GENERAL INTRODUCTION

Feed constitutes the major (*c.* 70%) cost incurred in all poultry production (meat, eggs, progeny). Because of this, any nutritional, genetic or managerial advances, either true or manipulative, which can reduce feed costs *per se* or increase the efficiency of utilization of feed for productive processes can result in considerable benefit to the poultry industry, particularly when the scale and intensity of production is considered. For egg producing stock, much research has been directed at determining the nutrient requirements for optimal growth during rearing, but there is much evidence to suggest that some degree of sub-optimal growth caused by nutritional deprivation during rearing can result in savings in feed costs and enhanced egg production and efficiency of feed utilization.

The general term 'restricted feeding' was applied to studies on poultry in which some attempt was made to reduce nutrient intake, usually during rearing. Such manipulation of nutrient intake in studies with other animal species would use the term undernutrition or reference the exact nutrient involved, but for poultry the term 'restricted feeding' could imply the regulation of either specific macro-nutrients such as protein and/or energy or total nutrients inclusive of protein, energy, vitamins and minerals. As it is currently applied in the poultry industry, restricted feeding probably developed from the classical studies in Canada by Gowe *et al.* (1960), who showed that under practical conditions it was possible to increase egg production when birds were subjected to feed restriction during rearing. Subsequent studies confirmed this effect (e.g. Strain *et al.* 1965), which resulted in a large amount of global research aimed at demonstrating the effect with different types and strains of birds and at the optimization of the effect by various procedures. Investigations commenced in Australia around the 1960s, and the results confirmed overseas studies (see for example, Cumming 1972).

Currently in Australia approximately 47% of layer-type birds are replaced by started pullets and 60% of these are subjected to some form of restriction during rearing, while only about 35% of farm-reared replacement stock are similarly restricted during rearing (Littleton 1981). Despite the apparent wide-spread acceptance of the practice by poultry producers, there is some confusion regarding the benefits obtained. The source of much of this confusion can probably be credited to the essentially empirical nature of the practice of restricted feeding as it has been developed, since there is currently no information of sufficient detail and appropriate orientation that conclusions can be made concerning the biological basis of the effects obtained. Without this information, future research on restricted feeding is without clear direction, and variable results can be expected when the practice is applied to the industry at the farm level.

The procurement of such information is clearly of vital importance to the perpetuation and evolution of the practice of restricted feeding of poultry. The studies presented in this thesis were aimed at this objective, primarily from three facets: (1) alterations in the important production characteristics of egg-producing poultry due to feed restriction; (2) the gross changes in body composition and their physiological importance; and (3) the nature of any alterations in energy metabolism both during rearing and egg production.

CHAPTER 1

LITERATURE REVIEW

Chapter 1

Literature Review

1.1. INTRODUCTION

The literature on restricted feeding during the rearing of poultry was initially reviewed by Lee *et al.* (1971a). The range of restricted feeding techniques used to achieve nutrient reductions were considered, and the overall effects, many of which were treated by statistical procedures, were discussed in detail in this review (Lee *et al.* 1971a). Pearson and Shannon (1979) have recently completed a less detailed review which considered some of the more recent information on the effects of restricted feeding. However neither of these reviews attempted to discuss the factors which could possibly affect the response to a restricted feeding programme and which could explain, to a limited extent, the variable results reported. This does not represent a criticism of either review because each fulfilled adequately the specific aims to which they were directed. Rather, it identifies an area of restricted feeding of poultry which, although complex, must reasonably be considered. Furthermore, certain facets of restricted feeding, such as the known differences in response between layer-type and broiler breeder birds, have not as yet been considered.

Although the apparent responses of poultry to restricted feeding during rearing are variable, these responses obviously rely on the criteria used for their assessment. The definition of such criteria, and the importance placed on each of them, have not been consistent throughout the published literature. This review therefore initially outlines the various criteria which have been used to determine the responses to restricted feeding programmes. The major emphasis of this literature review has been placed on restriction methods which control feed intake (quantitative methods). From this aspect the literature has been reassessed sometimes with a less stringent approach in order to gain an overview of the responses obtained. To further clarify the situation, this reassessment was also carried out on a geographical basis. This was done to determine if there were regional responses to restricted feeding perhaps due to strain differences or managerial practices.

Finally, this review attempts to define and discuss the factors that could influence the response to a restricted feeding programme, to discuss the physiological, metabolic and energetic alterations found in various experiments, and to review the reasons which were proposed to explain the observed biological responses.

1.2 CRITERIA USED IN THE ASSESSMENT OF RESTRICTED FEEDING PROGRAMMES

The results of restricted feeding experiments reported in the literature have been assessed by the use of many different criteria either singularly or in conjunction with others. The main criteria used can be summarised as follows:

(a) Feed intake during rearing
(b) Liveweight at the end of the restriction period
(c) Liveweight at the end of the laying period
(d) Time of sexual maturity
(e) Egg weight
(f) Egg production
(g) Efficiency of feed utilization
(h) Body composition
(i) Economics

1.2.1 Feed intake during rearing

The use of this criterion in the assessment of the response to restricted feeding depends on the method of restriction used. Dilution of the diet with either fibre or similar inert material results in increased feed intake over the rearing period (Isaacks *et al.* 1960; Deaton and Quisenberry 1963; Lillie and Denton 1966; Waldroup *et al.* 1966; Summers *et al.* 1967; Kondra *et al.* 1974; Peter *et al.* 1976). Depending on the inclusion level of the fibre or inert material, nutrient intake can be reduced. Low protein diets or diets deficient in a specific amino acid can result in either an increase or a decrease in feed intake depending on such factors as the level of the first limiting amino acid relative to requirement at a particular age (Couch and Trammell 1970; Maclachlan *et al.* 1977a and b) and the amino acid profile of the dietary protein (Gous 1978).

Feed allowances for birds on quantitative restriction programmes are often calculated on the basis of a group of birds allowed *ad libitum* feed intake. There are two problems with this approach:

(a) Birds allowed *ad libitum* feed intake may not eat in direct relation to their energy requirements but may overconsume energy particularly in the later stages of the rearing period (Scott *et al.* 1969). This could be influenced by a number of factors (e.g., environment, strain of bird, dietary energy concentration). Therefore changes observed in feed intake and liveweight between the birds allowed *ad libitum* feed intake and those on a restricted feeding programme are only "apparent" changes. Berg *et al.* (1963) had three feeding treatments where birds were either allowed *ad libitum* feed intake of a high metabolisable energy (13.01 MJ/kg) diet or a low metabolisable energy (10.04 MJ/kg) diet or were restricted-fed the high energy diet. The energy intake of the birds on the low energy diet during the rearing period was approximately 9% lower than that for the birds on the high energy diet. The birds on the low energy diet would have eaten to satisfy their energy requirements (Hill and Dansky 1954) which may indicate overconsumption of energy by the birds on the high energy diet. In addition, Berg and Bearse (1961) found substantial reductions in feed intake during rearing but no delay in sexual maturity and negligible reduction in liveweight at the end of the restriction period.

(b) Physiological development is often retarded in suitable quantitative feed restriction programmes. Birds allowed *ad libitum* feed intake therefore commence egg production at an earlier age with an associated increase in feed intake due to greater energy requirements which, correspondingly, means that the birds on the restricted feeding programme are allocated increased feed allowances (e.g., Milby and Sherwood 1956).

To overcome these disadvantages associated with quantitative feed restriction programmes, some workers have offered a prescribed quantity of feed throughout the rearing period irrespective of the intake for the group allowed *ad libitum* feed intake (Walter and Aitken 1961; Deaton and Quisenberry 1963) or an amount calculated on the basis of actual energy requirements (Singsen *et al.* 1958).

1.2.2 Liveweight at the end of the restriction period

This criterion has been recommended as the definitive one in the assessment of a restricted feeding programme (Cumming 1972; Pym and Dillon 1974). However, there are three main problems associated with the use of this criterion.

(a) True versus apparent reduction in liveweight. This is related to the previous section (1.2.1) of overconsumption during rearing by birds allowed *ad libitum* feed intake.

(b) This criterion does not take into account the pattern of liveweight development during the rearing period (Wells 1980), and will be discussed in more detail in a later section (1.4.2).

(c) Body composition at the end of the restriction period could be important as birds of similar liveweight could have different body compositions depending on the type of restriction programme (see Section 1.5.1.3).

1.2.3 Liveweight at the end of the egg production period

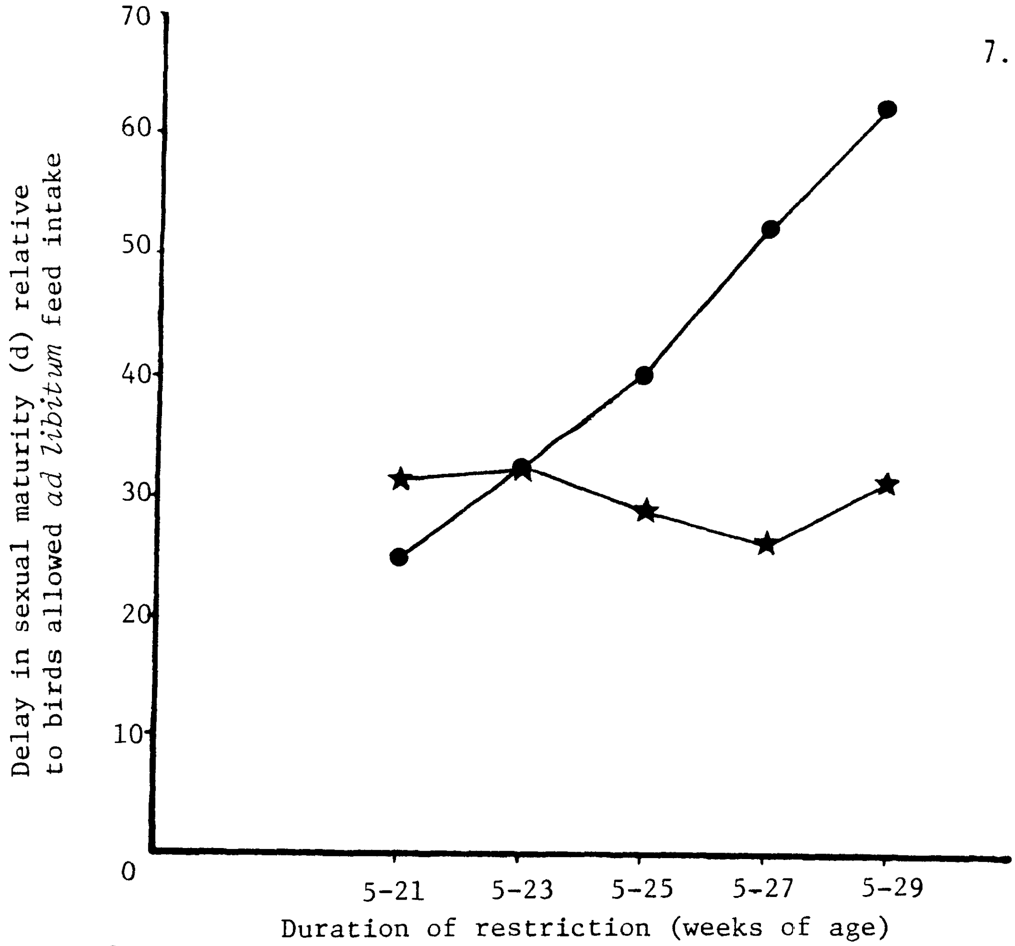
There are indications that liveweight may be permanently reduced in birds previously on a rearing feed restriction programme (Fuller and Dunahoo 1962; Berg *et al.* 1963; Deaton and Quisenberry 1963; Strain *et al.* 1965; Fuller *et al.* 1969). However it is impossible to draw sound conclusions from this criterion without making allowances for factors such as the rate of egg output over the laying period, the body composition at the start of the laying period, and the physiological age and rate of liveweight gain when the liveweight is measured.

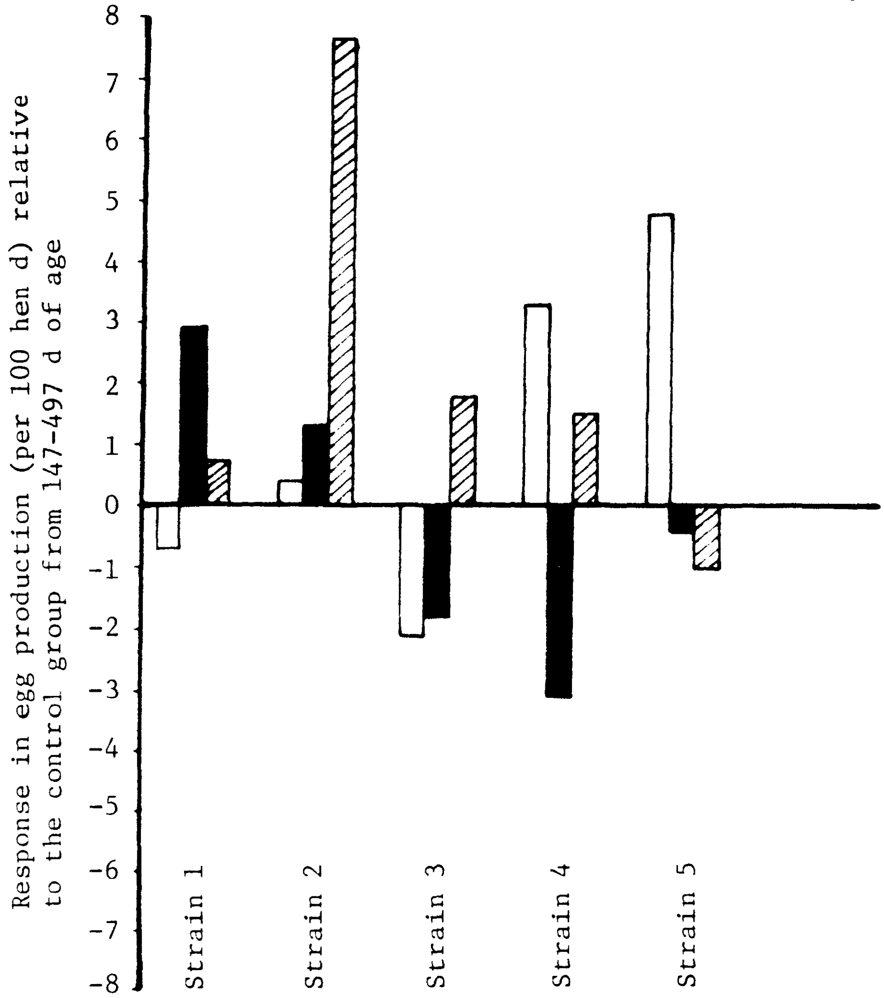
1.2.4 Age of sexual maturity

The precision of the estimation of this criterion determines its effectiveness (Lee *et al.* 1971a), as different indices have been used for its measurement (eg. age at first egg, age at 50% of egg production) (see Figure 1.1). This criterion is confounded between experiments by the lighting patterns used during the rearing period and according to one report (Summers *et al.* 1967) may not necessarily be indicative of prior nutritional deprivation. However, there is usually a significant relationship between delay in sexual maturity and the degree of liveweight reduction in restricted feeding programmes (Lee *et al.* 1971a; Gous and Stielau 1976), a finding not observed by Summers *et al.* (1967). Age at first egg should be an excellent measurement of attainment of sexual maturity in poultry. However this measurement requires that each individual bird is monitored for initial oviposition; although this was an impossible task in some experiments, in others it was easily measurable but was not recorded. The usual method is simply to record the age in each group that the first egg is observed. This can give misleading results because of precocious birds, irrespective of rearing treatment.

FIGURE 1.1: Results from MacIntyre and Gardiner (1964) which illustrate two different indicies used to determine the delay in sexual maturity for birds subjected to restricted feeding during rearing, either age at first oviposition (★) or age at egg production equal to 50 eggs/100 hen d (●).

