated temperatures (cyclic and constant) on egg production and shell quality.

Poultry Science 56 : 1178-1188.

Deaton, J.W. (1983) Alleviation of heat stress for avian egg production - a review.

World's Poultry Science Journal 39 : 210-217.

Degen, A.A., Kam, M., Rosenstrauch, A. (1992) Effect of restricted cooled drinking water on the performance of broiler breeder hens in a hot, dry climate.

British Poultry Science 33 : 917-924.

Deschepper, K., de Groote, G. (1995) Effect of dietary protein, essential and non-essential amino acids on the performance and carcass composition of male broiler chickens.

British Poultry Science 36:229-245

Digby, P., Galwey, N., Lane, P. (1989) *Genstat 5 : A Second Course*, Oxford Science Publications, Clarendon Press, Oxford.

Emmans, G.C. (1974) The effects of temperature on the performance of laying hens, in: T.R.Morris and B.M.Freemant (Eds) *Energy requirements of Poultry*, p.79-90 (British Poultry Science Ltd., Edinburgh).

Emmans, G.C. (1975) Problems in feeding laying hens : can a feeding system based on choice solve them?

World Poultry Science 31 : 311.

Emmans, G.C. (1979) Free choice feeding of laying poultry, in : Haresign, W. and Lewis, D. (Eds) *Recent Advances in Animal Nutrition*. (University of Nottingham, Butterworths).

Emmans, G.C., Charles, D.R. (1977) Climatic environment and poultry feeding in practice, in : Haresign, W., Swan, H. and Lewis, (Eds) *Nutrition and the Climatic Environment* p.31-49. (London, Butterworths).

Emmans, G.C. (1981) A model of the growth and feed intake of *ad libitum* fed animals, particularly poultry in : Hillyer, G.M., Whittemore, C.T., Gunn, R.G., (Eds), *Computers in Animal Production*, Occasional Publication No. 5 - British Society of Animal Production.

Emmans, G.C., Fisher, C. (1986) Problems in nutritional theory, in : Fisher, C., Boorman, K.N., (Eds) *Nutritional Requirements and Nutritional Theory* p.9-57. (London, Butterworths).

Emmans, G.C. (1987) Growth, body composition and feed intake.

Worlds Poultry Science Journal 43 : 208-227

Emmans, G.C., Oldham, J.D. (1988) Modelling of Growth and Nutrition in Different Species in : Karver, S., van Arendonk, J.A.M., (Eds), *Modelling of Livestock Production Systems*.

Emmans, G.C. (1989) The Growth of Turkeys in: C.Nixey and T.C.Grey (Eds) *Recent Advances in Turkey Science, Proceedings Poultry Science Symposium #21*, Butterworths, London.

Emmans - booklet of photostatted notes : property of Prof. R.M.Gous, University of Natal, Pietermaritzburg.

Emmans, G.C. (1994) Effective energy : a concept of energy utilization applied across species.

British Journal of Nutrition 71 : 801-821.

Emmans, G.C., Genetics and Behavioural Sciences Department, Scottish Agricultural College, Bush Estate, Penicuik, Midlothian, EH26 0QE.

Epol Booklet (1992) *Profitable Egg Production*, Bookpress, Johannesburg.

Etches, R.J. (1996) *Reproduction in Poultry*, CAB International Press.

Farrel, D.J. (1976) The influence of protein and amino acid balance in the diet of chickens on the efficiency of utilization of dietary energy, in : M.Vermorel, (Ed) *Proceedings of the 7th EAAP Symposium on the Energy Metabolism of Farm Animals*, Vichy, France, p97-100 (Clermont-Ferrand, Guy de Bussac).

Fisher, H., Griminger, P., Leveille, G.A., Shapiro, R. (1960) Quantitative aspects of lysine deficiency and amino acid imbalance.

Journal of Nutrition 71 : 213-220

Fuller, H.L., Dale, N.M., Smith, C.F. (1983) Comparison of heat production of chickens measured by energy balance and by gaseous exchange.

Journal of Nutrition 113 : 1403-1408.

Gous, R.M., (1981) Recent developments in poultry nutrition

South African Journal of Animal Science 11 : 187-193

Gous, R.M. (1986) Measurement of response in nutritional experiments in : Fisher, C. and Boorman, K.N., (Eds), *Nutrient Requirements of Poultry and Nutritional Research*, Poultry Science Symposium #19, Butterworths, London.

Gous, R.M., Head of Department: Animal Science and Poultry Science, University of Natal, Private Bag X01, Scottsville, Pietermaritzburg, 3209.

Guillaume, J., Summers, J.D. (1970) Influence of amino acid excess on energy utilization in the growing chick

Canadian Journal of Animal Science 50 : 355-362

Harper, A.E. (1959) Amino acid balance and imbalance 1. Dietary level of protein and amino acid imbalance.

Journal of Nutrition 68 : 405-418

Herremens, M., Decuyper, F., Siau, O. (1989) Effects of feather wear and temperature on prediction of food intake and residual food consumption.

British Poultry Science 30 : 15-22.

Hill, J.A., Charles, D.R., Spechter, H.H., Bailey, R.A., Ballantyne, A.J. (1988) Effects of multiple environmental and nutritional factors in laying hens.

British Poultry Science 29 : 499-511.

Kyarisiima, C.C., Balnave, D. (1996) Influence of temperature during growth on responses of hens to high or low temperatures during lay.

British Poultry Science 37 : 553-562.

