University of Alberta

Bio-economic Linkages between Broilers and Breeders: Optimizing the Chicken Production System

by

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"A fact is a simple statement that everyone believes. It is innocent, unless found guilty. A hypothesis is a novel suggestion that no one wants to believe. It is guilty, until found effective" Edward Teller

Abstract

This thesis studied the relationships between energetic efficiency, feed allocation, and technical and economic efficiency of broiler breeders, and their implications for broiler meat production. This objective was approached in three stages: 1) impact of broiler breeder feed allocation on chick production; 2) energetic efficiency in broiler breeders and its implications for reproduction and broiler production; and 3) technical and economic efficiency of broiler breeders. Two broiler breeder experiments were performed with different feed allocation strategies using Ross-708 birds. Individual hen data were collected during a production cycle. Three broiler experiments were carried out using a pedigree hatching system. Chick quality, broiler performance, and meat quality data were collected. Energetic efficiency was estimated based on a model of energy-mass balance. Effects of maternal energetic efficiency on broiler growth and yield, meat quality, feed conversion, energetic efficiency, and myofibre numbers were assessed. A new application of the data envelope analysis methodology was used to evaluate economic efficiency of individual hens.

Altering the BW profile of underweight pullets to reach a target BW increased considerably their egg production, although more small eggs were produced. Current models of energy balance were improved by utilization of mixed models to estimate individual maintenance requirements, which were function of absolute or relative energy intakes. Energetic efficiency was separated in two components: 1) energetic efficiency of maintenance, which was called residual maintenance ME requirement (RME_m), and 2) residual energetic efficiency, which was equivalent to residual feed intake (RFI). The RME_m was consistently related with egg production, chick production, and feed conversion rates of broiler breeders. High RME_m in broiler breeder hens was related with increased broiler muscularity and appeared to be advantageous for broiler growth when other efficiency traits (low RFI) were present. Even though minimizing maintenance requirements may increase broiler breeder productivity, it may not be compatible with maximizing broiler growth and meat yield. However, maximizing broiler and breeder energetic efficiency may be achieved

simultaneously. Utilization of data envelope analysis allowed separating technical-biological and allocative factors affecting economic efficiency. Therefore, this methodology may be used to develop specific strategies to improve economic efficiency in the supply chain.

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Dedication

Cata, I could not have done it without you, your loving smile always kept me going. A Luis Eduardo y Gloria Rosa, siempre los llevo en mi corazón, gracias por hacerme lo que soy. A Edgar y Nama, esta victoria también va por ustedes.

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List of Nomenclature and Abbreviations

ε……………………………….Residual error
ADG……………………………Average daily gain
ADG_P…………………………Positive average daily gain
ADG_N…………………………Negative average daily gain
BIC……………………………Bayesian information criterion
BW……………………………Body weight
BW^b…………………………Metabolic body weight
CP……………………………Crude protein
CRS……………………………Constant returns to scale
CV……………………………Coefficient of variation
DEA……………………………Data envelope analysis
e……………………………… Elasticity
E(a+u)…………………………Expected individual maintenance requirement
EM……………………………Egg mass production
EnE……………………………Energetic efficiency
EE……………………………Economic efficiency
F1……………………………Largest yellow follicle
FCR……………………………Feed conversion ratio
LYF……………………………Large yellow follicles
LWF……………………………Large white follicles
ME……………………………Metabolizable energy
MEI……………………………Metabolizable energy intake
ME_m…………………………Metabolizable energy requirement for maintenance
MSE……………………………Mean squared error
NE……………………………Net energy
O………………………………Origin
$\overline{OA}$ ……………………………Radial segment to point A
RFI……………………………Residual feed intake
RFI_{mat}……………………………Maternal residual feed intake
RME_m…………………………Residual maintenance ME requirement
RME_{mmat}………………………Maternal residual maintenance ME requirement

SRFI..............................Standardized residual feed intake

$SRME_m$..............................Standardized residual maintenance ME requirement

SYF..............................Small yellow follicles

T..............................Environmental temperature

TFN..............................Total fibre number

VRS..............................Variable returns to scale

Chapter 1. Introduction

1.1. Development of Modern Poultry Production

The world's poultry industry has experienced an accelerated growth from the middle of the 20^{th} century. Between 1961 and 2000, poultry meat production increased about five-fold in developed countries and about sixteen-fold in developing countries (FAO, 2001). From the early 1970s, the real price of poultry meat has fallen dramatically (Thurman, 1987), while the world's per capita consumption has risen to about 9.4 kg in 2007 (USDA, 2008). Chicken meat has become more affordable because of improved genetics and nutrition (Havenstein et al., 2003a), breakthroughs in disease control, improvements in equipment and infrastructure, vertical integration and economies of scale (Goodwin, 2005). Moreover, a greater variety in product presentation, increased product versatility and convenience, improved packing, and a large penetration in restaurants have contributed to increased consumption (Goodwin, 2005), especially in developed countries. Around the world, poultry has come from being a substitute of other meats to a position of independence (Thurman, 1987).