FIGURE 1.2: The effect of strain of bird on the response in egg production (number/100 hen d) during the laying period (147-497 d of age) measured from 50 eggs/100 hen d. Results were calculated relative to a group of birds which were reared with constant light (14 h/d) and *ad libitum* feed intake (Test number 3, Proudfoot and Gowe 1967). Rearing treatments were either (i) constant light - restricted (□); (ii) limited light - *ad libitum* (■); or (iii) limited light - restricted (▨).


Delay in sexual maturity (d) relative
to birds allowed *ad libitum* feed intake
70
60
50
40
30
20
10
0
5-21
5-23
5-25
5-27
5-29
Duration of restriction (weeks of age)


Response in egg production (per 100 hen d) relative
to the control group from 147-497 d of age
8
7
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
-6
-7
-8
Strain 1
Strain 2
Strain 3
Strain 4
Strain 5

1.2.5 Egg weight

There is conclusive evidence to show that egg weight is related to the chronological age of birds (eg. Williams and Sharp 1978). Therefore, since birds which had been on a restricted feeding programme begin egg production at a more advanced chronological age than birds which had been allowed *ad libitum* feed intake during rearing, heavier eggs are laid at the time of peak egg production. This can result in significant differences in average egg weight between groups which can be biologically misleading. Also, this effect can sometimes be modified by the lighting pattern used during the rearing period (Berg *et al.* 1963). However differences between treatments in egg weights, if measured appropriately, could be indicative of alterations in ovarian development and egg synthesis. Egg weight is therefore an extremely important criterion in the assessment of the biological response to restricted feeding. Also, egg weight is important economically because of the large price differentials prevalent in the Australian egg industry (Skaller 1976).

1.2.6 Egg production

This is clearly the major criterion in the commercial and biological assessment of a restricted feeding programme during rearing and refers to the number of eggs produced in a specified time interval. However the effectiveness of this criterion in the interpretation of experiments on restricted feeding is influenced by the method used for calculation. There are two methods of calculation of egg production, termed, at least in this thesis, with respect to either chronological or physiological age. Chronological age relates directly to temporal time from birth. Chronology (noun) is defined (Webster Dictionary) as the following: (1) the science that treats of measuring or computing time by regular divisions or periods and that assigns to events or transactions their proper dates; (2) a chronological table or list; (3) an arrangement (as of data, events) in the order of time of occurrence or appearance. Chronological and chronologic are the adjectives and chronologically the adverb. Physiological or physiologic are adjectives and are defined (Webster Dictionary) as the following: (1) of or relating to physiology; (2) characteristic of or appropriate to an organism's healthy or normal functioning; (3) differing in reactions or functional properties rather than in morphological features. Physiologically is the adverb. Physiological age with respect to egg producing poultry is conveniently expressed as a function of commencement of egg production and stage of egg production. The frequently reported method of calculation of egg production data is simply on a chronological age basis. Commercially, it is paramount to determine the ability of previously restricted birds to produce similar or greater quantities of eggs or egg mass prior to the termination of the egg production period. This is important due to the often substantial delay in sexual maturity which can occur in birds on restricted feeding programmes. However biologically, this is an inappropriate method for the determination of the egg production response to a restricted feeding programme. MacIntyre and Aitken (1959) were the first to stress the importance of method of calculation, and since then many workers have aided the biological interpretation of their results by presentation of egg production both on a similar age basis and also on the basis of similar durations of production after sexual maturity (e.g. Walter and Aitken 1961; Fuller and Dunahoo 1962; Connor *et al.* 1977b). Despite the known influence of method of calculation of egg production on interpretation, some workers have failed even to present basic information on egg production (eg. Powell and Gehle 1976; Abu-Serewa 1977), while others have continued to compare treatments only on a chronological age basis (Gous and Stielau 1976; Maclachlan *et al.* 1977a and b; Gous 1978).

1.2.7 Efficiency of feed utilization

Feed efficiency is an extremely important facet of modern poultry production, but few workers have given details of this parameter during either the rearing or laying periods. The index often used for this criterion during the laying period is the amount of feed per one dozen eggs (Lee *et al.* 1971a). This ignores differences between groups in average egg weights and therefore may be an imprecise estimator of actual feed efficiency. Feed efficiency calculated in this way also has no biological basis; rather it is largely a commercial index, and should only be used as such.

1.2.8 Body composition

This criterion has assumed increased importance in recent years with the postulate that body composition *per se* may affect reproductive performance (see Pearson and Shannon 1979). Body composition can be changed due to feed restriction during the rearing period, and this could contribute to the effects reported to be caused by restricted feeding (see Section 1.5.1.3). Gous (1972) reported an experiment on broiler breeders in which body composition was the major criterion used to assess the effects of restricted feeding programmes. Other workers have reported alterations to body composition and have attempted to relate the observed changes to the subsequent egg production (eg. Fuller *et al.* 1973).

1.2.9 Economics

Ultimately this is the final consideration in the evaluation of any nutritional programme. However in small scale experiments emphasis should be placed on the biological criteria outlined above. Some workers (eg. Gowe and coworkers) have given extensive treatment of both the biological and economic criteria, whereas others have concentrated on economics to the detriment of the biological interpretation of their results.

1.3 TABULATION OF RESULTS REPORTED FOR LAYER-TYPE STRAINS OF BIRDS

The majority of the experimental results reported in the literature on restricted feeding of layer-type strains of birds are given in Table 1.1. These results are classified according to the following parameters: strain type; the duration and method of restriction; the duration of the egg production period; lighting patterns during the rearing and egg production periods; the degree of liveweight reduction for the restricted-fed birds; the age at sexual maturity and the response in terms of egg production due to a restricted feeding programme during rearing. The data in Table 1.1 are not intended to include all experiments conducted on restricted feeding and were derived only from experiments that examined quantitative restricted feeding programmes during rearing. Lighting patterns given in Table 1.1 are estimates and were usually derived from the hatch dates reported in the references. Egg production responses, both on a chronological and a physiological age, are not statistically based. The physiological egg production response was assumed to be positive if the chronological egg production response was positive. This assumption is not necessarily a correct one due to the possibility of sudden changes in egg production, but is used to give an estimate of the biological response to a restricted feeding programme.

Much of the published research on restricted feeding of layer strains of birds has been carried out by Canadian workers and is of high quality in terms of procedure, and the precision and mode of presentation of results. Work carried out in Canada has also usually achieved a greater degree of liveweight reduction than work conducted elsewhere. Australian research has usually used time restriction methods which appear to have been extremely successful in achieving liveweight reductions and improving

TABLE 1.1 The effects of quantitative and time limitation methods of nutrient restriction during rearing on some production characteristics of layer-type poultry.

Reference	STOCK DESCRIPTION Type[1]	Mature W (kg)	Peak of egg production (per 100 hen d)	RESTRICTION PARAMETERS Duration (Weeks of age)	Method[2]	Laying Period[3] (Weeks)	PHOTOPERIOD[4] Rearing	Laying	LIVEWEIGHT (%)[5] Rearing	RESPONSE IN TERMS OF EGG PRODUCTION[6] Chrono-logical	Physio-logical	Delay in Sexual Maturity[7] (d)
1. <u>United States</u>												
Schneider *et al.* (1955)	SCWL/ NH	NA	65	6-28	TR	32	N,D8,I20	N,I4,D24,I4	84	+	+	15[A], 27[B]
Milby & Sherwood (1956)												
(a)	SCWL	2.5	75	7-23	QR	45	N,I5,D11	N,D12,I24,D9	87	+	+	12[A], 15[C]
(b)	SCWL	2.5	82	7-21	QR	45	N,I1,D13	N,D11,I24,D10	89	-	-	11[A], 10[C]
(c)	WR	3.1	77	7-22	QR	45	N,I1,D13	N,D11,I24,D10	88	-	-	15[A], 13[C]
Berg & Berse (1961)	SCWL	2.0		8-21	QR/C	44	C13	(D23,I8,D8,C5)*				
(a) Corn			91						99	-	-	0[B]
(b) Barley			90						97	-	-	0[B]
Fuller & Dunahoo (1962)	SCWL	2.0	72	6-24	QR/V	48	NA	C48	74	-	+	32[A]
Deaton & Quisenberry (1963)	NA	1.8	NA	8-21	QR/V	48	N,D8,I13	I7,D24,I17	76	-	+	8[C]
Lillie & Denton (1966)	SCWL	1.8	NA	8-20	QR/C	48	C12	C48	81	+	+	10[A]
Fuller & Chaney (1974)							I				+	21[A]
(a)	SCWL	1.8	NA	6-24	QR/E	72	C	C72	NA	-	-	26
							D				+	20
							I				+	38
(b)	SCWL	1.8	NA	6-28	QR/E	72	C	C72	NA	-	+	50
							D				-	35
Muir & Gerry (1978)	RR	NA	NA	10-22	QR/C	50	C12	C50	94	+	+	NA

(Cont.)

TABLE 1.1 (CONTINUED)

Reference	STOCK DESCRIPTION Type[1]	Mature W (kg)	Peak of egg production (per 100 hen d)	RESTRICTION PARAMETERS Duration (Weeks of age)	Method[2]	Laying Period[3] (Weeks)	PHOTOPERIOD[4] Rearing	Laying	LIVEWEIGHT (%)[5] Rearing	RESPONSE IN TERMS OF EGG PRODUCTION[6] Chrono-logical	Physio-logical	Delay in Sexual Maturity[7] (d)
2. <u>Canada</u>												
MacIntyre & Aitken (1959)												
(a)	SCWL/ Hybrid	2.2	78	8-22	QR/C	46	N,D14	(C18,I16,C14)*	91	-	+	NA
(b)	SCWL	2.1	85	8-22	QR/C	48	N,D14	(C18,I16,C14)*	86	-	+	NA
(c)	SCWL	2.0	83	8-22	QR/C	48	N,D14	(C18,I16,C14)*	73	-	-	NA
Gowe *et al.* (1960)	Mixed	2.0	82	7-21	QR/C	50	N,D14	(C15,I8,D8,C19)*	82	-	+	12
Walter & Aitken (1961)												
(a)	SCWL/ Inbred Cross											
(i)	Cages	2.3	70	9-20	QR/C	48	N,D11	N,D12,I24,D12	84	+	+	10-15[A]
(ii)	Floor	2.0	60	9-20	QR/C	48	N,D11	N,D12,I24,D12	86	+	+	10-15[A]
(b)	SCWL											
(i)	Cages	2.0	80	8-21	QR/C	48	N,D13	N,D12,I24,D12	87	-	+	10-15[A]
(ii)	Floor	1.8	72	8-21	QR/C	48	N,D13	N,D12,I24,D12	89	-	+	10-15[A]
Hollands & Gowe (1961)												
(a)	SCWL	2.0	83	3-21	QR/V	50	N,D18	(C23,I12,D4,C11)*	74	+	+	16[A]
(b)	SCWL	2.0	78	3-21	QR/V	50	N,D18	(C23,I12,D4,C11)*	74	-	-	14[A]
Gardiner & MacIntyre (1962)	SCWL	2.2	82	5-22	QR/C	48	N,I3,D14	(C26,I8,D8,C6)*	78	+	+	19[C]
Strain *et al.* (1965)												
(a)	Mixed	2.1	80	3-21	QR/V	50	N,I5,D12	(C28,I8,D8,C6)*	78	+	+	18[A]
(b)	Mixed	2.1	80	3-21	QR/V	50	N,I5,D12	(C28,I8,D8,C6)*	81	+	+	15[A]
Hollands & Gowe (1965)	SCWL	2.4	80	3-21	QR/V	50	N,I1,D16	(C23,I8,D8,C11)*	76	+	+	13[A]
Pepper *et al.* (1961)	SCWL (Incross bred pullets)	NA	NA	11-23	QR/C	36	N,D1,I11	N,I13,D23	97	-	-	0

(Cont.)

TABLE 1.1 (CONTINUED)

Reference	STOCK DESCRIPTION Type[1]	Mature W (kg)	Peak of egg production (per 100 hen d)	RESTRICTION PARAMETERS Duration (Weeks of age)	Method[2]	Laying Period[3] (Weeks)	PHOTOPERIOD[4] Rearing	Laying	LIVEWEIGHT (%)[5] Rearing	RESPONSE IN TERMS OF EGG PRODUCTION[6] Chrono-logical	Physio-logical	Delay in Sexual Maturity[7] (d)
3. <u>Australia</u>												
Keys (1974)	A x WL	2.4	79	7-22	TR	30	C16	C16	75	+	+	48^{A}, 32^{C}
Moffatt & Unicomb (1974)	WL x A											
(a) Breed 1		2.5							81	-	+	12^{A}
(b) Breed 2		2.4	NA	14-24	TR	52		C16	78	-	+	18^{A}
(c) Breed 3		2.4							77	-	+	21^{A}
McMahon *et al.* (1974)	WL x A	NA	NA	8-20	TR	42	C16	C16	79	+	+	NA
Morris (1974)	WL x A	2.0	NA									
(a)				8-22	Q/C	48	N,I14	N,I12,C36	93	-	-	NA
(b)				8-22	Q/C	48	D14	N,I12,C36	90	-	-	NA
Robinson & Dettmann (1976)	WL x A	2.1	NA	8-20	TR	48	C12	C48	86	-	+	NA
									67	-	+	
Connor *et al.* (1977b)												
Exp. 1	WL x A	2.5	80									
(a) 24 h/72				7-18,21 or 25	TR	43	C15	C15	87	+	+	4^{A}
(b) 40 h/72				7-18,21 or 25	TR	43	C15	C15	64	-	+	16^{A}
(c) 48 h/72				7-18,21 or 25	TR	43	C15	C15	49	-	+	24^{A}
Robinson *et al.* (1978)	WL x A	2.7	NA	8-20	TR	(a) 48	C16	C16	79	-	+	
						(b) 72				+	+	NA

(Cont.)

TABLE 1.1 (CONTINUED)

Notes: 1. Type of stock were coded as the following:
(a) SCWL - Single Comb White Leghorn
(b) WR - White Rock
(c) RR - Harco Red x Rock
(d) A x WL - Australorp x White Leghorn
(e) WL x A - White Leghorn x Autralorp

2. Method of retriction was:
(a) TR - time restriction
(b) QR - quantitative feed restriction
(c) QR/C - as above (b) but at one level
(d) QR/V - as above (b) but variable
(e) QR/E - quantitative energy restriction

3. Duration of the laying periods were on a chronological age basis except for Fuller and Chaney (1974).

4. Photoperiods were estimated from hatch dates of the chickens in the experiments:
(a) N - natural lighting
(b) D - decreasing
(c) I - increasing
(d) C - constant

* indicates minimum photoperiod of 13 h/d

5. Liveweight is the percentage which the restricted birds were of the *ad libitum* fed birds at the cessation of the restriction programmes.

6. Response of the restriction treatments relative to the *ad libitum* treatments.

7. Delay in sexual maturity of the restriction treatements relative to the *ad libitum* treatments:

A. Days to first oviposition
B. Days to 25% egg production
C. Days to 50% egg production

physiological egg production. Unfortunately much of the Australian work has been reported at scientific meetings and was not published in scientific journals, and the work has therefore not been subjected to rigorous scrutiny and often is given with insufficient detail. There also appears to be a large amount of experimental data on restricted feeding of poultry under Australian conditions which has not been reported in the scientific literature (personal observation). Australian work, as distinct from American and Canadian work has used relatively heavy cross-bred hens (White Leghorn X Australorp).

Lighting patterns during rearing in the majority of experiments reported on restricted feeding have been natural with a prevalence conducted using decreasing lighting regimens. Lighting during the laying periods was usually not permitted to decrease more than a preset minimum. This means however that there were periods of increasing or decreasing lighting during the laying periods in many of the experiments reported. The egg production response to a rearing restricted feeding programme was variable when estimated on a chronological age basis, but was apparently consistently increased when calculated on a physiological age basis.