Leclercq, B. (1986) Energy Requirements of Avian Species in : Fisher, C, Boorman, K.N., (Eds), *Nutrient Requirements of Poultry and Nutritional Research, Poultry Science Symposium No.19*, Butterworths, London.

Li, Y., Ito, T., Nishibori, M., Yamamoto, S. (1992) Effects of environmental temperature on heat production associated with food intake and on abdominal temperature in laying hens.

British Poultry Science 33 : 113-122.

Lokhorst, C. (1996) Mathematical curves for the description of input and output variables of the daily production process in aviary housing systems for laying hens.

Poultry Science 75 : 838-848

Luiting, P., Schrama, J.W., van der Hel, W., Urff, E.M. (1991) Metabolic differences between white leghorns selected for high and low residual feed consumption.

British Poultry Science 32 : 763-782.

Lundy, H., Macleod, M.G., Jewitt, T.R. (1978) An automated multi-calorimeter system: Preliminary experiments on laying hens

British Poultry Science 19: 173-186

MacDonald, P., Edwards, R.A., Greenhalgh, J.F.D.(1995) Evaluation of foods : energy content of foods and the partition of food energy within the animal. *Animal Nutrition 5th Edition* , Longman (Harlow, Essex).

Macleod, M.G. (1990) Energy and nitrogen intake, expenditure and retention at 20°C in growing fowl given diets with a wide range of energy and protein contents.

British Journal of Nutrition 64 : 623-637

Macleod, M.G. (1991) Fat deposition and heat production as responses to surplus dietary energy in fowls given a wide range of ME:protein ratios.

British Poultry Science 32 : 1097-1108

Macleod, M.G. (1992) Energy and nitrogen intake, expenditure and retention at 32°C in growing fowl given diets with a wide range of energy and protein contents.

British Journal of Nutrition 67 : 192-206

March, B.E., MacMillan, C. (1990) Linoleic acid as a mediator of egg size.

Poultry Science 69 : 634-639

Marsden, A., Wethli, E., Kinread, N., Morris, T.R. (1973) An investigation of the effect of environmental temperature on feed intake of laying hens.

World Poultry Science 29 : 286.

Marsden, A., Morris, T.R. (1975) Comparisons between constant and cycling environmental temperatures applied to laying pullets.

World's Poultry Science Journal 31 : 311.

Marsden, A., Morris, T.R. (1987) Quantitative review of the effects of environmental temperature on food intake, egg output and energy balance in layers.

British Poultry Science 28 : 693-704.

Marsden, A., Morris, T.R., Cromarty, A.S. (1987) Effects of constant environmental temperatures on the performance of laying pullets.

British Poultry Science 28 : 361-380.

May, J.D., Lott, B.D. (1992) Feed and water consumption patterns of broilers at high environmental temperatures.

Poultry Science 71 : 331-336

Meltzer, A. (1986) Efficiency of effect of high ambient temperatures on food utilization in male broilers.

British Poultry Science 27 : 349-351

Meltzer, A. (1987) Acclimitization to ambient temperature and its nutritional consequences.

World's Poultry Science Journal 43 : 33-44

Miller, P.C., Sunde, M.L. (1975) The effects of precise constant and cyclic environments on shell quality and other lay performance factors with Leghorn pullets.

Poultry Science 54 : 36-46.

Morris, T.R. (1968) The effect of dietary energy level on the voluntary calorie intake of laying birds.

British Poultry Science 9 : 285-295

Morris, T.R. (1972) Prospects for improving the efficiency of nutrient utilisation in : *Egg formation and Production*, Freeman, B.M., Lake, P.E., (Eds), British Poultry Science Ltd., Edinburgh, pg 139-159.

Morris, T.R., Blackburn, H.A. (1982) The shape of the protein response curve relating protein intake to egg output for flocks of laying hens

British Poultry Science 23 : 405-424

Morris, T.R., Al-Assawi, K., Gous, R.M., Simpson, G.L. (1987) Effects of protein concentration on responses to dietary lysine by chicks

British Poultry Science 28: 185-195

Mount, L.E. (1974) The concept of thermal neutrality, in : J.L.Monteith and L.E. Mount (Eds) *Heat Loss from Animals and Man, Assessment and Control*. p.425-439 (London, Butterworths).

Mueller, W.J. (1966) The effect of two levels of methionine on the biological performance of laying pullets in controlled environments.

Poultry Science 46 : 82-88.

Njoya, J. (1995) Effect of diet and natural variations in climates on the performance of laying hens.

British Poultry Science 36 : 537-551.

Okumura, J., Mori, S. (1979) Effects of deficiencies of single amino acids on nitrogen and energy utilization in chicks.

British Poultry Science 20: 421-429

Paton, N.D. (1994) The effect of environmental temperature on the performance of broilers, *M.Sc. Thesis*, University of Natal, Pietermaritzburg.

Payne C.G. (1966) Environmental Temperature and Egg Production in : C.Horton-Smith and E.C.Amoroso (Eds) *Physiology of the Domestic Fowl - British Egg Marketing Board Symposium #1*, Oliver and Boyd, Edinburgh and London.

Payne, C.G. (1967) The influence of environmental temperature on egg production : a review, in: T.C.Carter, (Ed) *Environmental Control in Poultry Production*, p. 40-54, (Edinburgh, British Poultry Science Ltd.).

Peguri, A., Coon, C. (1993) Effect of feather coverage and temperature on layer performance.

Poultry Science 72 : 1318-1329.