The poultry industry is one of the most vertically integrated of the agriculture and food businesses and is rapidly progressing towards being one of the most concentrated in the world (Goodwin, 2005). The structure of the breeding industry has changed dramatically in the past decades. A series of mergers and acquisitions have significantly reduced the number of breeding companies supplying chicken genetics for the world broiler production. Genetic companies offer a portfolio of strains developed to meet market demands of different areas of the world. In general, centralized pedigree lines produce great-grandparent and grandparent stocks that are transported to multiplication companies where parent stocks are produced and sold to farmers or integrated processors. It is estimated that close to 100,000 broiler chicks may be produced from a single pedigree bird (Pollock, 1999). Both changes in breeding programs and improvements in broiler breeder and broiler management at the commercial level have a great economic impact for the world's chicken meat production business.

1.2. The Modern Broiler

The emphasis of broiler selection programs has changed over the years from a focus on rapid growth, to one of improved conversion and yield of edible parts (Siegel and Wolford, 2003). However, growth rate has exhibited the greatest response to phenotypic selection because of its moderate heritability and high additive genetic variation (Siegel and Wolford, 2003). Since the economic benefits of selection for growth exceed the benefits of selection for other traits, primary breeding companies are expected to continue selecting for growth rate in the future (Pollock 1999). The genetic improvement of broiler growth rate has been enormous. It is estimated that growth rate to 56 d increased 58 g/yr from 1957 to 1976, 76 g/yr from 1976 to 1991, and 84 g/yr from 1991 to 2001 (Sherwood, 1977; Havenstein et al., 1994; Havenstein et al., 2003a). Additionally, the time and amount of feed consumed to produce a 1.8 kg broiler has seen a three-fold decrease over the last five decades (Havenstein et al., 2003a).

A reduction in the capacity to control their feed intake is recognized as a major factor driving changes in growth rate of broilers. Hypothalamic satiety mechanisms (Burkhart et al., 1983) as well as hormonal control (Kuo et al., 2005) have been affected by selection for growth traits. Bokkers and Koene (2003) reported that broilers do not seem to have a lower set point controlling the feed intake and only rely in an upper set point. Therefore, modern broilers eat to their maximal physical capacity.

Selecting for growth rate has also created a reduction in the development of the cardiopulmonary system in relation to the rest of the body. Hassanzadeh et al. (2005) found that relative lung weight, relative lung and heart volume, and volume of the thoracic cavity were lower in fast-growing broiler chickens than in layers and a slow-growing strain of chickens. Havenstein et al. (2003b) also reported that broilers show a reduction in relative weights of the lungs and heart at slaughter age. Modern broilers present high susceptibility to pulmonary hypertension and ascites (Hassanzadeh et al. 2005), which has a great economic impact for the industry (Pavlidis et al., 2007). Clearly, a balance of supply and demand tissues constitutes a limit for further increments in broiler growth rates and muscle yield (Rance et al., 2002).

Selection for broiler growth and yield has induced changes in myofibre hyperplasia and hypertrophy (Remignon et al., 1995). The *pectoralis major* muscle of high breast yield broilers exhibits more than twice as many myofibres as Leghorns do and 10% more than a classic broiler strain (Scheuermann et al., 2004). Macrae et al. (2006) reported that *pectoralis major* fibres had greater diameter than did *biceps femoris* fibres in broilers and broiler great-grandparents, but not in laying strains. Soike and Bergmann (1998) proposed that selective hypertrophy of fast-twitch glycolytic fibres in broilers increases the distance for oxygen diffusion and the vulnerability of the breast muscle to stressing conditions. Additionally, high breast yield has been associated with lower capillary density (Hoving-Bolink et al., 2000). Accordingly, Macrae et al. (2006) reported a higher incidence of degenerative changes in the muscle broilers than in slow-growing chickens.

Whether selection for growth and yield has produced changes in myofibre types is not clear. Soike and Bergmann (1998) found that layer-type chickens had relatively more slow-twitch oxidative and fast-twitch oxidative fibres than broilers in the *flexor cruxis medialis* muscle; and meat-type chickens had a higher proportion of glycolytic fibres than layer-type chickens in the *supracoracoideus* muscle. However, Remignon et al. (1995), who compared two strains divergently selected for growth, only reported a difference in the maturation of the fibres identified by myosin heavy chain isoform patterns, with no difference on fibre types. Nonetheless, lines selected for growth and breast yield have decreased the rate of protein degradation compared to slow-growing lines (Schreurs et al., 1995; Tesseraud et al., 2000).

The existence of the pale, soft and exudative (PSE) condition in chicken meat has been suggested from the 1990s as a correlated effect of selection for growth (Zhang and Barbut, 2005). Dransfield and Sosnicki (1999) proposed that a fast pH post-mortem decline of meat from fast-growing lines was responsible for PSE-like problems. However, the hypothesis that selection for growth and breast yield has had a detrimental effect on meat quality is not supported by studies of genetic variation on meat quality parameters in broilers (Le Bihan-Duval et al., 2001). Moreover, Berri et al. (2007) reported that myofibre hypertrophy has produced higher L* (lightness) values, but a greater water holding capacity in high yield broilers. It is not clear whether PSE-like problems will affect the potential of growth and meat yield improvements in the future.