1.4 FACTORS WITH THE POTENTIAL TO AFFECT THE RESPONSE TO A RESTRICTED FEEDING PROGRAMME

1.4.1 Strain effect

There has been a diverse range of strains and breeds of birds used in experiments on restricted feeding, with mature liveweights ranging from 1.8 kg to over 4 kg. Patchell (1977) and Proudfoot and Gowe (1967, 1974) showed that the response to a rearing feed restriction programme could be affected by the strain of bird. This is illustrated in Figure 1.2 for five different strains in terms of relative egg production calculated from Proudfoot and Gowe (1967). Peter *et al.* (1976) compared three strains of birds and found different responses between the strains on the same type of restriction programme. Robinson and Dettman (1976) also found strain differences in response to a common restriction programme and in addition found that strain may affect the responses obtained to dietary manipulation during the egg production period. On the basis of the differences found between two strains of broiler breeder hens, Pym and Dillon (1974) concluded that the optimum degree of liveweight reduction for birds on a restricted feeding programme may depend on the mature liveweight of the particular strain. However, Packham (1978) found no evidence of a strain effect for two Australian cross-breds (WL x A).

The varied selection methods and criteria used for selection in modern poultry breeding arguably make it reasonable to expect some differences in the response of different strains to common husbandry practices. Hearn (1978) has shown that rearing conditions and management practices can substantially affect subsequent egg production and profitability even with common conditions and management during the laying period. Strain effects can be illustrated by comparison of layer-type strains and broiler breeder strains in their response to restricted feeding programmes. The majority of experiments published on restricted feeding which have used layer-type strains of birds have found either decreased egg production or no effect on egg production due to prior restriction programmes when calculated on a chronological age basis, yet have found an increased rate of egg production over the egg production period and therefore an increased egg production calculated on a physiological age basis (see Table 1.1). This latter effect is usually of only small magnitude. For example, Strain *et al.* (1965) found good and consistent responses to restriction during rearing, but obtained no differences between groups in egg production to 500 d of age and only a 2.6% increase from 50% production for 45 seven day periods.

Conversely, many of the experiments carried out on restricted feeding of broiler breeder birds found large responses in terms of egg production even when this was calculated on a chronological age basis (Singsen *et al.* 1965; Fuller *et al.* 1969; Fuller *et al.* 1973; Voitle *et al.* 1974; Pym and Dillon 1974; Watson 1976; Peter *et al.* 1976; Powell and Gehle 1977). Studies in Australia on different levels of quantitative feed restriction (Pym and Dillon 1974; Watson 1976) found an approximate average increase in egg production (hen d basis) of 13% when compared with groups allowed *ad libitum* feed intake during rearing and with egg production calculated on a chronological age basis. The differences would probably have been extremely large if egg production was calculated on a physiological age basis. Peter *et al.* (1976) in a single experiment, found a 23% increase in egg production (chronological) for a broiler breeder strain which had been fed on an alternate day starvation programme during rearing but only a 12% increase in egg production for the same rearing treatment for a layer strain. Powell and Gehle (1977) reported a 28% increase in egg production (chronological) for a quantitatively restricted group of broiler breeders above that of the group allowed feed *ad libitum* during rearing.

Many factors could contribute to these apparent strain differences. The partition of dietary energy between maintenance and production was found to vary between strains of laying hens (Farrell 1975). This could influence the magnitude of any energetic alterations caused by restriction. There are also differences in the potential rate of egg production between strains of poultry, particularly between layer-type and broiler breeder strains. Proudfoot and Gowe (1967) suggested an environmental effect on the maximum genetic egg production potential of a strain, which may affect the response of different strains to a restricted feeding programme. Lee *et al.* (1971a) did not account for differences between layer-type and broiler breeder strains in their calculations.

Summary

The available evidence indicates that different strains of birds may react quite differently to similar feed restriction programmes. The best illustration of this is gained by a comparison of the magnitude of the egg production responses in layer-type and broiler breeder type of birds to restriction programmes. However, there is also clear evidence of differences between genotypes within each of these gross strain classifications (Proudfoot and Gowe 1967, 1974; Pym and Dillon 1974; Peter *et al.* 1976; Patchell 1977). Some factors were identified which could contribute to the observed strain differences (e.g., maximum genetic egg production potential), but these are by no means clearcut.

1.4.2 Liveweight pattern during rearing

The pattern of liveweight change during rearing can be influenced by a restricted feeding programme in three ways:

(a) the time of commencement of feed restriction;
(b) the severity of feed restriction;
(c) the time of cessation of feed restriction.

There can obviously be a large degree of interaction between these factors and other factors. For example, the severity of feed restriction will depend not only on the quantity of feed offered but also on the quality of the feed. Gardiner and MacIntyre (1962) showed the effect that time of commencement of a restricted feeding programme can have on subsequent egg production (see Table 1.2). Gous and Stielau (1976) found a tendency for hens which had been restricted in liveweight gain from three weeks of age rather than from nine weeks of age to have an increased egg production. Although their (Gous and Stielau 1976) results were on a chronological age basis which makes interpretation difficult, there appears to be some evidence of an interaction between the severity of feed restriction and the time of commencement of restriction (ie. severity x time) when peak and terminal rates of egg production are considered. For example, Gous and Stielau (1976) found differences in peak and terminal rates of egg production after restriction was commenced at the same age (three weeks) but severity of restriction varied. However these patterns were not evident for birds which had commenced restriction at six weeks of age.

MacIntyre and Gardiner (1964) examined the effect of time of cessation of a restriction programme and found a marked delay in age at 50% egg production as duration of the restriction period was increased. Estimations made by the present author from the egg production graphs given by MacIntyre and Gardiner (1964) indicate that there was a higher peak egg production for those treatments in which restriction was prolonged to 23 and 25 rather than 21 weeks of age. Also the treatments in which restriction was continued to 23, 25, 27 or 29 weeks of age had a higher rate of egg production than either of the other treatments (an *ad libitum* feed treatment and a treatment in which restriction was terminated at 21 weeks of age). Fuller and Dunahoo (1962) found no increase in physiological egg production for birds restricted in feed intake from 6 to 12 weeks of age but an increase of 3.5% for birds restricted from 6 to 18 weeks of age relative to birds which had been allowed *ad libitum* feed intake during rearing. However liveweights at 24 weeks of age were 1.62 kg and 1.64 kg for the groups which were restricted from 6 to 12 and 6 to 18 weeks of age respectively, a difference of only 1%. Other results of importance from Fuller and Dunahoo (1962) include a 3% increase in egg production for birds restricted to 24 weeks rather than 18 weeks of age, and a slight increase in egg production for birds restricted from 6 to 24 weeks rather than from 12 to 24 weeks of age, although both these groups had the same liveweight (1.21 kg) at 24 weeks of age. Recent results have also shown an effect of liveweight pattern during rearing on subsequent egg production (Wells 1980).

Connor *et al.* (1977b) found significant increases in egg production over 30 weeks of age of egg production measured from sexual maturity when restriction was continued to 21 or 25 weeks of age rather than to 18 weeks of age. Although severity of restriction was examined in the work of Connor *et al.* (1977b), the mode of presentation of results prevents estimation of the interaction between severity of restriction and time of cessation of restriction. However Connor *et al.* (1977b) concluded that

TABLE 1.2 Results derived from Gardiner and MacIntyre (1962) in which feed restriction (70% of group allowed *ad libitum* feed intake) was commenced at either 5, 9, 13 or 17 weeks of age and continued to 22 weeks of age (Experiment 1).

Age of commencement of feed restriction (weeks)	Degree of liveweight reduction (%)[1]	Delay in sexual maturity[2] (d)	Increase in egg production (%)[3]
5	22	19	2.4
9	19	15	4.0
13	14	12	6.7
17	11	13	2.4

Notes: 1. Liveweight reduction at 22 weeks of age as a percentage of the group allowed *ad libitum* feed intake.

2. Relative to *ad libitum* group.

3. Egg production (no./100 hen d) in 336 d for each group as a percentage of the group allowed *ad libitum* feed intake during rearing.

the severity of restriction may not be as important as the age at which restriction is terminated and that "maximum benefits from growing period restriction would probably be achieved if restriction ceased when the restricted flock was laying at a very low level of production".

Summary

There is good evidence to suggest that the time of commencement of restriction programmes, their severity and their duration can influence the responses obtained during egg production. The interaction of these factors could be as important as the individual factors. With standard feed restriction programmes the available information indicates that the time of cessation of restriction is an important consideration for maximisation of the egg production responses obtained (MacIntyre and Gardiner 1964; Connor *et al.* 1977b).

1.4.3 Method of restriction

Restricted feeding is often considered a unified concept which consists of both quantitative and qualitative methods. However the published literature has shown a diverse within method variation which is noteworthy in the assessment of restricted feeding programmes.

1.4.3.1 Quantitative restriction methods

1.4.3.1.1 Proportion allowances. Birds on the restricted feeding programmes are allocated a feed allowance based on the feed intake obtained in a previously designated period by a group allowed feed *ad libitum*. However the manner in which this feed allowance has been offered has varied between experiments. Pym and Dillon (1974) calculated the feed allowance to be given daily to the groups on the restricted feeding programme as one-seventh the intake of the *ad libitum*-fed group during the previous 7 d but fed twice this calculated quantity every 2 d. Gardiner and MacIntyre (1962) and Connor *et al.* (1977a) calculated the feed allocation of the groups on the restricted feeding programme on the same basis, but Gardiner and MacIntyre (1962) offered half the daily allowance twice daily (morning and afternoon), while Connor *et al.* (1977a) fed the restricted groups twice weekly with three times the daily allowance offered on Tuesday and four times the daily allowance on Friday. Restriction programmes used by Pym and Dillon (1974) and Connor *et al.* (1977a) were equivalent to the limited-time restriction methods described in Section 1.4.3.1.2.

Deaton and Quisenberry (1963) offered the birds on the restricted feeding programme 45 g/bird d^{-1} irrespective of their age. Calculations from the data given by Scott *et al.* (1969) on the *ad libitum* feed intake by birds of similar liveweights showed that the restriction method imposed by Deaton and Quisenberry (1963) represented a scaled restriction of zero between 8 to 10 weeks of age, 80% of *ad libitum* from 10 to 12 weeks of age, 75% from 12 to 14 weeks, 71% from 14 to 16 weeks, 69% from 16 to 18 weeks and 66% from 18 to 21 weeks of age. Gous and Stielau (1976) offered quantities of feed which were sufficient for birds to reach a specific liveweight at 20 weeks of age, with feed supplied every 2 d.

1.4.3.1.2 Time methods. These methods allow *ad libitum* feed intake for only a specified number of hours during a prescribed period. Lee *et al.* (1971a) concluded that methods which limit the time of access to feed were not successful in reducing feed intake during the rearing period. This was a valid conclusion at that stage in the development of such programmes. However, in Australia particularly, time restriction methods have undergone considerable refinement since the early 1970s (see Cumming 1972). Time restriction methods as used in Australia have proved to be extremely effective in achieving the aims of feed restriction (see Section 1.3 and

Table 1.1). Long periods of feed availability (McMahon *et al.* 1974; Connor *et al.* 1977b), or short periods (Schneider *et al.* 1955; Schumaier and McGinnis 1969; Moffatt and Unicomb 1974; Abu-Serewa 1978) over periods of 1 to 4 d have been examined. Other forms of time restriction include alternate day feeding, in which feed is removed every other day but birds are either allowed *ad libitum* feed intake (Peter *et al.* 1976) or given specified quantities (Fuller *et al.* 1973), and double frequency feeding, in which birds are allowed *ad libitum* feed intake either for two 1 h periods (Peter *et al.* 1976) or for two 15 min periods (Powell and Gehle 1976) every 24 h. The omission of feed on one day every 5 or 7 d was also successfully used as a method of quantitative feed restriction (Luther *et al.* 1976).

1.4.3.1.3 Pair feeding methods. These involved the allocation of feed to the birds on the restricted feeding programme of an equivalent amount of feed which was consumed in the previous 7 d period by a group allowed *ad libitum* feed intake, but with the diet offered either at reduced energy concentration or at lower protein content or both (Bullock *et al.* 1963; Fuller *et al.* 1969; Fuller *et al.* 1973; Fuller and Chaney 1974; Chaney and Fuller 1975). Such methods can only be used in experimental situations.

1.4.3.2 Qualitative restriction methods

1.4.3.2.1 High fibre diets. Many workers have used diets with high fibre levels as a means of reducing energy and protein intakes of birds (Isaacks *et al.* 1960; Waldroup *et al.* 1966; Lillie and Denton 1966; Kondra *et al.* 1974), but this method has been shown to be difficult and uneconomical in practice (see Lee *et al.* 1971a).

1.4.3.2.2 Diets low in protein or imbalanced in amino acids. Rather surprisingly the majority of experiments on restricted feeding which have used broiler breeder strains of birds have used these methods of restriction (see Table 1.3). The response to these diets in terms of feed intake and therefore pattern of liveweight change varies depending on both the amino acid levels and the severity of certain amino acid imbalances (Tobin *et al.* 1973; Gous 1978). The main advantage of these methods is that such diets can be offered on an *ad libitum* basis, thereby reducing the managerial expertise required for the restriction programme. However the surprising aspect of the large volume of research reported on the use of these methods is the continued

TABLE 1.3 References which have reported the use of diets low in protein or imbalanced in amino acids as restriction methods for broiler breeder strains of birds.

Reference	Method of restriction
Singsen *et al.* (1964)	Low lysine
Singsen *et al.* (1965)	Low lysine
Britzman *et al.* (1965)	Low protein
Waldroup *et al.* (1966)	Low protein
Summers *et al.* (1967)	Low protein
Harms *et al.* (1968)	Low protein
Summers *et al.* (1969)	Low protein
Sherwood *et al.* (1969)	Low lysine
Couch and Trammell (1970)	Low lysine
Abbott and Couch (1971)	Low lysine, low protein
Lee *et al.* (1971b)	Low lysine
Gous (1972)	Low protein
Fuller *et al.* (1973)	Low lysine, low protein
Voitle *et al.* (1974)	Low lysine, low protein
Luther *et al.* (1976)	Low lysine, low protein
Powell and Gehle (1977)	Low tryptophan

persistence of research workers in the examination of such methods despite the excellent responses obtained with quantitative feed restriction methods (Pym and Dillon 1974; Watson 1976; Peter *et al.* 1976). The degree of technical expertise and mechanisation currently available to poultry producers reduce the problems associated with the use of quantitative feed restriction methods.

Summary

A wide range of techniques have been employed in attempts to subject birds to undernutrition during rearing. It is impossible to determine the influence of different restriction techniques on the responses obtained. The main methods reported were quantitative restriction methods in which birds are allocated a feed allowance which is some proportion of *ad libitum* feed intake. Time restriction methods have proved increasingly successful, particularly as developed and applied in Australia.

1.4.4 Lighting patterns during the rearing and egg production periods

Subsequent rate of egg production is increased by a decreasing lighting pattern during the rearing period (Morris and Fox 1960; King 1961; Smith and Noles 1963; Sykes 1968; Bornstein and Lev 1969), and this may be moderated by the lighting pattern used during the laying period (King 1961; Smith and Noles 1963; Harrison *et al.* 1969). The egg production curves given by Sykes (1968) and Bornstein and Lev (1969) are similar to those often found in restricted feeding experiments (eg. Strain *et al.* 1965).

The confounding effects of lighting pattern on the estimation of the response to a restricted feeding programme *per se* have been demonstrated (Berg and Bearse 1961; Berg *et al.* 1963; Lacassagne and Jacquet 1965; Proudfoot and Gowe 1967, 1974). Proudfoot and Gowe (1974) postulated that the beneficial effects reported for restricted feeding experiments (eg. Strain *et al.* 1965; Hollands and Gowe 1965) may have been caused by the lighting pattern during rearing. Proudfoot and Gowe (1974) concluded that a decreasing lighting pattern may be equivalent to a restricted feeding programme during rearing in terms of subsequent egg production. Other workers have reached a similar conclusion (Morris 1974; Robinson 1978).