Pesti, G.M., Thomson, E., Farrel, D.J. (1986) The energy metabolism of two breeds of hens in respiration chambers, in : *Energy metabolism in farm animals , Proceedings of 11th symposium.*

Pesti, G.M., Dorfman, J.H., Gonzalez-a, M.J. (1992) Comparison of equations for predicting metabolizable energy intake of laying hens.

British Poultry Science 33 : 553-559.

Pullar, J.D., Brockway, J.M, McDonald, J.D. (1969) A comparison of direct and indirect calorimetry in Blaxter, K.L, Kielanowski, J., Thorbek, G, (Eds) *Proceedings of the 4th EAAP Symposium on the Energy Metabolism of Farm Animals*, Warsaw, Poland, Oriel Press Ltd, Newcastle-upon-Tyne.

Reid, B.L., Weber, C.W. (1973) Dietary protein and sulfur amino acid levels for laying hens during heat stress.

Poultry Science 52 : 1335-1343.

Romijn, C., Lokhorst, W. (1966) Heat Regulation and Energy Metabolism in the Domestic Fowl in: C. Horton-Smith, E.C.Amoroso (Eds) *Physiology of the Domestic Fowl - British Egg Marketing Board Symposium #1*, Oliver and Boyd, Edinburgh and London.

Schulz, A.R. (1978) Simulation of energy metabolism in the simple stomached animal
British Journal of Nutrition 39 : 235-254

Sibbald, I.R. (1979) The gross energy of avian eggs.

Poultry Science 58 : 404-409.

Smith, A.J., Oliver, J. (1972) Some nutritional problems associated with egg production at high environmental temperatures : the effect of environmental temperature and rationing treatments on the productivity of pullets fed on diets of differing energy content.

Rhod.J.agric.Res. 10 : 3-21.

Smith, A.J., Oliver, J. (1972) Some nutritional problems associated with egg production at high environmental temperatures.

Rhod., J.agric.Res. 10:43-60.

Steel, R.G.D., Torrie, J.H. (1980) *Principles and Procedures of Statistics : A Biometrical Approach 2nd edition*, McGraw Hill International Editions, Singapore.

Stockland, W.L., Blaylock, L.G. (1974) The influence of temperature on the protein requirement of cage reared replacement pullets.

Poultry Science 53 : 1174-1187.

Sykes, A.H. (1972) The Energy Cost of Egg Production in : Freeman, B.M., Lake, P.E., (Eds), *Egg Formation and Production*, British Poultry Science Ltd, Edinburgh..

Sykes, A.H. (1977) Nutrition - Environment Interactions in Poultry, in: Haresign, W., Swan, H and Lewis, D., (Eds), *Nutrition and the Climatic Environment*, p.17-29 (London, Butterworths).

Sykes, A.H., Salih, F.I.M. (1986) Effect of changes in dietary energy intake and environmental temperature on heat tolerance in the fowl.

British Poultry Science 27 : 687-693.

Tasaki, L., Sugahara, K., Okumura, J. (1976) Effect of amino acid deficiency on energy and protein utilization in growing chicks, in : M.Vermorel, (Ed) *Proceedings of the 7th EAAP Symposium on the Energy Metabolism of Farm Animals*, Vichy, France, p101-104 (Clermont-Ferrand, Guy de Bussac).

Waring, J.J. (1967) Calorimetric studies on the utilization of dietary energy by the laying White Leghorn hen in relation to plane of nutrition and environmental temperature.

J.agric.Sci., Camb. 68 : 149-155.

Whittow, G.C. (1976) Regulation of body temperature, in : *Avian Physiology, 3rd Edition*, Sturkie, P.D., (Ed), Springer-Verlag, New York, pg 147-173

Wilson, W.O., Itoh, S., Siopes, T.D. (1972) Production traits of leghorn pullets in controlled temperatures.

Poultry Science 51 : 1014-1023.

APPENDIX I

Energy Balance in Layers		BIRD DATA:		FEED DATA:		CONSTANTS:	
FI	96.000 g/d	ME	11.350 MJ/kg	H=ME+egge-chBE			
EW	64.150 g	CP	15.600 %	egge=ROL(7.57304EW-82.4248)			
ROL	71.450 %	EE	9.930 MJ/kg	BE=14.941*chBW			
EO	45.835 g			(after Marsden & Morris, 1987)			
chBW	-5.454 g/d						
BW	1.816 kg						
ENERGY BALANCE:							
EEI	153.582 kcal/d						
MEI	169.310 kcal/d						
egge	27.933 kcal/d						
BE	17.026 kcal/d						
HP	124.351 kcal/d						
MH	118.119 kcal/d						
HIF	1.489 kcal/d						