1.3. The Modern Broiler Breeder

Reductions in appetite control have made feed restriction of broiler breeders necessary for acceptable reproductive performance (Renema and Robinson, 2004). Broiler breeder hens fed *ad libitum* exhibit increased rates of mortality and reduced settable egg production, fertility and hatchability (Robinson et al., 1991; Yu et al., 1992a). The "erratic ovoposition and defective egg syndrome" (EODES) has been reported for *ad libitum* fed meat-type breeders from the 1960's and 1970's (Jaap and Muir, 1968; Van Middelkoop, 1971, 1972). Yu et al. (1992a) reported that as much as 41% of the eggs produced by *ad libitum* fed hens to 34 wk were laid outside the prime laying hours, compared with a 13% in restricted hens. Accordingly, a 33% of the eggs from *ad libitum* birds presented shell formation abnormalities versus a 4% in restricted birds. As part of the mechanisms leading to multiple ovulations, Yu et al. (1992b) reported that the second-largest yellow follicle increased progesterone secretion to a level similar to the largest yellow follicle, indicating that both follicles matured at the same time. Onagbesan et al. (1999) proposed that a lack of interaction between gonadotrophins and IGF-I on progesterone production of *ad libitum* fed birds results in the simultaneous differentiation of several large yellow follicles of similar physiological state that the ovary cannot handle, causing erratic and multiple ovulations. Additionally, Chen et al. (2006) suggested that triacylglycerol accumulation in non-adipose tissue of overfed broiler breeders may be related with ovarian abnormalities and granulosa cell susceptibility to apoptosis, which may reduce reproductive performance.

Even small changes of feed allocation during sensitive stages of the bird development can impact reproduction. Robinson et al. (1998) reported that egg production and embryo viability were greater when broiler breeder hens received slow increments in feed allowance prior to sexual maturity than when feed increments were fast. Bruggeman et al. (1999) concluded that feed restriction from 7 to 15 wk led to improved hen reproductive performance as compared to restriction at other age periods during rearing. Additionally, interactions among nutrient availability, photostimulation and genotype may affect reproduction. Robinson et al. (2007) reported that an early photostimulation age (18 wk) negatively impacted settable egg production compared to a later photostimulation age (22 wk) regardless of BW profile, since greater development was achieved before the hypothalamus-hypophysis-ovary axis was stimulated by light. Different strains of broiler breeders exhibit differences in their ability to mobilize nutrients to maintain egg production; therefore, their sensitivity to changes in feed allocation is also different (Robinson et al., 2007).

The divergence of objectives of broiler selection and broiler breeder production emphasizes the importance of detailed broiler breeder management. Further selection for yield may reduce the ability of hens and roosters to mate naturally as has happened in turkey production (Pollock, 1997). So far, selection for growth has produced heavier broiler breeder males, which can exhibit mechanical difficulties in mating (Bilcik et al., 2005). Additionally, Millman and Duncan (2000) reported that broiler breeder roosters displayed more frequent aggressive behaviour towards females than laying-strain and fighting-strain male chickens did. They concluded that aggressive behaviour was not related to feed restriction. Overall, the reproductive challenges in broiler breeders may increase and, simultaneously, greater muscularity may determine greater metabolic demands diverting nutrients away from reproduction.

1.4. The Concept of Efficiency

Based on the definition of efficiency used in production economics (Coelli et al., 2005; Fried et al., 2008), efficiency was defined throughout this thesis as the extent to which a feasible optimization objective is obtained. Feasible optimums are defined by a biologic process, a production function or a behavioural goal of the producer. Natural and/or market constraints determine the relationships between inputs and outputs. Efficiency measures normally involve comparing observed output to maximum potential output obtainable, or comparing potential input to minimum potential input required, or a combination of the two (Fried et al., 2008). Measures of efficiency are commonly expressed in relative terms, as a proportion of the feasible outcome. The term "experimental unit" was preferred to "decision making unit", used in economics, since input-output relations are not always the result of rational decisions, but may be caused by natural optimization processes.

The poultry meat production system may be defined from a global perspective; the inputs are natural resources and human labour, and the main outputs are food for humankind and an environmental impact. The objective of the system is to minimize the cost of chicken meat and minimize the environmental impact. This thesis studied of input-output relationships using the animal organism as experimental unit, with the aim to make inferences applicable to the aggregated system. Therefore, a hierarchical system of biological and economic units affecting the system (cell, tissue, organ, animal, flock, farm, company, local, national and global industry) was assumed. Studying individual animals allowed accurately measuring inputs and outputs at the organism level and relating biologic, technical and economic efficiency. However, this approach did not allow considering important parts of the system such as labour and the environmental impact of poultry production.