However, as previously discussed, the production response to a rearing programme in layer strains of birds is usually small, and much of the published work on the effect of lighting pattern has presented egg production only on a chronological basis, which makes the biological interpretation of results difficult. Fuller and coworkers (1969, 1973) examined the effect of lighting pattern during rearing on the response to a restricted feeding programme which used a common broiler breeder poultry strain (White Plymouth Rock). Their results showed that irrespective of feeding regimen a decreasing lighting pattern during rearing caused a greater subsequent egg production than when an increasing lighting pattern was used during rearing. Fuller *et al.* (1969) found that the response, based on physiological egg production, was over twice as large after birds were on a restricted feeding programme with an increasing rather than a decreasing lighting pattern during rearing. However this effect was not evident in later results (Fuller *et al.* 1973). In these experiments (Fuller *et al.* 1969, 1973) the restricted feeding programmes gave an increased egg production which was in addition to that increase caused by a decreasing lighting pattern during rearing. Robinson (1978) found a similar result using a layer-type strain. Fuller and Chaney (1974) carried out similar experiments to those with broiler breeders (Fuller *et al.* 1969; 1973) but used a layer-type strain (White Leghorn), and the results obtained again illustrated the effect of lighting pattern on the response to a restricted feeding programme: in Experiment 1 the increase in egg production (physiological age basis) was 6% for a restricted feeding programme with an increasing lighting pattern but only a 3% increase on a decreasing lighting pattern; in Experiment 2 the changes were 13% and -3% respectively. The reasons for the differences found between the experiments of Fuller and Chaney (1974) could be that different hatches of chicks were used and the experiments were conducted at different times of the year. In this context it is interesting to note the different response between experiments for the birds reared on a constant daylength of 12 h/d. There was a 1% increase in egg production versus a 5% increase for birds reared on the restricted feeding programmes in Experiments 1 and 2 respectively.

Summary

There is an undoubted interaction between the lighting pattern during the rearing period and the responses obtained due to restriction programmes. Many workers found a decreasing lighting pattern during the rearing period caused a subsequent improvement in egg production (Morris and Fox 1960; King 1961; Smith and Noles 1963; Sykes 1968; Bornstein and Lev 1969; Proudfoot and Gowe 1974; Fuller *et al.* 1969, 1973). Whether a feed restriction programme in conjunction with a decreasing lighting pattern during rearing results in an additive effect on egg production remains unclear. However it appears that restricted feeding in time of a rapidly increasing lighting pattern has large benefits (Fuller *et al.* 1969; Fuller and Chaney 1974).

1.4.5 Experimental procedures, presentation and interpretation of results

As mentioned throughout this review, the mode of presentation of results from experiments on restricted feeding programmes, principally the differentiation between chronological and physiological age, is crucial to their biological assessment. Although this is commonly accepted (see Lee *et al.* 1971a) many workers ignored the effect that this can have on the biological interpretation of their results. Canadian workers (eg. MacIntyre and Aitken 1959; Gowe *et al.* 1960; Hollands and Gowe 1965; Strain *et al.* 1965) consistently showed the egg production patterns obtained on their restricted feeding experiments. This is important in the estimation of the effect of a restricted feeding programme on peak of egg production, subsequent rate of egg production and any anomalies of egg production caused by environmental factors (eg. temperature, lighting, disease). For example, Walter and Aitken (1961) obtained variable responses to restricted feeding programmes. However the egg production curves given by Walter and Aitken (1961) show that only in one out of four trials given in the two experiments was the pattern of egg production similar to that expected (*viz.*; peak egg production after sexual maturity followed by a slow decline). The reason for this was apparently that natural lighting patterns were used during the laying period, where the birds were reaching peak of egg production with a declining lighting pattern (see Table 1.1). Egg production curves also allow a better estimation of the biological response to a restricted feeding programme in reports which present only chronological egg production (eg. Hollands and Gowe 1965). The presentation of egg production figures should therefore be encouraged in published reports.

Since a strain effect cannot be discounted in restricted feeding experiments (see Section 1.4.1), the responses obtained in some published experiments may have been modified due to either mixing strains (eg. Gowe *et al.* 1960; Walter and Aitken 1961) or combining strains in the presentation of results (eg. Schneider *et al.* 1955). This effect is illustrated by the results of Walter and Aitken (1961) in which two experiments were carried out, the first of which contained equal numbers of two layer-type strains (White Leghorns and an inbred cross strain), whereas the second experiment contained only the White Leghorn strain. There was a large difference in liveweights between experiments and the response to the restricted feeding programme also differed in terms of egg production between experiments. Schneider *et al.* (1955) carried out separate experiments but combined the results of White Leghorn and New Hampshire strains for calculation.

The results of Schneider *et al.* (1955) are often quoted as illustrating the increased rate of egg production obtained with a rearing restricted feeding programme (eg. see Gowe *et al.* 1960). However the effect observed by the group on the restricted feeding programme (slow grower) may have been due to a suboptimal performance by the groups fed for rapid growth (fast grower). These birds were fed a diet that contained 250 g protein/kg and post-morten results showed that the kidneys of birds that died were congested with urates. Also, the authors (Schneider *et al.* 1955) stated that all adult birds in this group were affected by a condition diagnosed as gout, and that the feet were chronically inflammed. Mortality during the laying period (20 to 60 weeks of age) was 28.9 and 15.7% for the fast and slow grower groups respectively. The validity of inclusion of the above experiment (Schneider *et al.* 1955) in the overall assessment of restricted feeding is doubtful. Pepper *et al.* (1961) also obtained results which contained certain anomalies. There was only a small reduction in liveweight and no delay in age at sexual maturity despite a 25% reduction in feed intake for the restricted fed birds. Lillie and Denton (1966) concluded that there were no significant differences in egg production or efficiency of egg production on the basis of rearing regimen. However, comparison of the quantitative restriction groups indicates that there were differences between these restriction treatments (see Table 1.4).

TABLE 1.4 Results from Lillie and Denton (1966) which show apparent differences between treatments.

Treatment	Number of birds	Egg production (number/100 hen d)+	Feed (kg)/ 12 eggs	Liveweight change ≠ (g)
Ad libitum	668	57.5	2.59	440
Restricted 80%	200	59.1	2.56	572
Restricted 75%	60	64.6	2.36	705
Restricted 70%	60	65.2	2.30	653

\+ Chronological age basis.

≠ From cessation of feed restriction to end of laying period.

Criteria for the removal of birds from an experiment can clearly have an effect on results obtained. Gowe and coworkers (eg. Gowe *et al.* 1960; Strain *et al.* 1965) used rigorous procedures in their experiments to ensure completely random selection. Milby and Sherwood (1956) in one experiment culled 20 to 30% of the "poorest" birds after ten months of egg production. Powell and Gehle (1977) selected birds at 22 weeks of age after various restricted feeding programmes by "discarding obvious culls and excessively heavy birds". When such procedures are used before commencement of egg production the experiment becomes of doubtful value.

Summary

Certain experimental procedures reported in the literature were identified as being inappropriate for proper scientific investigation. Other procedures may have influenced the interpretation of the results obtained. One experiment was shown to be unacceptable in the overall assessment of restriction programmes (Schneider *et al.* 1955). Presentation of egg production figures should be encouraged in reports concerning restricted feeding of poultry.

1.5 PHYSIOLOGICAL, METABOLIC AND ENERGETIC RESPONSES TO RESTRICTED FEEDING PROGRAMMES

1.5.1 Physiological responses

1.5.1.1 Anatomical alterations

A liveweight reduction is often the major effect of a restricted feeding programme (see Lee *et al.* 1971a). Other anatomical alterations reported to be caused by restricted feeding programmes include an increased gizzard weight (g/kgW) (Hollands *et al.* 1965; Lee *et al.* 1971b; Watson 1976; Gous and Stielau 1976), increased pancreas, thyroid gland and liver weights (Hollands *et al.* 1965), and increased intestinal length (Gous and Stielau 1976) or weight (Lee *et al.* 1971b). This latter effect was consistently observed in rats subjected to intermittent starvation periods (eg. Holeckova and Fabry 1959; Lojda and Fabry 1959). The persistence of such alterations after realimentation has not been investigated.

1.5.1.2 Frequency of abnormal eggs

The classification of abnormal eggs and the physiological reasons for their occurrence were reviewed and discussed by van Middelkoop (1978). There are few detailed studies on the influence of a feed restriction programme on the frequency of abnormal eggs (Berg *et al.* 1963; Fuller *et al.* 1969, 1973). Lacassagne and Jacquet (1965) and Lacassagne and Mogin (1965) found that the frequency of abnormal eggs (double-yolks, thin shells, shell-less) was directly related to age at sexual maturity, and the more delayed the age at sexual maturity the greater the shell strength. A lower incidence of cracked shells in hens which were previously on a restricted feeding programme during rearing was found by Gous and Stielau (1976) and MacIntyre and Gardiner (1964), but not by other workers (Robinson *et al.* 1978; Robinson 1978). The lighting pattern during rearing (Fuller *et al.* 1969; Fuller and Chaney 1974; van Middelkoop 1978), due to the effect it has on sexual maturity, and restricted feeding (Fuller *et al.* 1969; Fuller and Chaney 1974), were shown to influence the frequency of abnormal egg production. Egg classification may also be influenced by the rate of egg production (Hollands and Gowe 1961). Fuller and Chaney (1974) found that the main effect of a restricted feeding programme irrespective of the rearing lighting pattern was to decrease the number of small sized eggs produced (see Figure 1.3). Other workers have found similar trends (MacIntyre and Aitken 1959; MacIntyre and Gardiner 1964).

The production of eggs which have inadequate shells and which are subsequently unrecorded have special significance in experiments on restricted feeding. Maximum production of such eggs was shown to occur at peak egg production (Roland 1977). Differences in rate of production of abnormal eggs between treatments may therefore cause substantial errors in comparisons between treatments.

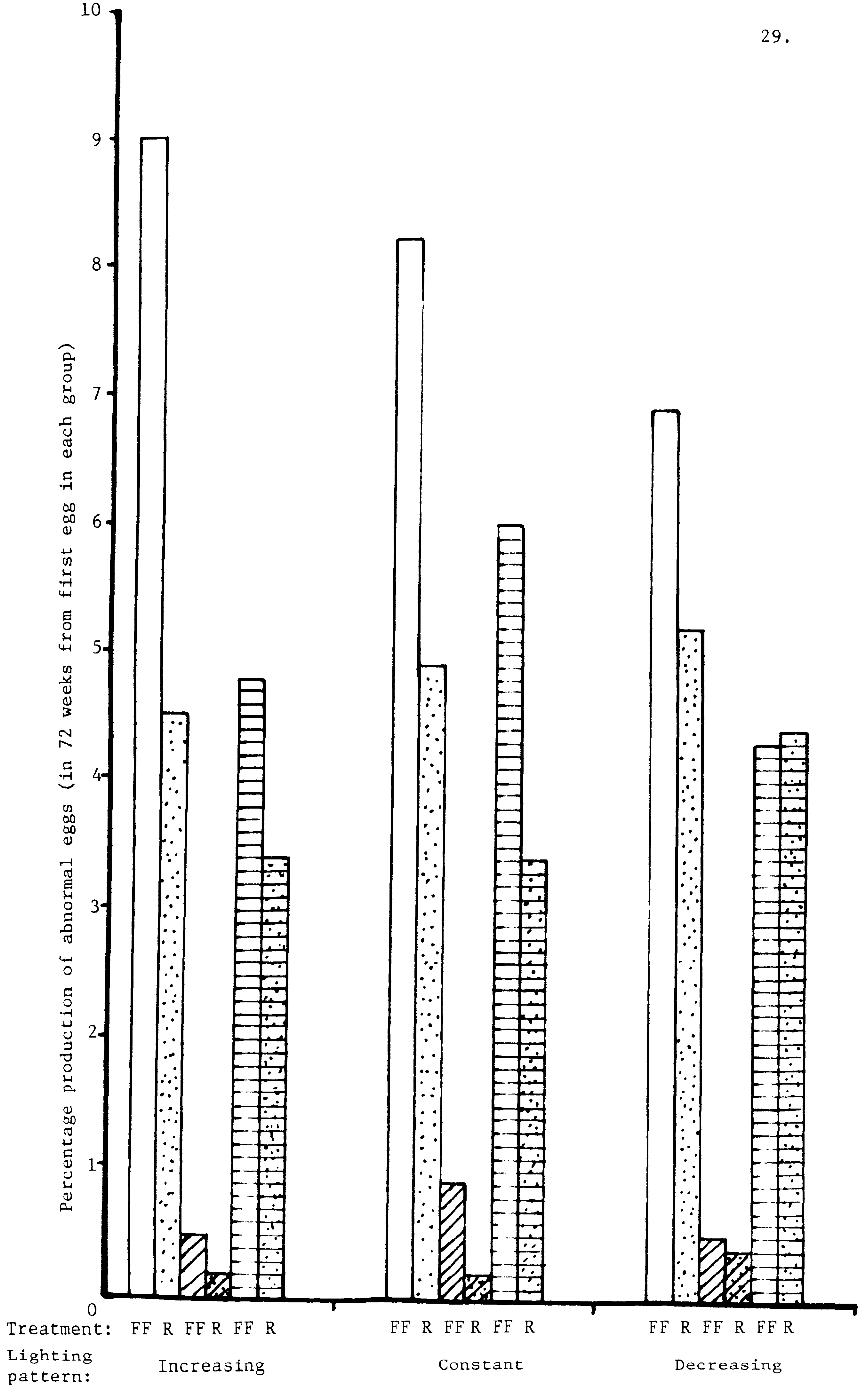
1.5.1.3 Body composition

Alterations in body composition, particularly body fat, are direct and major consequences of feed restriction programmes. The extent and direction of these changes is dependent on variables such as method of restriction (Gous 1976; Powell and Gehle 1976, 1977; Maclachlan *et al.* 1977a), liveweight pattern during rearing (Gous and Stielau 1976), time of measurement (Gous 1972; Fuller and Chaney 1974), nutrient concentration of the diet (Donaldson *et al.* 1956; Gous 1972) and severity of restriction (Lee *et al.* 1971b; Connor *et al.* 1977b). The relationship between liveweight reduction and body fat reduction (both as a proportion of the groups allowed *ad libitum* feed intake) at the termination of feed restrictions, derived from data in the literature, is shown in Figure 1.4. The results from Gous and Stielau (1976) have not been included in Figure 1.4 due to certain facets of their data which will be discussed later. Although it would be inappropriate to derive an equation for the data shown in Figure 1.4, there appears to be a tendency for the proportionate reduction in body fat to approach a plateau in the region 70-80% of *ad libitum* liveweight.

Scott *et al.* (1969) postulated that excess fat may cause suboptimal egg production. Gous (1972) therefore concluded that leaner birds would produce a greater quantity of eggs and although the influences of dietary

FIGURE 1.3: Classification of eggs produced by birds which were allowed either *ad libitum* feed intake (FF) or were restricted in feed intake (R) during rearing as influenced by lighting pattern during rearing (Fuller and Chaney 1974). Egg categories and treatments were:

	Treatment	
Category of egg	*ad libitum*	restricted
Small (<52 g)		
Double yolk		
Soft shelled, broken or abnormal		


Percentage production of abnormal eggs (in 72 weeks from first egg in each group)
0
1
2
3
4
5
6
7
8
9
10
Treatment: FF R FF R FF R FF R FF R FF R FF R FF R FF R
Lighting pattern: Increasing Constant Decreasing

manipulation on body composition of broiler breeders was investigated, Gous (1972) did not provide liveweights or measure subsequent egg production yet concluded that the leanest birds "would be expected to show greatest reproductive fitness in the laying stage". Work directed at determining the real effect of body fat on reproductive performance (Fuller *et al.* 1969, 1973; Chaney and Fuller 1975) has in fact failed to associate reduced rates of lay with increased body fat using current procedures.