TEMP	UNITS	1959a	1959b	1972a	1972b	1972c	1972d	1972e	1972f	1972g	1972h
EEI	kcal	277.37	248.06	153.58	153.58	241.78	218.16	153.58	153.58	153.58	153.58
MEI	kcal	313.70	296.65	169.31	169.31	272.11	240.92	169.31	169.31	169.31	169.31
egge	kcal	51.33	53.77	27.93	27.93	75.49	71.14	27.93	27.93	27.93	27.93
BE	kcal	1.56	1.07	-17.03	-17.03	8.21	10.71	-17.03	-17.03	-17.03	-17.03
HP	kcal	280.81	241.81	124.35	124.35	186.40	159.06	124.35	124.35	124.35	124.35
MH	kcal	151.61	148.58	118.12	118.12	165.30	118.12	118.12	118.12	118.12	118.12
HIF	kcal	26.10	22.28	1.49	1.49	5.52	-1.49	1.49	1.49	1.49	1.49
FI	g/day	102.70	125.50	125.00	100.00	90.00	80.00	143.00	120.00	105.00	90.00
EW	g	53.50	54.70	60.30	60.30	60.30	66.70	66.90	64.70	64.70	63.90
ROL	%	66.50	67.80	86.00	85.30	84.40	78.90	88.30	69.00	69.00	66.50
EO	g/day	35.60	37.10	51.86	51.44	50.89	47.89	45.68	45.82	45.23	42.49
chBW	g	0.44	0.30	2.00	0.60	2.30	3.00	1.61	1.07	0.10	6.20
BW	kg	1.83	1.78	2.06	2.06	2.06	2.06	2.31	2.31	2.31	2.31
ME	MJ/kg	12.78	9.89	12.53	12.41	12.65	12.60	12.60	12.52	12.55	12.51
CP	%	17.64	13.55	17.77	20.24	21.90	16.97	16.97	14.85	16.51	20.40
EE	MJ/kg	11.30	8.27	11.29	11.01	11.24	11.41	11.41	11.38	11.37	11.12

Experimentier	TEMP	UNITS	1959a	1959b	1972a	1972b	1972c	1972d	1972e	1972f	1972g	1972h
Bolton			277.37	248.06	153.58	153.58	241.78	218.16	153.58	153.58	153.58	153.58
Sykes			313.70	296.65	169.31	169.31	272.11	240.92	169.31	169.31	169.31	169.31
			51.33	53.77	27.93	27.93	75.49	71.14	27.93	27.93	27.93	27.93
			1.56	1.07	-17.03	-17.03	8.21	10.71	-17.03	-17.03	-17.03	-17.03
			280.81	241.81	124.35	124.35	186.40	159.06	124.35	124.35	124.35	124.35
			151.61	148.58	118.12	118.12	165.30	118.12	118.12	118.12	118.12	118.12
			26.10	22.28	1.49	1.49	5.52	-1.49	1.49	1.49	1.49	1.49
			102.70	125.50	125.00	100.00	90.00	80.00	143.00	120.00	105.00	90.00
			53.50	54.70	60.30	60.30	60.30	66.70	66.90	64.70	64.70	63.90
			66.50	67.80	86.00	85.30	84.40	78.90	88.30	69.00	69.00	66.50
			35.60	37.10	51.86	51.44	50.89	47.89	45.68	45.82	45.23	42.49
			0.44	0.30	2.00	0.60	2.30	3.00	1.61	1.07	0.10	6.20
			1.83	1.78	2.06	2.06	2.06	2.06	2.31	2.31	2.31	2.31
			12.78	9.89	12.53	12.41	12.65	12.60	12.60	12.52	12.55	12.51
			17.64	13.55	17.77	20.24	21.90	16.97	16.97	14.85	16.51	20.40
			11.30	8.27	11.29	11.01	11.24	11.41	11.41	11.38	11.37	11.12

Experimentier	TEMP	UNITS	1959a	1959b	1972a	1972b	1972c	1972d	1972e	1972f	1972g	1972h
Bolton			277.37	248.06	153.58	153.58	241.78	218.16	153.58	153.58	153.58	153.58
Sykes			313.70	296.65	169.31	169.31	272.11	240.92	169.31	169.31	169.31	169.31
			51.33	53.77	27.93	27.93	75.49	71.14	27.93	27.93	27.93	27.93
			1.56	1.07	-17.03	-17.03	8.21	10.71	-17.03	-17.03	-17.03	-17.03
			280.81	241.81	124.35	124.35	186.40	159.06	124.35	124.35	124.35	124.35
			151.61	148.58	118.12	118.12	165.30	118.12	118.12	118.12	118.12	118.12
			26.10	22.28	1.49	1.49	5.52	-1.49	1.49	1.49	1.49	1.49
			102.70	125.50	125.00	100.00	90.00	80.00	143.00	120.00	105.00	90.00
			53.50	54.70	60.30	60.30	60.30	66.70	66.90	64.70	64.70	63.90
			66.50	67.80	86.00	85.30	84.40	78.90	88.30	69.00	69.00	66.50
			35.60	37.10	51.86	51.44	50.89	47.89	45.68	45.82	45.23	42.49
			0.44	0.30	2.00	0.60	2.30	3.00	1.61	1.07	0.10	6.20
			1.83	1.78	2.06	2.06	2.06	2.06	2.31	2.31	2.31	2.31
			12.78	9.89	12.53	12.41	12.65	12.60	12.60	12.52	12.55	12.51
			17.64	13.55	17.77	20.24	21.90	16.97	16.97	14.85	16.51	20.40
			11.30	8.27	11.29	11.01	11.24	11.41	11.41	11.38	11.37	11.12