1.4.1. Biological Efficiency

In this thesis, biological efficiency was approached from the energy perspective, although in nature, the optimization objective is frequently survival rather than energetic efficiency (Yun et al., 2006). Energy is defined as the capacity to do work, and work as the action of a force in moving a mass through a distance (Brafield and Llewellyn, 1982). Energy cannot be measured directly, but through the transformation from one form to another.

The transfer of heat and work in thermodynamic processes is governed by thermodynamic axioms that have been developed from the 19th century based on the work of scientists as Sadi Carnot, Robert Mayer, Hermann Helmholtz, William Thompson, and Rudolf Clausius (Ebeling et al., 2005). The first law of thermodynamics states that the total amount of energy in the universe remains constant (Lehninger, 1971). This law allows a description of any energetic system in which energy inputs equal energy outputs. The second law of thermodynamics states that the entropy of a system that is not in equilibrium will increase over time, approaching a maximum value at equilibrium (Lehninger, 1971). This law determines that a proportion of energy in a changing system is irreversibly transformed into heat.

All biological organisms on earth derive their energy directly or indirectly from the sun. Living organisms preserve their internal order by taking in free energy (useful energy) of nutrients or sunlight and returning to their surroundings an equal amount of energy in a less useful form (Lehninger, 1982). Therefore, the energetic efficiency objective can be described as the minimization of the energy input transformed in heat per unit of time, such that the system remains organized (functional).

1.4.2. Energetic Efficiency in Animal Production

A reduction of energy wasted as heat in animal production is assumed to improve productivity because more energy would be retained for animal products. However, measuring heat production alone does not provide a complete picture of the energy partitioning process within the animal organism. From the early 20th century, studies on heat production and energy partitioning in animals allowed the development of a general theory of energy partitioning that have been refined since then. Armsby and Fries (Armsby, 1903; Armsby and Fries, 1915) were among the first to characterize a hierarchical partition of digestible energy in farm animals, separating out energy losses from energy available for productive processes (i.e. growth and reproduction). Although some of the assumptions of Armsby and Fries have been refuted since then (Emmans, 1994), their theoretic model of energy partitioning has been the basis of the modern study of bioenergetics in animal production. Figure 1-1 shows a general version of the model (Leeson and Summers, 2001).

The percentage of gross energy that can be taken into the animal body depends upon the ability of the animal to digest and absorb feed; this portion of energy is named digestible energy. Further losses occur in the urine, primarily because the synthesis of uric acid (or urea in mammals) to excrete excess nitrogen has a metabolic cost. The remaining energy, available to support the metabolic process in the animal is termed metabolizable energy (ME). A major proportion of ME consumed by an animal is transferred to the surroundings as heat since both anabolic and catabolic reactions require a release of unusable energy. Part of this heat expenditure is caused by the process of absorption, transport and breakdown of nutrients from the diet to become available to support cell metabolism; that portion is termed heat increment of feeding. The energy that is left for maintenance and retention is called net energy (NE). Although this model considers these processes to be hierarchical and independent, in reality, energy retention and tissue maintenance are simultaneous and share common biochemical pathways and regulatory mechanisms, so they permanently affect each other.

Maintenance has traditionally been defined as the energy necessary to maintain the vital processes of the animal at a state of zero energy retention (Emmans, 1994). From the work of Armsby and Fries (1915), the need to separate heat increment of feeding from maintenance heat production has been recognized. The heat increment of feeding has been demonstrated to be a function of diet composition and feeding level (Emmans, 1994). Researchers have attempted to disaggregate total heat expenditure in their theoretical components in order to rank feedstuffs by their ability to yield productive NE (Lofgreen and Gareett, 1968). Others have attempted to estimate maintenance ME requirements for animals (Yan et al., 1997). In general, methodologies based on NE systems have been imprecise to represent animal energy utilization whereas ME systems have been imprecise to represent diet effects (Birkett and de Lange, 2001). Since energy is measured by its potential heat production, methodologies to assess energy partitioning present difficulties to discern the origin of heat expenditure. Additionally, artifacts may appear due to the sensitivity of the animal metabolic rate to specific experimental conditions.

The processes of synthesis and turnover of organic components that constitute animal products have an energetic cost. Therefore, the efficiency of energy retention (k; Figure 1-1) normally is lower than one. From the work of Kielauowski (1965), a difference in the metabolic cost of energy retention in form of protein and fat has been recognized. In chickens, efficiency of protein deposition is lower than efficiency of fat deposition (Petersen, 1970; Boekholt et al., 1994). Therefore, the metabolic cost of retention of lean and fat tissue depends on the relative rates of retention. Most modern energy partitioning methodologies consider this assumption. Nonetheless, Birkett and de Lange (2001) pointed out that marginal energy efficiencies of retention may also change as a function of level of production, metabolic state, and level of intake. Again, the difficulty to separate sources of heat production makes calculation of efficiencies of retention dependent on estimations of maintenance requirements and measures of gross energy in animal products (Lopez and Leeson, 2005; Rabello et al., 2006).