The influence of restriction programmes on the major body components are given in Table 1.5. The components were derived, where possible, on a fat-free basis to give a clearer indication of the alterations (Moulton 1923). Apart from the marked reduction in body fat (g/kgW) found by most authors (Fuller *et al.* 1969; Lee *et al.* 1971b; Gous and Stielau 1976; Powell and Gehle 1976; Maclachlan *et al.* 1977a), there appears to be no consistent trends, irrespective of the strain of bird used. Some results, however, indicated that water content of the fat-free mass (WFFM) may be increased due to undernutrition during rearing (Gous and Stielau 1976; Powell and Gehle 1976; Connor *et al.* 1977b). However determination of body composition at a chronological age is not as important as at a physiological age. Body composition at sexual maturity is therefore the more appropriate age to compare differences. There is a disparity between the two reports in which body composition was determined at sexual maturity (ie. first oviposition) (see Table 1.5). Fuller and Chaney (1974) found no differences in either liveweight or body fat (g/kgW) between birds which were allowed *ad libitum* feed intake and those which were restricted in energy intake during rearing. Connor *et al.* (1977b) found major differences between treatments. Clearly though, body composition at sexual maturity will be determined by the amount of compensatory growth which occurs between cessation of restriction, and the consequent allowance of *ad libitum* feed intake, and the age at sexual maturity. This represents a major area where the influence of lighting pattern could be important. The results given by Connor *et al.* (1977b) represent mean values from treatments which also compared the age at cessation of restriction. The observed changes may therefore indicate that some of the birds sampled from the restriction treatments were still on feed restriction.

Low protein and low lysine diets when fed to poultry during the rearing period as a method of restriction can result in a body composition which is different from that which would be assumed from the liveweight reduction obtained (Gous 1976). Powell and Gehle (1976) fed broiler

TABLE 1.5 The influence of feeding regimen during rearing on body composition.

Strain	Age	Treatment[1]	Liveweight (W, kg)	Fat (g/kgW)	Derived components[2] WFFM	PFFM (g/100g)	PFFDM	Reference
Layer type	Sexual maturity	*Ad libitum*	1.6	130	-[+]	-	-	Fuller and Chaney (1974)
		R70	1.5	130	-	-	-	
	20 weeks	*Ad libitum*	1.4	163	72.2	-	-	Gous and Stielau (1976)
		R90	1.3	123	73.2	-	-	
		R80	1.1	131	73.0	-	-	
		R60	0.9	83	73.4	-	-	
	20 weeks	*Ad libitum*	1.5	144	70.2	24.2	81.1	Maclachlan *et al.* (1977a)
		R90	1.4	93	69.9	23.7	78.7	
		R87	1.3	83	69.9	22.6	75.0	
		R82	1.3	82	71.2	22.4	78.0	
	Sexual maturity	*Ad libitum*	1.9	256	71.9	-	-	Connor *et al.* (1977b)
		T24	1.9	249	72.3	-	-	
		T40	1.8	207	72.5	-	-	
		T48	1.7	202	72.6	-	-	
Broiler breeder	Sexual maturity	*Ad libitum*	3.1	222	74.5	20.2	79.3	Fuller *et al.* (1969)
		R70	2.7	179	75.3	19.8	80.3	
	22 weeks	*Ad libitum*	3.1	575	68.6	20.4	64.8	Powell and Gehle (1976)
		R44	1.7	168	73.6	19.7	74.4	
	20 weeks	*Ad libitum*	3.0	250	72.7	23.1	84.3	Lee *et al.* (1971b)
		R90	2.6	178	69.8	22.1	73.3	
		R70	2.1	143	72.5	21.0	76.3	

Notes: 1. Restriction treatments coded to either R (quantitative restriction) or T (time restriction). Number after code letter R refers to the proportion of the *ad libitum* intake which birds were allocated; after T refers to amount of time (h) which feed was denied in every 72 h.

2. Components derived from data in text:

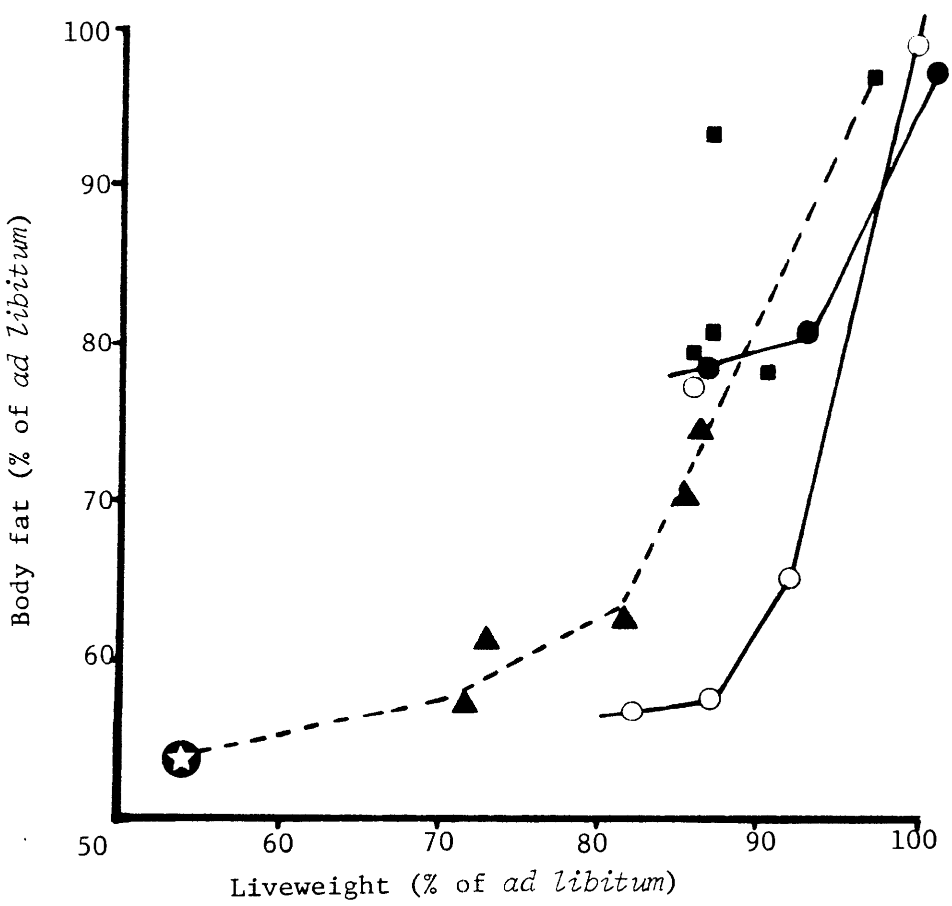
WFFM is Water of the fat-free mass;
PFFM is Protein of the fat-free mass;
PFFDM is Protein of the fat-free dry matter.

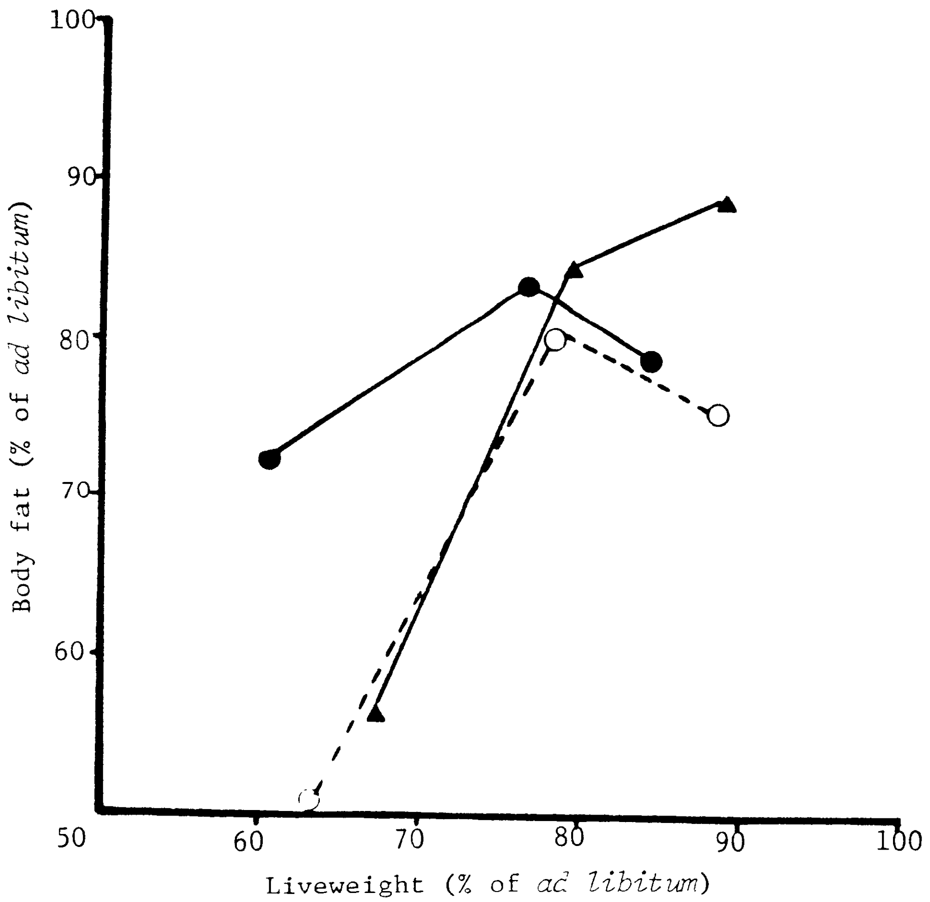
\+ Not able to be derived from information presented.

FIGURE 1.4: The percentage reduction in body fat (g/kgW) and liveweight of birds restricted during rearing relative to birds allowed *ad libitum* feed intake. Results were derived from published reports where birds were slaughtered at approximately 20 weeks of age:

Type of poultry	Reference
Broiler breeders	Powell and Gehle 1976 (✪)
	Fuller *et al.* 1969 (■)
	Lee *et al.* 1971b (▲)
Layers	Connor *et al.* 1977b (●)
	Maclachlan *et al.* 1977a (○)

FIGURE 1.5: Results recalculated from Gous and Stielau (1970) which show the percentage reduction in body fat (g/kgW) and liveweight of birds which commenced quantitative feed restriction at three different ages and with varied levels of restriction relative to birds allowed *ad libitum* feed intake during rearing. Restriction was commenced at either 3 weeks of age (▲), 6 weeks of age (○), or 9 weeks of age (●).


100
90
80
70
60
50
60
70
80
90
100
Body fat (% of *ad libitum*)
Liveweight (% of *ad libitum*)


100
90
80
70
60
50
60
70
80
90
100
Body fat (% of *ad libitum*)
Liveweight (% of *ad libitum*)

breeder pullets diets which were deficient in tryptophan; there were substantial liveweight reductions but significant increases in carcass fat measured at 22 weeks of age relative to a group offered a normal diet *ad libitum*. The pattern of liveweight development may also influence the alterations which occur in body composition due to a restricted feeding programme. Results recalculated from Gous and Stielau (1976) are used to illustrate this effect, and are shown in Figure 1.5. The birds restricted from 3 weeks of age had a body fat content, expressed as a proportion of that for the group allowed *ad libitum* feed intake, which was greater at 20 weeks of age than for those birds restricted from 6 weeks of age at three levels of severity of restriction. For birds restricted from 6 or 9 weeks of age there was not a rectilinear relationship between proportionate liveweight and fat reduction. The divergent reductions in body fat at approximately the same proportionate reduction in liveweights for the three ages of commencement of restriction at the most severe level of restriction provide evidence of the importance of liveweight pattern on the development of final body composition.

1.5.1.4 Response to heat stress

The mortality during the egg production period associated with elevated temperatures was substantially reduced for birds that had previously been on a restricted feeding rather than on an *ad libitum* feeding programme during rearing (*broiler breeders*: Fuller *et al.* 1973; Pym and Dillon 1974; *layers*: Moffatt and Unicomb 1974). Pym and Dillon (1974) postulated that certain behavioural aspects were altered in the restricted-fed birds which allowed them to alleviate the effects of heat stress more efficiently. However, Washburn *et al.* (1980) showed a highly significant correlation between liveweight and time to heat prostration in young chickens. Pym and Dillon (1974) found a positive correlation between extent of mortality at 25 weeks of age and degree of feed restriction during rearing, and liveweights at this age (estimated from the liveweight diagrams given by Pym and Dillon (1974)) were substantially lower for the restricted-fed birds, thus substantiating the findings of Washburn *et al.* (1980). Certainly there is the possibility of large differences in response due to type of stock, because broiler breeder birds allowed *ad libitum* feed intake are usually heavier with a greater fat content than the restricted birds relative to the same treatments with layer-type birds (see Table 1.5). Many other factors (eg. time of last feed, quantity consumed) were shown to influence the response to heat stress (van Kampen 1977), and it would therefore require precisely controlled experiments to determine if any differences *per se* exist between birds reared on restricted feeding programmes and birds allowed *ad libitum* feed intake during rearing.

1.5.2 Metabolic responses

1.5.2.1 Short-term effects of starvation and realimentation

The metabolic responses to varied periods and intensities of starvation and realimentation have been studied extensively in both rats (reviewed by Leveille 1972) and birds (reviewed by Pearce 1974). Hepatic lipogenesis, the major site of *de novo* lipid synthesis in birds (Goodridge 1968 ; O'Hea and Leveille 1969), was markedly increased by certain patterns of feed intake (Leveille 1966; Yeh and Leveille 1970; Leveille and Yeh 1972; Simon and Brisson 1972). Glucose and glycogen metabolism, specific enzyme activities, substrate transport and digestive enzyme secretions were also influenced by periods of starvation and realimentation in young birds (Leveille 1966; Yeh and Leveille 1970; Belo *et al.* 1976; Shen and Mistry 1979; Nir and Nitson 1979). These short-term responses to restricted feeding programmes are dependent on the method of restriction (Simon and Brisson 1972; Simon and Rosselin 1979) and also on the amount and frequency of feeding (Smith *et al.* 1978). Diets deficient in amino acids can give major changes in metabolism of birds (Pastro *et al.* 1969; March and Walker 1970).

1.5.2.2 Long-term effects of restricted feeding programmes

Few studies have examined the metabolic alterations caused by prolonged feed restriction programmes of the type poultry are commonly subjected to in practice. Because of the importance of the liver in carbohydrate metabolism in birds (Pearce 1974), some studies have investigated the weight and function of this organ, but the results obtained have been inconsistent. Lee *et al.* (1971b) and Ballam and March (1979) found that the relative weight (g/kgW) of the liver at 20 weeks of age in birds on feed restriction programmes was almost constant when compared with birds allowed *ad libitum* feed intake during rearing. Connor *et al.* (1977b) found liver moisture to be significantly increased (rectlinearly) with increasing severity of limited time feed restriction. However Balnave *et al.* (1979) found a significant increase in liver weight (g/kgW) at 13 and 20 weeks of age in birds subjected to limited-time feed restriction relative to birds which were allowed *ad libitum* feed intake during rearing. Liver lipid (g/100 g) was increased, and there was a tendency for some hepatic lipogenic enzymes to be increased at 13 weeks of age for the restricted-fed birds (Balnave *et al.* 1979). Variable results found between different studies on the long-term effects of restricted feeding programmes are probably due to differences in physiological age between birds on the restricted feeding programmes and birds allowed *ad libitum* feed intakes. The metabolic response to approaching sexual maturity in the domestic fowl is well documented (eg. Heald and Badman 1963; Husbands and Brown 1965), and failure to take this into account will give erroneous comparative differences between birds which were allowed *ad libitum* feed intake during rearing and those which were on restricted feeding programmes due to the usual delay in sexual maturity caused by feed restriction in poultry.