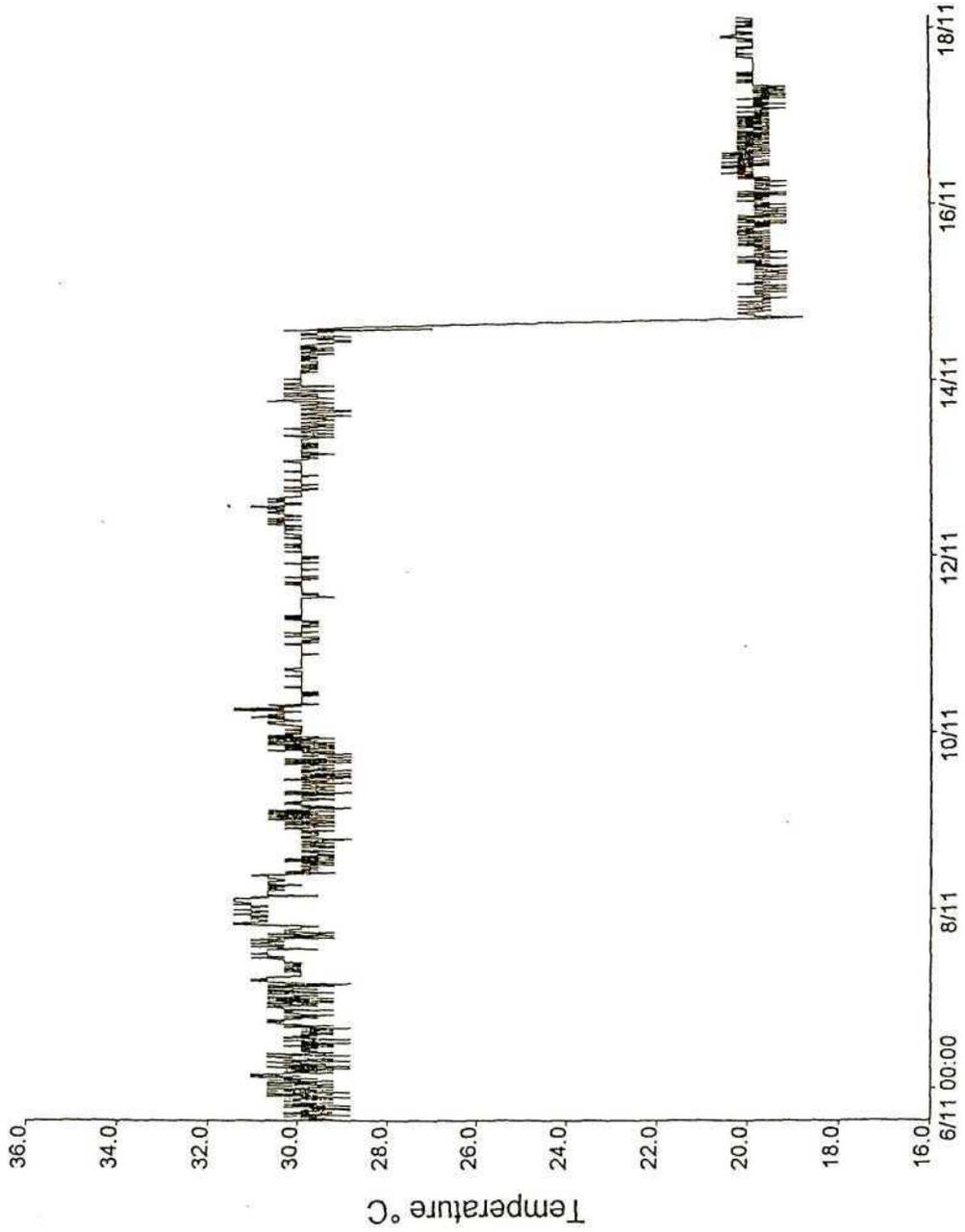
Experimentier	TEMP	UNITS	1959a	1959b	1972a	1972b	1972c	1972d	1972e	1972f	1972g	1972h
Bolton			277.37	248.06	153.58	153.58	241.78	218.16	153.58	153.58	153.58	153.58
Sykes			313.70	296.65	169.31	169.31	272.11	240.92	169.31	169.31	169.31	169.31
			51.33	53.77	27.93	27.93	75.49	71.14	27.93	27.93	27.93	27.93
			1.56	1.07	-17.03	-17.03	8.21	10.71	-17.03	-17.03	-17.03	-17.03
			280.81	241.81	124.35	124.35	186.40	159.06	124.35	124.35	124.35	124.35
			151.61	148.58	118.12	118.12	165.30	118.12	118.12	118.12	118.12	118.12
			26.10	22.28	1.49	1.49	5.52	-1.49	1.49	1.49	1.49	1.49
			102.70	125.50	125.00	100.00	90.00	80.00	143.00	120.00	105.00	90.00
			53.50	54.70	60.30	60.30	60.30	66.70	66.90	64.70	64.70	63.90
			66.50	67.80	86.00	85.30	84.40	78.90	88.30	69.00	69.00	66.50
			35.60	37.10	51.86	51.44	50.89	47.89	45.68	45.82	45.23	42.49
			0.44	0.30	2.00	0.60	2.30	3.00	1.61	1.07	0.10	6.20
			1.83	1.78	2.06	2.06	2.06	2.06	2.31	2.31	2.31	2.31
			12.78	9.89	12.53	12.41	12.65	12.60	12.60	12.52	12.55	12.51
			17.64	13.55	17.77	20.24	21.90	16.97	16.97	14.85	16.51	20.40
			11.30	8.27	11.29	11.01	11.24	11.41	11.41	11.38	11.37	11.12