Whether maintenance or energy retention costs play a more important role in determining productivity depends on the growth rate, and the specific tissue or organic compound of interest for production. For instance, maintenance has the most important share in the metabolic budget of broiler breeders (Spratt et al., 1990a). In broilers, efficiency of muscle mass retention appears as the most important factor determining individual productivity (Lopez et al., 2007). The efficiency objective may be defined as minimization of energy inputs transformed in non-useful outputs, or maximization of retained energy relative to energy input per unit of time. A comprehensive definition of energetic efficiency in animal production should include both maintenance and retention because both are likely to present some variation simultaneously. Nonetheless, experimental methods frequently fail to measure both accurately. Hence, different approaches may be taken to measure efficiency depending on the nature of the production system and the quantitative and analytic methods of choice.

1.4.2.1. Measuring Energetic Efficiency in Animals

A direct relationship between feed input and animal products (feed conversion) is a straight forward measure of energetic efficiency in animals with high growth rates (Skinner-Noble and Teeter, 2004; Orejano-Dirain, 2004). In this case, the difference between energy input and body weight gain is basically the sum of energy losses in Figure 1-1. Selection for feed conversion has been practiced in poultry breeding programs from the 1970s and has been supported mainly by increments in growth rate, since this is a correlated trait (Zhang and Aggrey, 2003). The heritability of feed conversion is moderate (h^2=0.21 to 0.35; Chambers et al., 1994). This implies that rates of genetic improvement are below those for growth rate. Additionally, since feed conversion does not consider energy partitioning within the animal, measurement standardization on commercial breeding programs has presented difficulties. For instance, selecting efficient animals in a fixed age period penalizes heavier birds since they have greater maintenance requirements (Emmerson, 1997).

In animals where maintenance requirements are proportionally more important, measures of energetic efficiency must recognize metabolic BW as a scaling factor determining part of the heat expenditure. In this case, two basic approaches may be taken to assess energetic efficiency: 1) direct estimation of variability in energy requirements for maintenance; or 2) quantification of residual variability in energy balance models. Although the first method has been tested in vivo in cattle (Shuey et al., 1993), estimation of individual requirements for maintenance using calorimetric techniques has proven to be difficult for application due to low repeatability, small sample sizes and identification of the sources of heat expenditure. The second approach presents practical advantages; however, these measures comprise a mixture of factors that affect the energy balance and inferences should be cautious.

From the 1980s, an approach known as residual feed intake (RFI) has been used to assess energetic efficiency in different species (Bordas and Merat, 1981; Johnson et al., 1999; Herd et al., 2003). RFI is defined as the difference between observed and predicted ME (or feed) intakes.

An efficient animal is one that consumes less energy than the estimated requirement. As individual requirements vary as a function of the metabolic size and production level, an accurate estimation of energetic demands is necessary to compare individual energetic efficiency. Estimations of ME requirements in RFI calculations have incorporated some of the assumptions of ME models of energy partitioning. The following general function has been traditionally used in the RFI literature in hens (Katle, 1991; Bordas et al., 1992).

$$MEI = aBW^{0.75} + bADG + cEM$$

Where MEI is ME intake, $BW^{0.75}$ is metabolic BW, ADG is average daily gain, and EM is daily egg mass production. However, a number of issues in the assumptions attached to this model make it inconsistent with the energy partitioning theory in animals:

- The assumption of $BW^{0.75}$ as metabolic scaling factor has been controverted as general theory (Glazier, 2005).
- The coefficients for ADG and EM are linear; hence, weight gain and egg mass production are assumed to have a fixed composition and efficiency of retention.
- The ME requirement for maintenance (ME_m) is assumed to be independent of feed intake, even though the feed increment of feeding is one of the components of ME_m.

Although sources of variation in RFI may include genotypic differences related with energy utilization at the cellular and tissue level, they may also include environmental effects that were not properly modeled. Some attempts to improve models of ME intake estimation have been proposed (Luiting and Urff, 1991a), but assumptions of the model have not been improved. Nonetheless, selection for RFI has had positive results for productivity in laying hens (Bordas et al., 1992), meat cattle (Nkrumah et al., 2004) and pigs (Cai et al., 2008). This measure presents high phenotypic variability and moderate to high heritability in laying hens (h^2=0.42 to 0.62; Luiting and Urff, 1991b, 1991c). Therefore, it may be subject to selection with fairly quick genetic improvement rates. The concern of using RFI as a selection criterion is the possibility of negative correlated responses. For instance, divergent selection experiments for RFI have demonstrated a correlated reduction of voluntary feed intake in laying hens (Schulman et al., 1994).

1.4.2.2. Factors Affecting Energetic Efficiency in Poultry Production

Inter-bird variation in rates of nutrient absorption affects individual estimates of energetic efficiency. Maisonnier et al. (2001) concluded that anatomical characteristics of the gastrointestinal tract are responsible for part of the individual variation in nutrient digestibility. Additionally, nitrogen balance affects quantification of ME because of energy requirements for nitrogen excretion (Leeson and Summers, 2001). This effect is a reflection of the interaction between diet composition (Lopez and Leeson, 2008), and protein and essential amino acid requirements of the birds (Eits et al., 2005).