1.5.3 Energetic responses

1.5.3.1 Starvation heat production

Fuller and Dunahoo (1962) and Balnave *et al.* (1979) have investigated the effect of rearing feed restriction programmes on starvation heat production (SHP) of layer-type strains of poultry during both the rearing and subsequent laying periods. A reduced starvation heat production, relative to birds allowed *ad libitum* feed intake during rearing, was reported at 18 and 52 weeks of age by Fuller and Dunahoo (1962) for birds which were or had been on restricted feeding programmes during rearing. However Balnave *et al.* (1979) found no differences between groups at any age as influenced by feeding treatment during rearing. The differences between the two experiments could be due to technical and procedural problems in the measurement of starvation heat production. Fuller and Dunahoo (1962) measured oxygen consumption and carbon dioxide production only during a 10 to 15 minute period, a procedure with high inherent error (Cairnie and Pullar 1959), especially in poultry, which have pronounced circadian rhythms (Berman and Meltzer 1978). Also, Fuller and Dunahoo (1962) did not state that all measurements were carried out at a similar time of the day. Farrell and coworkers (see Balnave *et al.* 1979) used equipment of proven reliability (see Farrell 1972), and carried out all measurements over the accepted period of 24 h.

However neither study adequately considered the factors which could influence the comparisons between groups of birds, particularly the effects of sexual maturity and activity on starvation heat production. Also, Balnave *et al.* (1979) did not report to a sufficient degree those indices (see Section 1.2 of this review) which are commonly used in the assessment of restricted feeding programmes. It is of paramount importance that adequate details on indices such as feed intake during rearing, temperature, liveweight and egg production be given with such studies so that the results obtained on energy metabolism can be interpreted properly.

1.5.3.2 Efficiency of utilization of feed during the rearing and laying periods

Efficiency of feed utilization during the rearing period can be influenced by factors such as the level of feeding, the composition of the liveweight gain, diet composition, environmental and husbandry conditions, and strain of bird. Data derived from the literature were used to estimate the effect of a feed restriction programme during rearing on an index of feed efficiency, *viz.*, feed conversion ratio (FCR), during the rearing (g feed/gW gain) and laying periods (g feed/g egg output). Comparisons between groups of birds were limited to reports on quantitative restriction methods (see Section 1.4.3.1) which used similar diets for the groups allowed *ad libitum* feed intake and those on a restricted feeding programme. These results, segmented on the basis of the strain of bird used (layer-type or broiler breeder), are given in Table 1.6. Initial liveweights were often not given, and these were estimated for layer-type strains from the data of Scott *et al.* (1969), and for broiler breeder strains were assumed to be 0.64 kg and 0.82 kg at 6 and 8 weeks of age respectively. It was also assumed that initial liveweights did not differ between groups.

Results recalculated to give feed conversion ratio during the rearing period and liveweight at the termination of the restriction programme for the groups on the restricted feeding programmes as a percentage of the values obtained when birds were allowed *ad libitum* feed intake are shown in Figure 1.6 and Figure 1.7 for layer-type and broiler breeder strains respectively. It should be noted that many of these results were by necessity calculated on a chronological age basis. For layer-type strains the relationship between severity of feed restriction and efficiency of feed utilization indicates a minimum reduction in feed conversion ratio in the region of a 75 to 90% reduction in liveweight relative to birds allowed *ad libitum* feed intake. The few results for broiler breeder strains show a similar trend towards an increased feed conversion ratio as severity of restriction is increased.

The effect of time and severity of restriction on the feed conversion ratio during rearing is shown by results derived from Wells (1980). These results are given in Figure 1.8, and indicate that feed restriction can

TABLE 1.6 Feed conversions (g feed) for the rearing (per gW gain) and laying (per g egg output) periods calculated or derived from the literature.

Type of bird	Reference	Feed conversion (g feed:)			
		Rearing period (per gW gain)		Laying period (per g egg output)	
		Ad libitum	Restricted	*Ad libitum*	Restricted
Layer-type	Gous 1978	8.74	11.65	3.24	3.22
	Berg *et al.* 1963	8.23	7.88	3.38	3.41
		7.24	6.80	3.18	3.37
		7.87	7.17	3.31	3.24
		7.99	7.60	3.23	3.30
	MacIntyre & Gardiner 1964	NA		3.01	3.06
		NA		3.01	2.96
	Connor *et al.* 1977b	5.72	5.71	NA	
		5.72	6.59	NA	
		5.79	7.94	NA	
	Hollands & Gowe 1965	5.83	5.54	3.52	3.37
	MacIntyre & Aitken 1959	NA		3.50	3.40
		NA		3.54	3.39
		NA		4.07	3.92
	Gardiner & MacIntyre 1962	NA		3.15	3.08
		NA		3.15	3.03
		NA		3.15	3.03
		NA		3.15	3.10
	Lillie & Denton 1966	8.44	8.26	3.62	3.60
		8.44	9.66	3.62	3.28
		8.44	9.33	3.62	3.21
	Denton & Quisenberry 1963	7.19	7.94	2.66	2.73
		7.19	7.94	2.72	2.71
	Muir & Gerry 1978	NA		2.05	2.02
	Maclachlan *et al.* 1977b	6.30	6.40	2.79	2.79
		6.30	6.90	2.79	2.77
	Bullock *et al.* 1963	7.52	7.45	NA	
		7.18	6.99	NA	
	Sherwood *et al.* 1969	9.20	8.56	3.22	3.12
Broiler breeders	Isaacks *et al.* 1960	7.93	8.36	5.62	5.31
		8.11	8.44	4.68	4.10
	Schumaier & McGinnis 1969	4.84	4.75	NA	
	Lee *et al.* 1971b	6.72	7.09	6.54	5.97
		6.72	7.74	6.54	5.92
	Powell & Gehle 1977	5.33	4.74	5.19	4.48
	Harms *et al.* 1968	4.88	8.18	4.55	4.65
	Watson 1976	4.78	5.18	NA	
		4.78	5.17	NA	
		4.78	5.57	NA	

The relationship between feed conversion ratio and liveweight at cessation of feed restriction both expressed as a percentage of values found for an *ad libitum* control treatment during the same experiment. Results were calculated from published reports, often with certain assumptions (see Section 1.5.3.2).

FIGURE 1.6: Feed conversion ratio (g feed/g liveweight gain) during rearing of layer-type birds. References used were: Gous 1978 (✖); Berg *et al.* 1963 (○); Connor *et al.* 1977b (■); Hollands and Gowe 1965 (□); Strain *et al.* 1965 (△); Fuller and Dunahoo 1962 (▲); Lillie and Denton 1966 (●); Deaton and Quisenberry 1963 (⊗); Maclachlan *et al.* 1977b (⊙); Bullock *et al.* 1963 (⊠); Maclachlan *et al.* 1977a (◣); and Sherwood *et al.* 1969 (◺).

FIGURE 1.7: Feed conversion ratio (g feed/g liveweight gain) during rearing of broiler breeder birds. References used were: Schumaier and McGinnis 1969 (○); Isaacks *et al.* 1960 (✖); Lee *et al.* 1971b (●); Powell and Gehle 1977 (△); Watson 1976 (▲); and Blair *et al.* 1976 (□).

FIGURE 1.9: Feed conversion ratio (g feed/g egg output) during the egg production period of layer-type birds. References used were: Gous 1978 (◺); Berg *et al.* 1963 (○); MacIntyre and Gardiner 1964 (■); Wells 1980 (●); Hollands and Gowe 1965 (□); Strain *et al.* 1965 (▲); MacIntyre and Aitken 1959 (△); Gardiner and MacIntyre 1962 (⊗); Lillie and Denton 1966 (⊙); Deaton and Quisenberry 1963 (⊠); Muir and Genry 1978 (•); Maclachlan *et al.* 1977b (⊞); Gous and Stielau 1976 (▵); and Sherwood *et al.* 1969 (◢).

FIGURE 1.10: Feed conversion ratio (g feed/g egg output) during the egg production period of broiler breeder birds. References used were: Powell and Gehle 1977 (○); Lee *et al.* 1971b (●); Harms *et al.* 1968 (×); and Isaacks *et al.* 1960 (▲).

FIGURE 1.6

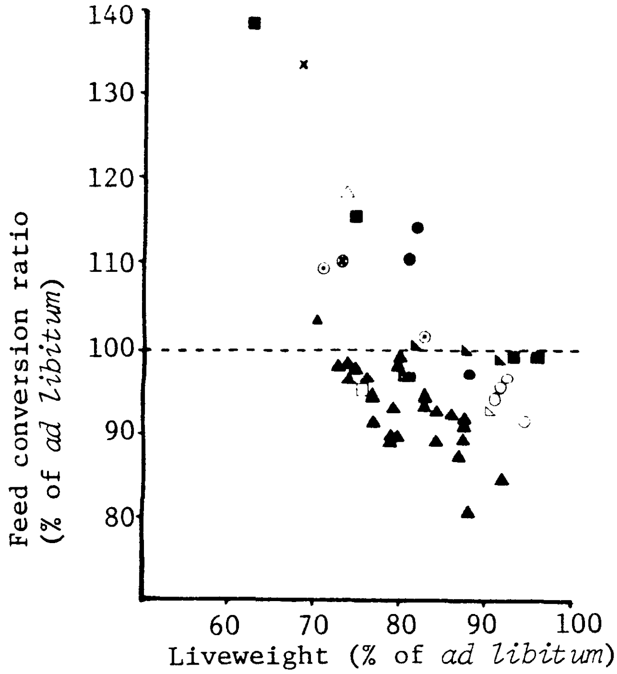


FIGURE 1.7

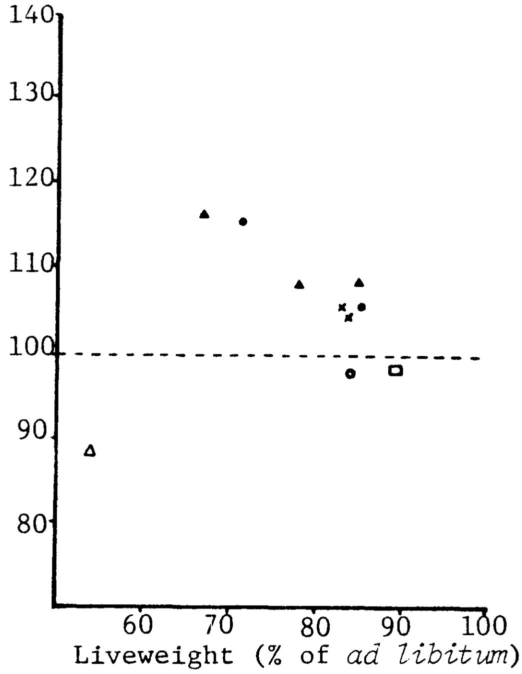


FIGURE 1.9

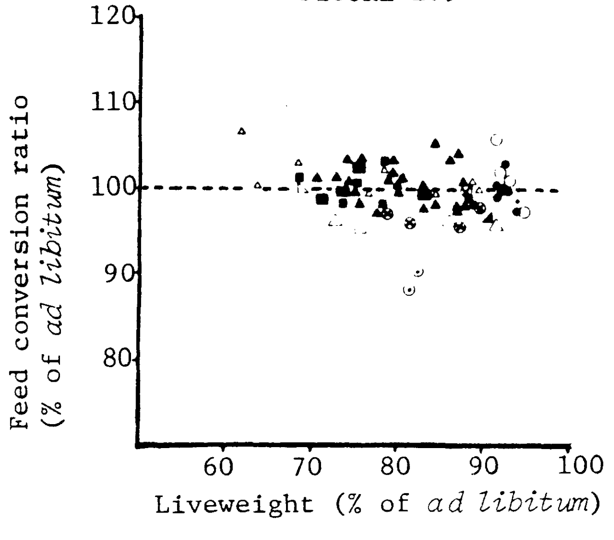


FIGURE 1.10

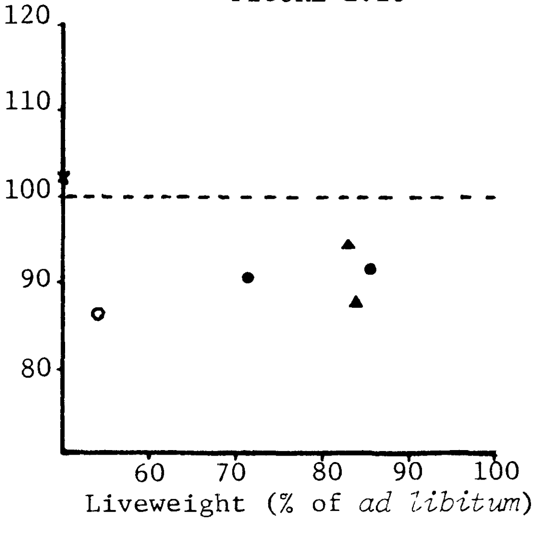
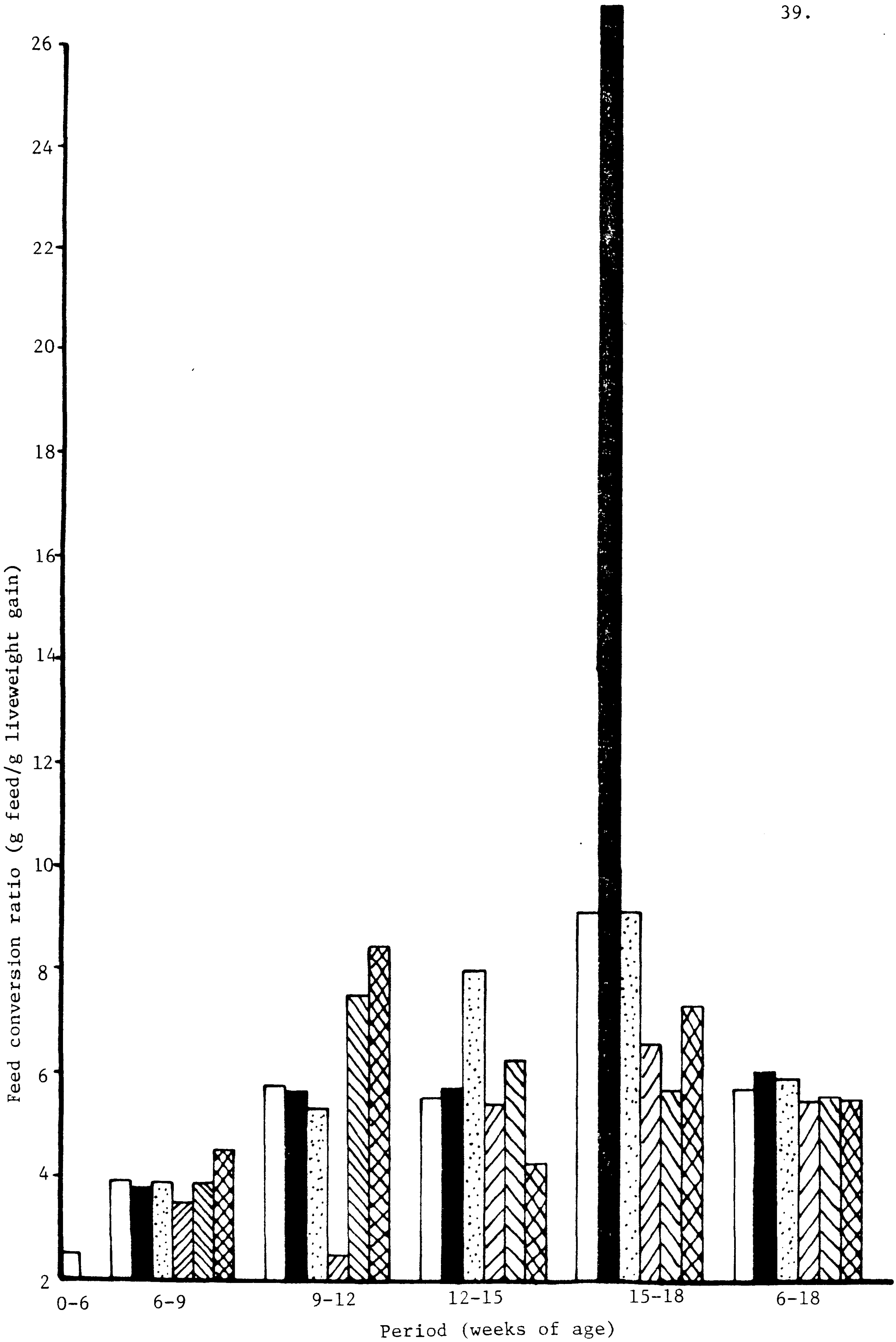


FIGURE 1.8 Data recalculated from Wells (1980) to give feed conversion ratios (g feed/g liveweight gain) for birds on differing feeding treatments during rearing:

Symbol	Treatment	Period and restriction* 6-9	9-12	12-15	15-18
	1	-	-**	-	-
	2	-	-	-	40%
	3	-	-	20%	20%
	4	10%	20%	20%	10%
	5	15%	30%	30%	-
	6	20%	40%	-	-

* Restriction as a percentage reduction in feed intake relative to birds allowed *ad libitum* feed intake.