Experimentier	TEMP	UNITS	1959a	1959b	1972a	1972b	1972c	1972d	1972e	1972f	1972g	1972h
Bolton			277.37	248.06	153.58	153.58	241.78	218.16	153.58	153.58	153.58	153.58
Sykes			313.70	296.65	169.31	169.31	272.11	240.92	169.31	169.31	169.31	169.31
			51.33	53.77	27.93	27.93	75.49	71.14	27.93	27.93	27.93	27.93
			1.56	1.07	-17.03	-17.03	8.21	10.71	-17.03	-17.03	-17.03	-17.03
			280.81	241.81	124.35	124.35	186.40	159.06	124.35	124.35	124.35	124.35
			151.61	148.58	118.12	118.12	165.30	118.12	118.12	118.12	118.12	118.12
			26.10	22.28	1.49	1.49	5.52	-1.49	1.49	1.49	1.49	1.49
			102.70	125.50	125.00	100.00	90.00	80.00	143.00	120.00	105.00	90.00
			53.50	54.70	60.30	60.30	60.30	66.70	66.90	64.70	64.70	63.90
			66.50	67.80	86.00	85.30	84.40	78.90	88.30	69.00	69.00	66.50
			35.60	37.10	51.86	51.44	50.89	47.89	45.68	45.82	45.23	42.49
			0.44	0.30	2.00	0.60	2.30	3.00	1.61	1.07	0.10	6.20
			1.83	1.78	2.06	2.06	2.06	2.06	2.31	2.31	2.31	2.31
			12.78	9.89	12.53	12.41	12.65	12.60	12.60	12.52	12.55	12.51
			17.64	13.55	17.77	20.24	21.90	16.97	16.97	14.85	16.51	20.40
			11.30	8.27	11.29	11.01	11.24	11.41	11.41	11.38	11.37	11.12

Experimenter		Miller 1975			Njoya 1995				Kyarisiima 1996		de Andrade 1976				Smith & Oliver 1976			Ahmad 1974			
TEMP	UNITS	10	21	32	21	21	31	31	15	30	21	21	32	32	29.5	32	35	22	30	22	30
EEl	kcal	214.14	226.11	200.39	350.80	289.36	267.59	250.02	297.80	236.11	255.22	260.19	189.50	203.69	244.47	224.60	176.56	213.92	202.27	153.58	218.76
MEI	kcal	238.04	251.50	222.98	401.55	342.33	306.30	295.78	355.02	281.48	285.99	288.80	212.35	226.09	261.58	240.31	188.92	247.16	233.70	169.31	235.56
eggE	kcal	69.13	57.91	48.16	73.83	70.57	62.99	58.54	70.49	60.02	73.96	78.49	54.82	63.26	67.80	62.00	47.49	60.79	62.93	27.93	53.12
BE	kcal	7.93	3.96	5.95	14.64	15.36	7.14	8.21	14.34	11.65	0.00	0.00	0.00	0.00	0.94	1.66	4.89	2.59	2.47	17.03	2.34
HP	kcal	160.97	189.62	168.87	313.08	256.40	236.17	229.03	270.18	209.80	212.04	210.31	157.53	162.82	192.85	176.66	136.54	183.78	168.29	124.35	180.10
MH	kcal	143.67	131.13	124.69	173.37	173.55	148.76	151.43	185.13	175.66	0.00	0.00	0.00	0.00	136.64	133.23	125.08	137.14	133.99	118.12	133.23
HIF	kcal	4.14	13.98	10.56	33.39	19.80	20.89	18.55	20.33	8.16	50.68	50.27	37.65	38.92	13.43	10.38	2.74	11.15	8.20	1.49	11.20
FI	g/day	99.00	88.50	68.00	142.50	136.80	108.70	118.20	140.00	111.00	99.80	92.10	74.10	72.10	73.80	67.80	53.30	112.16	106.05	55.30	74.78
EW	g	62.50	59.00	54.50	60.70	59.60	56.00	55.70	57.25	53.40	58.90	61.90	53.60	56.10	58.00	55.60	52.80	56.06	55.91	48.69	53.28
ROL	%	74.00	66.50	61.00	81.88	80.03	77.14	72.17	84.00	78.00	85.10	85.00	70.90	77.30	79.50	76.60	62.60	74.35	77.22	40.82	69.23
EO	g/day	48.25	39.24	33.25	49.70	47.70	43.20	40.20	48.09	41.65	50.12	52.62	38.00	43.37	46.11	42.59	33.05	41.68	43.17	19.88	36.89
chBW	g	2.22	1.11	1.67	4.10	4.30	2.00	2.30	4.02	3.26					0.26	-0.46	-1.37	0.72	0.69	-4.77	-0.66
BW	kg	1.70	1.50	1.40	2.20	2.20	1.78	1.83	2.41	2.24					1.59	1.53	1.41	1.60	1.55	1.30	1.53
ME	MJ/kg	10.06	11.89	13.72	11.79	10.47	11.79	10.47	10.61	10.61	11.99	13.12	11.99	13.12	14.83	14.83	14.83	9.22	9.22	12.81	13.18
CP	%	12.54	14.43	16.32	19.08	17.00	19.08	17.00	18.07	18.07	14.52	17.59	14.52	17.59	26.78	26.78	26.78	14.50	14.50	26.14	14.50
EE	MJ/kg	9.05	10.69	12.33	10.30	8.85	10.30	8.85	8.90	8.90	10.70	11.82	10.70	11.82	13.86	13.86	13.86	7.98	7.98	11.62	12.24
breed :		SC WLgH			Lohmann Brown				Tegel Super Brown		SC WLgH		Hyline WLgH			Hyline 934-E WLgH					
age (wks):		34-47			22-46				18-50		20-48		20-34			26-46					