Factors affecting utilization of ME may be divided in two types: 1) those affecting ME_m, and 2) those affecting composition and efficiency of retention. Variables affecting maintenance have been studied through calorimetry and divergent selection experiments of RFI. Factors affecting retention have been studied through calorimetry and feed conversion experiments. In the case of RFI and feed conversion experiments, a mixture of maintenance and retention effects is analyzed. In the case of calorimetric studies, variation of energy requirements is always omitted on either the maintenance or the retention side.

Body size has a great importance in determining energetic efficiency in animals. The relationship between size and metabolic rate is typically expressed as a power function ($R=aM^b$; R=metabolic rate; M=body mass). The exponent b=0.75 has been widely accepted for animals in the scientific literature (Brody, 1945; Kleiber, 1961; Blaxter, 1989). However, recent studies have demonstrated that 0.75 is not universal within or among species. Surface-area limits on resource/waste exchange processes and mass/volume limits on power production do not explain all the variation in the exponential relationship (Glazier, 2005). Lopez and Leeson (2005) reported that the assumed scaling exponent (0.60 vs. 0.75) significantly affected estimation of energy partitioning and efficiencies of protein and fat retention in birds.

Environmental temperature and thermal isolation barriers affect heat transfer from the animal to its surroundings. The thermoneutral temperature is defined as the temperature at which the body temperature is kept constant at the lowest energy cost. For chickens, the thermoneutral zone changes with age as a consequence of reduction in body surface area per unit of body mass (Leeson and Summers, 2001) and the development of thermoregulatory mechanisms (McNabb and Olson, 1996). Maintenance ME requirements increase when environmental temperature gets further from the thermoneutral temperature (Sakomura, 2004). Feather coverage also affects heat expenditure. Neme et al. (2005) found a higher ME_m for laying pullets with poor feather coverage compared with normally feathered birds. Similarly, Bordas and Minvielle (1999) attributed differences in RFI between two divergently selected lines of laying hens to morphological traits involved in heat loss, such as wattle size.

Differences in heat expenditure between inefficient (high RFI) and efficient (low RFI) laying hen lines have been explained by a greater dietary thermogenesis (Gabarrou et al., 1997) and feeding activity levels (Gabarrou et al., 1998) of inefficient birds. Gabarrou et al. (1998) found that high RFI hens exhibited a greater regulatory thermo genesis at high feed intakes than low RFI hens, although no differences in basal heat production were found. However, it is not clear to what extent voluntary intake levels or diet induced regulatory thermogenesis are responsible for differences in energetic efficiency in hens because selection for high RFI has simultaneously resulted in high voluntary intakes (Swennen et al., 2007) and strains have not been compared at equal feed intake levels.

The relative size of visceral organs is an important factor determining requirements of ME_m (Konarzewski et al., 2000). Spratt et al. (1990b) reported that the liver, gut and reproductive tract accounted for 26 to 30% of the energy expenditure of adult broiler breeder hens. Intra-bird variation in the energetic metabolism of these tissues may affect efficiency too. Orejano-Dirain et al. (2004) reported that low feed efficiency was related to a greater electron leak of duodenal mitochondria in broilers, which causes oxidative stress and may increase energy requirements to maintain cellular integrity.

Activity level also determines ME_m and plays a role in energetic efficiency. Rabello et al. (2004) reported that ME_m were 21.8% higher for broiler breeders raised on floor than those in cages. Li et al. (1991) also reported that heat expenditure during the day was 33% greater than it was at night in laying hens. In contrast, activity levels may have a different relation with feed efficiency in fast-growing animals where maintenance is less important. Skinner-Noble et al. (2003) reported that more active broilers had higher feed efficiency than less active birds, probably because it improved their ability to access feed.

Body composition affects energetic efficiency through changes in maintenance and retention requirements. First, fat depots in the body have a lower metabolic rate than lean tissue (Blaxter, 1989). Second, energy density is greater in the fat than lean tissue; not only because fats have greater free energy than proteins, but also because there is a greater amount of water associated with lean tissue (Leeson and Summers, 2001). And third, efficiency of fat retention is greater than efficiency of protein retention (Kielauowski, 1965). Genetic and environmental differences in composition and efficiency of retention may be responsible for variability in energetic efficiency in hens (Luiting, 1990). In the case of eggs, the yolk contains more energy than albumen (USDA, 2007), but efficiency of yolk retention may be greater because of the lack of turnover of $VLDL_Y$ to be deposited in the follicles (Walzem et al., 1999) and the high ATP requirement for egg white protein and calcium carbonate synthesis in the oviduct (Etches, 1996). In the case of body weight gain, body fat contains about 9.1 kcal/g while body protein contains about 5.5 kcal/g (Leeson and Summers, 2001). However, there is evidence of variability in efficiency of energy retention in animals, which may be a reflection of diet composition and the origin of substrates for tissue synthesis (Emmans, 1994). For instance, Sakomura et al. (2004) reported an efficiency of fat deposition of 1.04 for broiler breeder hens and 0.69 for broiler chicks and attributed this difference to the fact that broilers were fed *ad libitum*. Possibly, a greater amount of retained fat was the result of *de-novo* fatty acid synthesis in broilers than in broiler breeders.