** No restriction imposed.


26
24
22
20
18
16
14
12
10
8
6
4
2
Feed conversion ratio (g feed/g liveweight gain)
0-6
6-9
9-12
12-15
15-18
6-18
Period (weeks of age)

cause an increase or a decrease in feed conversion dependent on the age of commencement and degree of severity of restriction. Mild restriction at an early age followed by moderate restriction during the middle of the rearing period (9-15 weeks of age) then mild restriction during the final stage of rearing (15-18 weeks of age) gave the lowest feed conversion ratio (treatment 4). Severe restriction during the final stage of rearing (treatment 2) gave a substantial increase in feed conversion ratio, and resulted in the highest overall feed conversion ratio (6-18 weeks of age).

Efficiency of feed utilization for egg production is determined by factors such as feed intake, liveweight, average egg weight and egg production rate (Brody 1945). The possibility that rearing feed restriction programmes may cause an increased feed intake during the laying period was discussed by Pym and Dillon (1974). This implies that there is an alteration in the basic factors which control feed intake due to restricted feeding. However the feed conversion ratio (g feed/g egg output) gives a total assessment of the effect of a restricted feeding programme and incorporates all the factors outlined above.

The relationship between feed conversion ratio (g feed/g egg output) and liveweight at the end of the restriction period, for the restricted-fed birds, both as a percentage of the values for the birds allowed *ad libitum* feed intake during rearing, is given in Figure 1.9 and Figure 1.10 for layer-type and broiler breeder strains respectively. There appears to be no apparent relationship between the percentage reduction in liveweight and percentage change in feed conversion ratio for layer-type strains during the egg production period. Results for broiler breeder strains show a similar lack of this relationship, but feed conversion ratio during the egg production period appears to be lower for those birds which were on the quantitative restricted feeding programmes during rearing.

Summary

Information reviewed on the physiological, metabolic and energetic responses to restricted feeding programmes in poultry highlighted the current lack of data on the continued effects of such programmes after realimentation. Frequency of abnormal egg production was identified as an important factor in comparisons of egg production between treatments. Marked alterations in body composition, particularly body fat, have been reported by most workers when this was determined at the same chronological age near or at cessation of restriction. However the alterations in body composition at the more important physiological ages such as at sexual maturity and after equal duration of egg production have received little attention. The influence of body fat *per se* on egg production, although easy to hypothesize, is difficult to determine and the current evidence indicates no correlation. Adaptability to heat stress reported for birds on restriction programmes (Fuller *et al.* 1973; Pym and Dillon 1974; Moffatt and Unicomb 1974) was explained on the basis of reduced liveweight in conjunction with possible other factors.

Although the short-term effects of starvation and realimentation are well known, few studies have considered the metabolic effects of prolonged feed restriction programmes, particularly during the egg production period after subsequent realimentation. Whether starvation heat production is influenced during or after feed restriction in poultry remains unclear. Feed conversion efficiency during rearing appears to be related to the severity of feed restriction, whereas during egg production, relative to that for birds allowed *ad libitum* feed intake during rearing, it may be increased or decreased by feed restriction programmes during rearing.

1.6 REASONS PROPOSED TO EXPLAIN THE RESPONSES TO RESTRICTED FEEDING PROGRAMMES

1.6.1 Delay in sexual maturity

Bullock *et al.* (1963) proposed that the effect of a restricted feeding programme during the rearing period was to delay sexual maturity and cause a simple shift in the egg production curve. Criticisms of this approach have been put forward by Strain *et al.* (1965) and Pym and Dillon (1974) in that the model fails to account for either the increased peak of egg production or the subsequent slower rate of decline often found in experiments on restricted feeding of poultry (see also Lee *et al.* 1971a). However, Bullock *et al.* (1963) also explained that the proposed egg production model had these deficiencies, a point which was overlooked by many of the authors who have criticised their (Bullock *et al.* 1963) model. Nevertheless the model undoubtedly explains some of the results reported for restricted feeding experiments, and it remains the only serious attempt to explain some of the disparities which were reported in these experiments.

1.6.2 Stress during the rearing period

Gowe and coworkers (Gowe *et al.* 1960; Hollands and Gowe 1961) tentatively hypothesized that the stress of a restricted feeding programme during rearing may cause optimal development of the endocrine glands, which would then allow a greater egg production when restriction was terminated and birds were allowed *ad libitum* feed intake. Sturkie (1976) described the endocrine glands or organs of the bird as the following: (a) the pituitary, (b) the thyroid, (c) the parathyroids, (d) the adrenals, (e) the pancreas, (f) the gonads, (g) the ultimobronchial glands, and (h) the intestine. The anterior lobe of the pituitary gland produces the gonadotropic hormones, follicle stimulating hormone (FSH) and luteinizing hormone (LH), prolactin, somatotropin (STH), adrenocorticotropin (ACTH), thyrotropin (TSH) and others. The influence of these hormones is not restricted to direct reproductive function, but govern many other processes which can indirectly affect reproductive function or efficiency. For example, thyroxine can affect the starvation heat production of young chickens (Keller and Piekarzewska 1976); somatotropin (STH) was shown to stimulate *in vitro* lipolysis of avian adipose tissue and to decrease liver lipogenesis (Harvey *et al.* 1977). Frankham and Doornenbal (1970a and b) found an increased gonadotrophin sensitivity of birds selected for increased egg production, and certain changes in thyroid and adrenal gland weights also in the selected lines of birds. These authors attempted to correlate their findings to the increased egg production of the selected lines. Other workers have also discussed the possibility of direct correlations between certain plasma hormone levels and egg production in poultry (for example, see Michels *et al.* 1980).

Proudman and Opel (1981) found that turkeys (6-11 weeks of age) on quantitative feed restriction programmes (50% of *ad libitum* consumption) had significantly greater plasma somatotropin (STH) levels than birds allowed *ad libitum* feed intake, and that this change occurred within 7 d of the imposition of feed restriction. Levels of somatotrophin remained higher even after the cessation of restriction. An increased response to thyrotropin-releasing hormone (TRH) was also observed in the restriction treatments. However the significance of such observations in terms of dietary energy utilization and production remains to be elucidated. Wilson (1978) found that the concentration of plasma luteinizing hormone (LH) in pullets at commencement of egg production was related to subsequent egg production. Current research appears to be directed at establishing clear relationships between hormone status at certain ages and subsequent egg production in poultry (eg. Sharp *et al.* 1981); future work on these foundations will undoubtedly examine the influence of restricted feeding programmes on such relationships, but at present evidence is not available either to refute or substantiate the tentative reason advanced by Gowe and coworkers (Gowe *et al.* 1960; Hollands and Gowe 1961) to explain the responses obtained by restricted feeding.

1.6.3 Absorption of nutrients

On the basis of alterations in intestinal length and weight shown to be caused by restricted feeding programmes (see Section 1.5.1), Gous (1977) investigated the effect on the rate of uptake of certain amino acids *in vitro*. Results were non-significant and inconsistent and Gous (1977) concluded that amino acid uptake in the intestine was not altered due to a restricted feeding programme during rearing. Michael and Hodges (1973) investigated the effects of a 7 d period of severe feed restriction (25% of *ad libitum*) on cockerels six weeks of age. Birds were slaughtered on the eighth day of feed restriction (15% loss in liveweight) and intestinal enzyme activities measured; activities of alkaline phosphatase, leucine naphthylamidase, acid phosphatase, β-glucuronidase, non-specific esterase and succinic dehydrogenase were increased in the restricted birds relative to those found in normally fed birds. These changes were seen to provide evidence of enhanced nutrient absorption in birds on restricted feeding regimens. There are insufficient studies in this area of restricted feeding, and the effects after prolonged periods of feed restriction and after subsequent realimentation are unknown.

1.6.4 Development of reproductive organs

Jones *et al.* (1967) found that male White Leghorns had a higher sperm concentration peak and slower rate of decline after they received diets which were low in protein during the rearing period. Watson (1975) and Ballam and March (1979) found a greater development of the reproductive organs of hens aged approximately 42 weeks that had been on a restricted feeding programme during rearing.

However Brody *et al.* (1980) in birds and Schenck *et al.* (1980) in rats showed that undernutrition during rearing caused delayed development of the reproduction organs when compared to full-fed control animals at sexual maturity. This may imply that the effects observed by Watson (1975) were due to the elevated rate of egg production rather than the cause of the elevated rate of egg production. Ballam and March (1979) did not present egg production details of their experiment. However both studies (Watson 1975; Ballam and March 1979) used broiler breeder hens, and

Watson (1975) found substantially higher egg production for the groups which had been restricted during rearing. If the increased development of the reproductive organs observed in laying hens after a considerable period of egg production (Watson 1975; Ballam and March 1979) was caused by, but was not the cause of the increased egg production found in the restriction treatments, at least by Watson (1975), then this could partially explain the continued increase in egg production during succeeding years in production as indicated by one report (Walter and Aitken 1961) and found unequivocally in others (Fuller and Dunahoo 1962; Hollands and Gowe 1961, 1965). The results of Fuller and Dunahoo (1962) indicate that egg production in the second and third years of production was closely correlated to that in the first year of production irrespective of rearing treatment. Hollands and Gowe (1965) found a larger difference in egg production between the *ad libitum* and restricted treatments in the second year rather than the first year of production. However this disparity was caused by the 13 d delay in sexual maturity in the restricted birds in the first year of production; after all birds were force-moulted at the end of the first production year, both treatments commenced egg production at a similar time.

1.6.5 Feed intake following restriction

Feed intake was increased immediately after the cessation of a quantitative feed restriction programme (Gardiner and MacIntyre 1962; Keys 1974; Pym and Dillon 1974; Watson 1976; Connor *et al.* 1977b; Proudman and Opel 1981). Logically this should be a major response to previous nutritional deprivation, and the extent of the increase in feed intake would probably depend on the severity of the restriction programme previously imposed. This was verified by Pym and Dillon (1974). Polin and Wolford (1973) postulated that some of the effects (eg. increased egg size) reported for restricted feeding experiments could be due to the increased feed intake following cessation of restriction. However, there is no reason *a priori* to assume that restricted feeding during rearing should cause an alteration in the regulatory mechanisms associated with feed intake. Therefore the increased feed intake found for birds at the cessation of restriction should be in direct relationship to the normal factors which determine feed intake (*viz.*, liveweight, liveweight gain, egg output, etc.). However this area remains an important area for further investigation. Many workers have found a reduced feed intake to a certain age for the restricted treatments during rearing, but have found similar feed intakes up to sexual maturity when compared with birds allowed *ad libitum* feed intake during rearing (see Lee *et al.* 1971a). The pattern of feed intake after cessation of feed restriction in relation to commencement of egg production has not so far been described, although detailed studies were carried out with respect to this for birds allowed *ad libitum* feed intake during rearing (Foster 1968a; Hurwitz *et al.* 1971).

1.6.6 Alterations in energy utilization

Fuller and Dunahoo (1962) and Balnave *et al.* (1979) ostensibly attempted to explain the effects of a restricted feeding programme in terms of altered energetics. These studies, and their limitations, were described previously (Section 1.5.3.1). Fuller *et al.* (1969, 1973) and Chaney and Fuller (1975) investigated the effect of fat deposition, and therefore the partition of feed energy between different areas of production (ie. body fat versus egg synthesis), on egg production, but could not detect any effect *per se* of body composition. Walker and Garrett (1970) found marked alterations in the energetics of rats during periods of undernutrition and also after subsequent realimentation. Other workers found similar results (eg. Lee and Lucia 1961; Miller and Wise 1975).

Although the effect of feed restriction on the energy metabolism of laying hens has been studied (MacLeod and Shannon 1978; MacLeod *et al.* 1979), there has been no study on the effect of a rearing feed restriction programme on energy partition during both the growing and subsequent laying periods. The results derived from the literature, shown in Figures 1.6, 1.7, 1.9 and 1.10, indicate that feed utilization during rearing can be influenced by the severity of restriction, which implies a shift in energetics, and that feed utilization during the laying period may be increased or decreased by rearing feed restriction. There is the possibility that differences in response may depend on the strain of bird (Section 1.4.1); the method of restriction has also been shown to affect feed utilization during the rearing period (Simon and Brisson 1972); differences in activity (Wenk and van Es 1980), both between groups within an experiment, and in birds between experiments, cannot be discounted as possible causes of response differences. Hollands *et al.* (1965) noted that the birds on the restricted feeding programme in their experiment showed greater activity during rearing than birds allowed *ad libitum* feed intake. Wenk and van Es (1980) found that the energy required for physical activity was approximately 15 to 20% of the maintenance energy requirement (ME_m) for birds allowed *ad libitum* feed intake; this value was increased to 30% of the maintenance energy requirement by severe feed restriction. The energy required for physical activity in laying hens depends on the amount of time spent standing and sitting and on the amount of resting activity and oviposition (van Kampen 1976a and c). These activities could be influenced by a restricted feeding programme during rearing, and may account for the variable changes observed in feed conversion ratios during the egg production period for birds previously restricted-fed (see Figure 1.9). Studies so far conducted on the energy metabolism of birds to determine the effects of a restricted feeding programme have failed to consider the contribution that differences in activity between groups of birds may have on comparisons (eg. Fuller and Dunahoo 1962; Balnave *et al.* 1979).

1.7 DETERMINATION OF ENERGY METABOLISM

1.7.1 Preliminary

The complexities involved in the energy metabolism of animals are enormous. Often, simply to determine energy metabolism involves a myriad of theoretical assumptions and calculations which have considerable inherent uncertainties (Farrell 1974a). Energy metabolism studies involve the theoretical partition of dietary energy between the processes of maintenance and production; this represents an obvious but necessary oversimplification of biological chemistry (Blaxter 1962). The primary initiation point for any energy metabolism study is from the utilization of energy which is available to the animal. For most animals the majority of the energy available for productive processes is derived from dietary sources; however for cattle in milk production and poultry in egg production the utilization of energy for these specific production processes cannot be determined accurately (Blaxter 1962; Grimbergen 1970; De Groote 1974) because of milk or egg synthesis from carcass tissue reserves (fat and/or protein). The following parts of this review outline the basic terminology associated with energy metabolism studies, presents a detailed diagram for energy partition in animals, and considers the alterations in energy metabolism found for various animal species as caused by undernutrition.

1.7.2 Terminology used in energy metabolism studies

There is a range of terminology associated with energy metabolism studies and which was considered for adoption in the studies to be reported in this thesis. The basic scheme used at the National Institute of Animal Science, Copenhagen (G. Thorbek, pers. comm.) was implemented for literature considerations and for reporting the results obtained. There was some modification with regard to the partition of dietary energy between the production processes in egg producing poultry. The scheme is given in Table 1.7.

1.7.3 Partition of dietary energy

Dietary energy which is available to an animal is termed the metabolisable energy (ME). A simplified scheme for the partition of metabolisable energy in egg producing poultry is given in Table 1.8. The heat increment (HI) is the quantity of metabolisable energy which is not retained and is lost as heat energy (HE). The remaining portion of the metabolisable energy is used directly by an animal for maintenance and production; this is termed the net or productive energy (NE). The efficiency of utilization of metabolisable energy for maintenance (km) is defined as follows:

$$km = \frac{\text{Starvation heat production (SHP)}}{\text{Metabolisable energy for maintenance } (ME_m)}$$

The starvation heat production, determined under appropriate conditions (Blaxter 1962), closely approximates the basal metabolic rate (BMR) and is an estimation of the net energy required for maintenance (ME_m).