Experimenter		de Andrade 1977				Marsden 1987						Smith & Oliver 1972				Peguri 1993						
TEMP	UNITS	21	21	31	31	15	18	21	24	27	30	15	18	21	24	27	30	32	38	12.8	23.9	33.9
EEl	kcal	249.94	238.88	184.21	206.73	258.88	256.64	243.12	235.87	223.18	200.52	329.34	326.49	306.72	297.57	280.39	251.92	220.79	153.58	330.71	293.82	218.33
MEI	kcal	280.19	266.21	206.50	230.38	300.60	298.00	279.02	270.70	256.14	230.13	361.39	358.26	337.75	327.68	310.99	279.42	243.40	169.31	366.50	328.45	251.89
eggE	kcal	67.41	69.20	48.48	63.68	67.13	67.90	67.22	68.06	68.18	62.66	67.13	67.90	67.22	68.06	68.18	62.66	57.50	27.93	65.60	71.89	63.43
BE	kcal	4.07	6.57	6.48	0.04	0.11	0.14	1.46	0.68	2.07	0.29	0.11	0.14	1.46	0.68	2.07	0.29	2.36	17.03	0.96	0.82	1.18
HP	kcal	208.71	190.43	151.54	166.66	233.37	229.97	210.34	201.96	185.89	167.18	294.15	290.22	269.07	258.94	240.74	216.47	183.54	124.35	299.94	255.75	187.28
MH	kcal	162.36	162.36	148.58	148.58	133.04	133.04	133.04	133.04	133.04	132.40	133.04	133.04	133.04	133.04	133.04	132.40	133.16	118.12	162.36	131.13	148.58
HIF	kcal	11.08	6.71	0.71	4.32	23.98	23.17	18.48	16.47	12.63	8.31	38.51	37.57	32.51	30.09	25.74	20.09	12.04	1.49	32.88	29.79	9.25
FI	g/day	98.10	84.70	72.30	73.30	115.60	114.60	107.30	104.10	98.50	88.50	115.60	114.60	107.30	104.10	98.50	88.50	79.50	55.30	128.00	115.00	90.00
EW	g	55.01	55.76	50.39	53.53	60.60	60.70	60.40	60.10	59.30	56.80	60.60	60.70	60.40	60.10	59.30	56.80	55.22	48.69	59.40	59.20	57.30
ROL	%	84.40	85.20	67.80	82.50	74.60	75.30	75.00	76.40	77.80	75.40	74.60	75.30	75.00	76.40	77.80	75.40	71.65	40.82	74.70	82.20	75.50
EO	g/day	46.43	47.51	34.16	44.16	45.21	45.71	45.30	45.92	46.14	42.83	45.21	45.71	45.30	45.92	46.14	42.83	42.83	42.83	42.83	42.83	42.83
chBW	g	1.14	1.84	-1.81	0.01	0.03	0.04	0.41	0.19	0.58	0.08	0.03	0.04	0.41	0.19	0.58	0.08	-0.66	-4.77	-0.27	-0.23	0.33
BW	kg	2.01	2.01	1.78	1.78	1.53	1.53	1.53	1.53	1.53	1.52	1.53	1.53	1.53	1.53	1.53	1.52	1.53	1.30	2.01	1.50	1.78
ME	MJ/kg	11.95	13.15	11.95	13.15	10.88	10.88	10.88	10.88	10.88	10.88	13.08	13.08	13.17	13.17	13.21	13.21	12.81	12.81	11.98	11.95	11.71
CP	%	14.50	18.33	14.50	18.33	11.50	11.50	13.82	13.82	15.40	15.40	14.50	14.50	16.21	16.21	18.30	18.30	26.14	26.14	12.48	13.52	17.03
EE	MJ/kg	10.66	11.80	10.66	11.80	9.37	9.37	9.48	9.48	9.48	9.48	11.92	11.92	11.96	11.96	11.91	11.91	11.62	11.62	10.81	10.69	10.15
breed :		S-C WLgH				WLgH Babcock B305						WLgH Babcock B305				WLgH Thorber 606			Dekalb XL WgH			
age (wks):		20-32				32-66						32-66				20-30			59-65			

EEchambers



Time (starting November 5, 1997 3:25:15 pm)

#7233

TABLE 26

*Extent of the change in performance of Amberlink hens at 20°C and 30°C as measured by pairwise comparisons,
D being the difference between the periods.*

DIFFERENCE : PERIOD THREE MINUS PERIOD ONE

DIET	feed intake (g/bird.d)		rate of lay (%)		egg weight (g)		egg output (g/bird.d)			
	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n
B1	-13.50	12.41	-24.77	23.35	1.65	0.35	-12.37	7.61		
B2	-5.57	16.69	-15.34	9.69	2.50	0.28	-6.26	2.92		
HIGH	6.43	11.01	-14.05	14.92	2.09	0.50	-5.43	4.75		
HIGH/LOW	2.18	15.27	-13.90	6.50	1.87	0.18	-6.05	2.37		
LOW	-13.07	31.32	-20.22	18.66	2.00	0.15	-8.77	5.45		
95	-0.83	34.15	-12.34	14.74	2.21	0.85	-1.81	5.67		
95/125	-1.41	54.13	-13.85	47.23	3.22	0.73	-5.08	16.66		
125	-6.80	35.61	-13.10	12.10	2.84	0.14	-5.43	3.89		