Energetic efficiency is a multifactorial trait. An appropriate analysis of individual variation in energetic efficiency requires: 1) a robust method of energetic efficiency estimation; 2) consistency of the assumptions of the energy balance model with scientific evidence of nutrient partitioning; 3) recognition of the sources of variation included and not included in the measure; and 4) differentiation between direct and indirect variables affecting energy balance.

1.4.3. Efficiency: An Economic Perspective

Economic efficiency is usually defined relative to the economic objective of profit maximization. In poultry meat production, that objective is often assumed to be consistent with the behavioural assumption of cost minimization. As producers have spatial and temporal limitations for output production decisions, and their portfolio is focused on a single output (chicks, broilers), short term producer decisions are limited to input utilization. In order to link biological and economic processes, a short term scenario was considered since that interaction occurs in the lifespan of the birds. However, a complete model of economic efficiency in the poultry meat industry should consider long term decisions that include scale of production and technical change.

Farrell (1957) was the first to propose that economic efficiency of a firm consists of technical and allocative efficiency. Purely technical factors can be analyzed separately from input utilization decisions because their causes are different. Based on Farrell's work, current methods of economic efficiency analysis have been developed. These methods have been primarily used to assess efficiency differences among firms or industries (Wu et al., 2003; Osborne and Trueblood, 2006) and to quantify factors affecting firm efficiency within an industry (Tauer and Mishra, 2006). Technical change has been often studied simultaneously with economic efficiency (Hadley, 2006). Applications of economic efficiency methods have been used in animal nutrition to minimize costs (Sonka et al., 1976; Brokken and Bywater, 1982) with emphasis in factor substitution. Only recently, economic efficiency methods have been applied in agriculture to link biological processes and producer decisions to maximize profit (Wang et al., 2006).

1.4.3.1. Technical, Allocative and Economic Efficiency

The terms efficiency and productivity are frequently confused and used interchangeably. However, their meaning is different. Figure 1-2 represents a production frontier f(x), which determines the maximum output (y) attainable from each input (x) level. It reflects the current state of the technology (Coelli et al, 2005). Firms in the industry operate either on the frontier if they are technically efficient or beneath if they are not. Firms A and B (Figure 1-2) are technically efficient. However, firm B has a lower productivity than firm A because it uses more input per unit of output than firm A. The slope of rays from the origin to each firm (y/x) provides a measure of productivity (Coelli et al, 2005). Due to the characteristics of the technology, no firm (point C; Figure 1-2) can produce the same amount of output as firm B and have the same productivity as firm A.

Technical efficiency refers to the ability of a firm to produce as large as possible an output from a given set of inputs, or, from an input perspective, to use the lowest amount of inputs to produce a given output (Farrell, 1957). Consider the unit frontier isoquant $\overline{UU'}$ (Figure 1-3; Farrell, 1957), in which combinations of inputs x_1 and x_2 are used to produce a unit of output y. The point A represents an inefficient firm using x_1 and x_2 at the same ratio as A', but at greater quantities. Technical efficiency of firm A is defined as $\overline{OA'}/\overline{OA}$. Allocative efficiency (**AE**) refers to the extent to which a firm uses the best proportion of inputs in view of their prices (Farrell, 1957). The tangency point of the isoquant $\overline{UU'}$ and the isocost line $\overline{VV'}$ (Figure 1-3), which slope is equal to the ratio of the prices of the two inputs, determines the cost minimizing proportion of inputs. Firm A (Figure 1-3) is technically inefficient but allocatively efficient because it is using the same ratio of inputs as the cost minimizing point A'. Firm B is technically and allocatively inefficient. Allocative efficiency of firm B is defined as $\overline{OB''}/\overline{OB'}$. An economically efficient firm is one that is technically and allocatively efficient. Economic efficiency of firm B is defined as $\overline{OB'}/\overline{OB}$. Therefore, the multiplication of technical and allocative efficiency measures economic efficiency.

1.4.3.2. Measuring Economic Efficiency

Methods to measure economic efficiency can be classified in parametric and non-parametric based on whether they require fitting mathematical functions, and stochastic or deterministic based on the assumptions regarding the error term. Most modern economic efficiency studies use either stochastic estimations of production frontiers (Aigner et al., 1977) or data envelope analysis (DEA; Charnes et al., 1978) to measure efficiency.

DEA is a non-parametric method to calculate efficiency based on a linear convex hull approach to frontier estimation (Charnes et al., 1978). DEA involves the use of linear programming to construct a non-parametric piece-wise surface (or frontier) over the data. Efficiency measures are then calculated relative to this surface (Coelli, 1996). The initial specification of DEA assumed constant returns to scale and strong input disposability. However, Byrnes et al. (1984) relaxed these assumptions in order to segregate technical efficiency in three components: 1) a measure or purely technical efficiency, 2) a measure of scale efficiency, and 3) a measure of congestion efficiency (overutilization of some inputs). DEA does not require assumptions of functional forms, which is an advantage compared with parametric methods. However, since it is a deterministic method, DEA assumes that all deviations from the production frontier are due to inefficiency. Thus, this method may be sensitive to outliers. Since efficiency indices are directly calculated using DEA, inefficiency is usually modeled in a second step (Wu et al., 2003). The Tobit model (Tobin, 1958) is considered more appropriate to analyze factors affecting efficiency than least square procedures because efficiency measures present a high bound at one.