The efficiency of utilization of metabolisable energy for production is defined as:

$$kp = \frac{\text{Retained energy (RE) (ME - HE)}}{\text{Metabolisable energy (ME) - Metabolisable energy required for maintenance } (ME_m)}$$

The metabolisable energy required for production (ME_p) is used for fat production (ME_{pf}) and protein production (ME_{pp}), with an overall efficiency (kp) as defined above, and with nutrient specific efficiencies of (kpf) and (kpp) for fat and protein deposition respectively:

$$kpf = \frac{RFATE}{ME - ME_m}$$

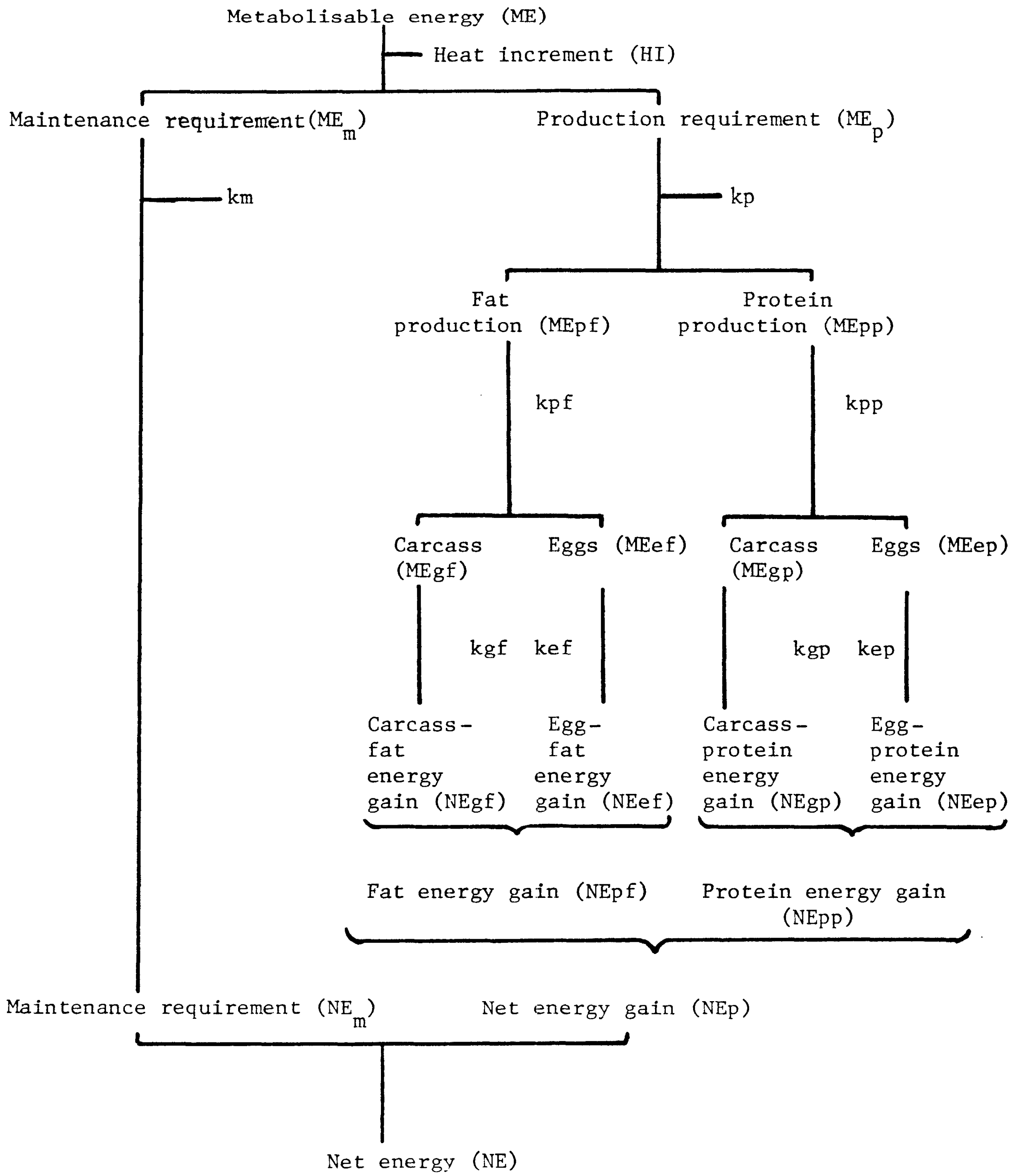
$$kpp = \frac{RPE}{ME - ME_m}$$

In young growing chickens or adult birds in the non-reproductive state the partition of dietary metabolisable energy up to this stage can be

Table 1.7 Terminology of energy metabolism for poultry.

Term	Parameter
IE(GE)	Intake of gross energy
FE	Faeces energy
UE	Urine energy
HE	Heat energy
ME	Metabolisable energy = IE - E(F + U)
NE	Net energy = ME - Heat increment
RE	Retained energy = ME - HE
RPE	Energy retained as protein
RFATE	Energy retained as fat
ME_m	Metabolisable energy (ME) required for maintenance
ME_p	ME required for production = $ME_{pf} + ME_{pp}$
ME_g	ME required for growth = $ME_{gf} + ME_{gp}$
ME_e	ME required for egg production = $ME_{ef} + ME_{ep}$
ME_{pf}	ME required for fat deposition
ME_{pp}	ME required for protein deposition
ME_{gf}	ME required for carcass fat deposition
ME_{gp}	ME required for carcass protein deposition
ME_{ef}	ME required for egg fat deposition
ME_{ep}	ME required for egg protein deposition
kp	Efficiency of utilization of ME for production = kg + ke
kg	Efficiency of utilization of ME for growth = kgf + kgp
ke	Efficiency of utilization of ME for egg production = kef + kep
kgf	Efficiency of utilization of ME for carcass fat deposition
kgp	Efficiency of utilization of ME for carcass protein deposition
kef	Efficiency of utilization of ME for egg fat production
kep	Efficiency of utilization of ME for egg protein production

Table 1.8 The partition of dietary metabolisable energy in poultry.



completed in the usual manner without major problems (De Groote 1974). Blaxter (1962) defined the three main groups of energy demanding processes as:

(1) Maintenance expenditures derived from energy released in the oxidation of food or from oxidation of body reserves.
(2) Synthetic processes exclusive of fat deposition, which can occur at the expense of body reserves.
(3) Fat deposition, which can only occur when excess energy is supplied, and is determined primarily by (2) above.

However, egg producing poultry have the metabolic capacity for continued substrate synthesis for egg production despite inadequate dietary metabolisable energy intake (see Snetsinger and Zimmerman 1974). Over 10% of the weight of an average egg is fat; the contribution of fat to the total energy content of an egg is therefore approximately 62.6%, on the assumption that the energy content of an egg is 6.7 kJ/g (eg. Hoffman and Schiemann 1973). It is clear then that the latter energy demanding category (3) as defined by Blaxter (1962) is inappropriate for poultry in egg production. Consequently, the determination of the true efficiency of utilization of dietary metabolisable energy for production (kp) in egg producing poultry is difficult, since body tissue reserves can be utilized for egg production. This could result in apparent efficiency being higher than the true efficiency. Although this problem was initially discussed by Grimbergen (1970), few studies have attempted further investigation.

When the quantity of retained energy is zero (ie. ME - HE = 0) then all of the metabolisable energy consumed is recovered as heat energy. Above this level of metabolisable energy intake, heat energy is increased depending on the efficiency of utilization of metabolisable energy for production (kp); this can be summarised as the following:

$$HE = (1 - kp)\ (ME - ME_m) + ME_m$$

This relationship facilitates the estimation of the efficiency of utilization of metabolisable energy for production and the maintenance metabolisable energy requirement by regression techniques. Values of these parameters (kp and ME_m) which have been determined by this method for poultry in egg production were described in detail by Grimbergen (1974) and De Groote (1974). The assumptions and inherent problems of this approach were summarised by Henckel (1976).

1.7.4 Approaches to determine energy metabolism

There are two methods which can be used to determine the energy metabolism of animals. These are (a) Calorimetry, and (b) Regression techniques. Calorimetry is a general term which covers both the direct and indirect determination of heat production. Measurement of gaseous exchange is the main calorimetric technique employed. These methods have been discussed in detail by Blaxter (1962) and Farrell (1974a). Other indirect methods used to determine the quantity of retained energy specifically in poultry were also described by Farrell (1974a). In summary, there are two main indirect methods for the estimation of retained energy:

(1) Measurement of heat production indirectly. This involves the initial measurement of gaseous exchange, i.e., carbon dioxide (CO_2) produced and oxygen (O_2) consumed. Blaxter (1962) has outlined the theoretical considerations on which the calculation of heat production from gaseous exchange is based. The formulae of Brouwer (1965) are commonly used for this purpose.

(2) Measurement of fat (RFATE) and protein (RPE) deposition. Methods used for this purpose measure the retained energy rather than estimating the retained energy from an initial estimation of heat energy. Carbon (C) and nitrogen (N) balance can be used to calculate retained energy by an equation given by Brouwer (1965). Farrell (1974a) discussed the assumptions involved. Components of liveweight gain can also be estimated by carcass composition analysis. This is the comparative slaughter technique (see Farrell (1974a) for errors involved).

The second method which can be used to determine the partition of dietary energy in animals is by regression techniques. Such techniques also involve several assumptions. The variables which must be measured are metabolisable energy intake, liveweight, liveweight change and, in the case of egg producing birds, egg output. Brody (1945) described the use of this technique to partition dietary energy in egg producing poultry and lactating dairy cows. Byerly (1979) discussed many of the factors relating to the use of such techniques, and many workers investigated specific nutritional and environmental effects on both growing and egg producing poultry by this approach (Hurwitz *et al.* 1978; Reid *et al.* 1978; Vohra *et al.* 1979; Valencia *et al.* 1980a,b; Byerly *et al.* 1980; Hurwitz *et al.* 1980). The main advantage of regression over calorimetric techniques is that expensive equipment and technical expertise is not required and a greater number of birds can be used. Their disadvantage is lack of precision.

1.8 CONCLUSIONS

This review has attempted to provide some basis for the biological responses obtained by subjecting growing poultry to undernutrition during rearing. The necessary criteria used to define such responses were outlined, and it was evident that a major reorientation of research aims may be required to gain an understanding of the true effects of restricted feeding during rearing on poultry performance. The inherent commercial ramifications of poultry research have not been conducive to such an understanding in this area. The criteria described were assessed on their ability, as commonly used, to determine the response to a restricted feeding programme. It is advocated that these criteria are essential to the correct interpretation of restricted feeding experiments and must be applied, not singularly, but jointly, in any one experimental situation. The overt emphasis on the response to a restricted feeding programme on subsequent egg production has resulted in an historically imbalanced appraisal of many restricted feeding experiments. Currently there are no adequate explanations for the biological responses sometimes obtained in restricted feeding experiments.

Major emphasis was given to the factors which can probably exert an influence on the response to a restricted feeding programme, for it is predominantly these factors which are the reasons for the variable results obtained in both experimental and practical situations. The main factors with the potential to affect the response to a restricted feeding programme were given (Section 1.4) as the strain of bird used, the liveweight pattern during rearing, the method of restriction used and the lighting pattern prevalent during the rearing and egg production periods. Certain experimental procedures and report pecularities were identified also as factors which could affect the apparent response to a restricted feeding programme. Many of the published reports on restricted feeding were summarised in tabular form (Table 1.1) to give an overview of the biological responses obtained. The major emphasis of these considerations, and of the review as a whole, was on quantitative methods of feed restriction. This was done, not out of deference to qualitative restriction methods, but simply for brevity and is justified on the basis that quantitative restriction methods have resulted in the necessary improvement in performance to a sufficient degree to allow the study of the reasons for the observed effects. However it was noted that the majority of the publications which reported the influence of restricted feeding on broiler breeder strains of birds used qualitative restriction methods. These reports often indicated that quantitative restriction techniques were superior to qualitative techniques (amino acid imbalanced diets, low protein diets) in terms of reducing feed intake during rearing and in the subsequent egg production obtained (e.g. Sherwood 1969; Fuller *et al.* 1973; Luther *et al.* 1976; Powell and Gehle 1977; Harms *et al.* (1968) found equivalent egg production over a chronological period of 224 d for broiler breeders which were reared on a skip-a-day limited feeding schedule or which were fed *ad libitum* on either a 10% protein or a 16% protein diet. However the skip-a-day limited feeding schedule resulted in a 51% reduction in liveweight at 30% egg production and a 28 d delay in peak of egg production. If results were calculated on the basis of physiological age then the skip-a-day treatment would probably have been considerably better in terms of egg production than the other two treatments. This illustrates a major theme of this review: that physiological parameters must be stressed in experiments on restricted feeding.

Quantitative feed restriction programmes (Section 1.4.3) gave a consistent improvement in physiological egg production (see Table 1.1). Many of the experiments reviewed were carried out with a naturally decreasing lighting pattern for most of the rearing period. The effect which this had on the results obtained remains open to debate (eg. Fuller *et al.* 1973). However, two points are clear: (a) the lighting pattern during rearing can influence the egg production subsequently obtained, and (b) there is an interaction between the lighting pattern used during rearing and restricted feeding. It is pertinent to observe in this context that the senior author of perhaps the classic restricted feeding publication (Gowe *et al.* 1960) should in co-authorship conclude later that a decreasing lighting pattern may be equivalent to a restricted feeding programme during rearing in terms of subsequent egg production (Proudfoot and Gowe 1974). Fuller *et al.* (1973) obtained some evidence with broiler breeder birds that a restricted feeding programme had a synergistic effect on egg production when a decreasing lighting pattern was used during rearing.

The strain of bird was shown to affect the response to a restricted feeding programme during rearing (Pym and Dillon 1974; Proudfoot and

Gowe 1967, 1974; Patchell 1977). The importance of this factor, particularly with the emerging new strains of egg-producing birds, is such that it has the potential to decide the future of restricted feeding in its entirety for use with layer-type birds. This review highlighted the differences in response between layer-type strains and broiler breeder strains of birds with similar restriction programmes.

The main physiological, metabolic and energetic responses to restricted feeding programmes were outlined and discussed in Section 1.5. The influence of abnormal egg production, particularly eggs without adequate shell formation, was considered an important aspect for further study to determine the true difference between treatment groups. Although some studies investigated possible alterations of such important parameters as liver lipogenesis and starvation heat production in birds on restricted feeding programmes, they were often deficient in experimental procedure. This has negated much of their contribution to the elucidation of the biological response to restriction (e.g. Balnave *et al.* 1979). The efficiency of utilization of feed during rearing was found to be variable but there was a clear indication that efficiency declined due to increased severity of restriction. Also, there appeared to be an optimal degree of restriction which caused an improvement in feed efficiency in comparison to birds allowed *ad libitum* feed intake (Section 1.5.3.2). Further emphasis should be given to feed efficiency during rearing in an attempt to reduce feed costs. There was not a clear indication that feed efficiency was improved during the egg production period by prior restriction (Section 1.5.3.2).

The reasons proposed to explain the responses to restricted feeding programmes were given in Section 1.6. Overseas publications (e.g. Proudman and Opel 1981) indicate that major emphasis is at present being placed on the identification of hormonal influences on subsequent egg producation (Section 1.6.2). However more basic considerations were identified (Section 1.6.5) to provide clarification of the effects of restriction programmes. Alterations in energy metabolism (Section 1.6.6) were discussed in a range of animal species due to undernutrition, and it is concluded that this area of investigation offers one of the most suitable ways to determine the biological response to a restriction programme. The background, terminology and problems of this approach were considered in detail (Section 1.7).