DIET	body weight (g)		BW change (g/bird.d)		ME intake (kJ/bird.d)		EE intake (kJ/bird.d)		HP (kJ/bird.d)	
	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n
B1	-3.73	0.35	-6.89	5.87	-170.90	1987.64	-143.90	1409.55	-26.99	49.55
B2	-25.64	0.99	-6.04	3.40	-68.16	2501.09	-58.27	1827.73	-9.90	52.69
HIGH	-14.00	0.64	-5.00	1.63	75.73	1529.25	66.38	1173.25	9.35	23.31
HIGH/LOW	3.64	0.33	-2.36	1.76	17.75	2163.18	19.22	1642.45	2.99	25.93
LOW	-30.78	0.60	-5.11	21.04	-172.30	5450.67	-142.50	3728.56	-29.79	163.00
95	21.00	1.70	-1.80	5.16	-10.31	5176.36	-9.22	4130.45	-1.10	58.96
95/125	-23.20	0.63	-0.46	5.65	-17.14	8219.20	-15.06	6576.00	-2.08	91.65
125	-22.50	0.44	-4.03	9.24	-83.98	5437.30	-75.36	4379.40	-8.61	57.16

TABLE 26

*Extent of the change in performance of Amberlink hens at 20°C and 30°C as measured by pairwise comparisons,
D being the difference between the periods.*

DIFFERENCE : PERIOD THREE MINUS PERIOD TWO

DIET	feed intake (g/bird.d)		rate of lay (%)		egg weight (g)		egg output (g/bird.d)			
	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n		
B1	34.50	35.21	16.65	17.57	1.94	0.35	10.95	6.96		
B2	26.74	16.63	11.55	14.57	6.41	0.49	7.04	4.10		
HIGH	19.41	10.63	8.39	7.53	1.20	0.32	5.56	1.95		
HIGH/LOW	7.64	13.80	9.36	8.68	1.19	0.55	6.34	2.92		
LOW	22.94	35.17	4.42	19.03	2.21	0.68	3.48	5.88		
95	21.64	31.07	0.91	38.26	1.36	1.23	1.85	6.52		
95/125	23.26	35.76	15.87	29.57	3.46	0.44	12.20	9.66		
125	27.94	45.17	5.48	14.21	2.33	0.62	4.94	5.66		

DIET	body weight (g)		BW change (g/bird.d)		ME intake (kJ/bird.d)		EE intake (kJ/bird.d)		HP (kJ/bird.d)	
	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n
B1	120.10	8.83	9.11	8.83	436.50	5640.82	367.60	44001.00	68.93	140.64
B2	127.50	3.65	8.13	3.65	327.20	2494.00	279.70	20048.00	47.50	52.55
HIGH	139.00	2.07	4.96	2.07	228.70	1472.42	200.50	13575.00	28.24	22.44
HIGH/LOW	69.09	4.42	2.61	4.42	106.20	2198.00	83.33	17294.00	22.82	36.73
LOW	76.33	22.53	8.79	22.53	302.40	6126.22	250.10	37717.00	52.30	18.32
95	41.73	8.99	9.09	8.99	266.30	4713.55	237.90	41372.00	28.42	53.69
95/125	144.20	5.52	4.78	5.52	286.40	5443.20	256.00	13753.00	30.34	58.25
125	127.50	6.67	7.09	6.67	345.00	6881.00	309.60	55422.00	35.37	72.35

TABLE 26

Extent of the change in performance of Amberlink hens at 20°C and 30°C as measured by pairwise comparisons, D being the difference between the periods.

DIFFERENCE : PERIOD ONE MINUS PERIOD TWO

DIET	feed intake (g/bird.d)		rate of lay (%)		egg weight (g)		egg output (g/bird.d)	
	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n
B1	-21.00	20.02	8.12	4.20	-3.59	0.19	1.42	13.47
B2	-21.17	28.15	3.79	14.82	-3.14	0.47	-0.78	4.21
HIGH	-25.83	16.11	5.66	20.58	-3.30	0.67	-0.13	7.25
HIGH/LOW	-9.82	4.07	4.55	3.96	-3.06	0.83	-0.29	1.68
LOW	-9.87	28.83	16.33	8.41	-3.95	0.61	5.79	2.60
95	-20.81	40.24	13.57	41.62	-2.78	0.91	4.62	16.82
95/125	-21.85	37.96	-2.02	12.10	-6.68	1.62	-7.12	71.55
125	-21.14	23.80	7.62	10.62	-5.16	0.52	0.49	4.51

DIET	body weight (kg)		BW change (g/bird.d)		ME intake (kJ/bird.d)		EE intake (kJ/bird.d)		HP (kJ/bird.d)	
	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n	D	S ² _n
B1	-111.64	0.59	-2.22	1.19	-265.60	3201.73	-223.60	2269.73	-41.94	79.83
B2	-101.80	0.52	-1.48	3.57	-259.10	4214.45	-221.50	3079.91	-37.60	88.79
HIGH	-125.00	0.62	0.04	1.51	-304.40	2236.83	-266.90	1718.67	-37.59	34.10
HIGH/LOW	-72.73	0.34	-0.25	4.35	-145.60	4847.00	-119.80	3671.00	-25.81	14.56
LOW	-45.56	1.19	-4.99	3.94	-130.10	5015.00	-107.60	3430.56	-22.50	150.00
95	-62.73	0.49	-6.30	6.43	-256.00	636.18	-228.70	4860.00	-27.32	69.37
95/125	-121.00	1.25	-2.48	2.22	-269.20	5753.20	-241.00	4598.20	-28.27	64.77
125	-105.00	0.57	-3.44	3.03	-261.00	3627.60	-234.20	2921.80	-26.76	38.15