A stochastic frontier production function specification was proposed in the 1970s (Aigner et al., 1977; Meeusen and van den Broeck, 1977) in order to separate the error term of production functions in two components: one that accounts for random effects and one that accounts for technical inefficiency. Therefore, stochastic production function estimation not only relies on assumptions of the production function, but also regarding the distribution of inefficiency error term (Forslund et al., 1980; Mbaga et al., 2003). In stochastic efficiency analysis, a second step regression of inefficiency variables is considered inconsistent with the assumption of independence of inefficiency effects in the two estimation stages. Kumbhakar et al. (1991) addressed this issue by specifying explicitly technical efficiency as composed by a deterministic component of firm-specific characteristics and a random component. This one-stage efficiency analysis is used in most modern stochastic efficiency studies. Cost function frontiers (Chambers, 1988) have also been used to assess economic (or cost) efficiency (Hailu et al., 2005) since, in some cases, industry cost data is more readily available than input-output data.

1.5. The Problem

Increments of growth rate and yield in modern broilers have increased broiler productivity by maximizing feed utilization on time, and diverting more nutrients towards meat production. Although phenotypic selection for broiler growth and yield is still possible, technical improvement in broiler chicken production is a finite process constrained by physiological homeostasis. Additionally, the self regulation of broiler breeders has been compromised. Selection for high energetic efficiency may help to sustain advancements in the chicken meat production frontier while affecting positively the chick production frontier.

Feed is the main input of poultry production and feedstuff prices may continue a tendency to increase in the future. In modern broilers, maximization of feed utilization is consistent with maximizing nutrient intake. In modern breeders, maximization of feed utilization is consistent with maximizing reproduction while minimizing energy losses. The process of maximizing economic efficiency of meat poultry industry would greatly benefit by understanding the bio-economic relationships between broilers and broiler breeders. Accordingly, implementation of strategies to optimize technical and economic efficiency in the industry requires the development of more consistent and accurate measurement and analytic methodologies.

1.6. Objectives

1.6.1. General Objective

The objective of this thesis was to study the relationships between feed allocation, energetic efficiency, and technical and economic efficiency of broiler breeders, and their implications for broiler meat production. Studying these bioeconomic linkages will provide primary breeders and producers with a platform to develop strategies to optimize economic efficiency of chicken meat production systems.

1.6.2. Specific Objectives

- To determine the effect of individual-based feed allocation on ovary morphology and carcass composition at sexual maturity.
- To determine if hens with superior rates of lay can be selected by allocating feed on an individual hen rather than a flock basis.
- To develop more accurate prediction equations of ME intake in broiler breeders.

- To develop robust methods to evaluate energetic efficiency in broiler breeders.
- To phenotypically characterize broilers breeders categorized by energetic efficiency.
- To relate maternal energetic efficiency to broiler growth, feed efficiency, yield and functional properties of the meat.
- To relate maternal energetic efficiency and feed allocation to muscle fibre characteristics on a semi-pedigree basis.
- To evaluate the effect of broiler breeder feed allocation on the technical efficiency of individual hens and quantify factors contributing to inefficiency.
- To assess the effect of feed allocation decisions on economic efficiency of broiler breeder flocks under different feed price scenarios.

1.7. Approach

The objectives of this thesis were approached in three stages: 1) impact of broiler breeder feed allocation on chick production; 2) energetic efficiency in broiler breeders and their implications for reproduction and broiler production; and 3) technical and economic efficiency of broiler breeders. Two broiler breeder experiments were performed using Ross-708 birds with different feed allocation strategies. Hen-based data of body weights, feed intake, egg and chick production, and egg characteristics were collected during a complete production cycle. Three broiler experiments were carried out using a pedigree hatching system. Data of chick quality, broiler performance, and functional properties of breast meat were collected.

Broiler breeder reproduction and management were studied based on phenotypic information. This study continued previous broiler breeder research done at the University of Alberta (Renema et al., 1999; Robinson et al., 2007). Study of the impact of feed allocation on broiler breeder reproduction focused on the effect of hen body weight and feed intake variability. Individual-based feed allocation was used to evaluate broiler breeder females at a common BW target. Improvements on current methods to estimate ME intake requirements in hens were made. Energetic efficiency was estimated based on a model of energy-mass balance. A new method to calculate energetic efficiency relative to the requirement for maintenance was developed. Effects of maternal energetic efficiency on broiler growth and yield, meat quality, feed conversion, energetic efficiency, and myofibre numbers were assessed. Finally, a new application of DEA at the animal level was used to evaluate technical efficiency of individual hens and to make economic efficiency inferences for broiler breeder management.

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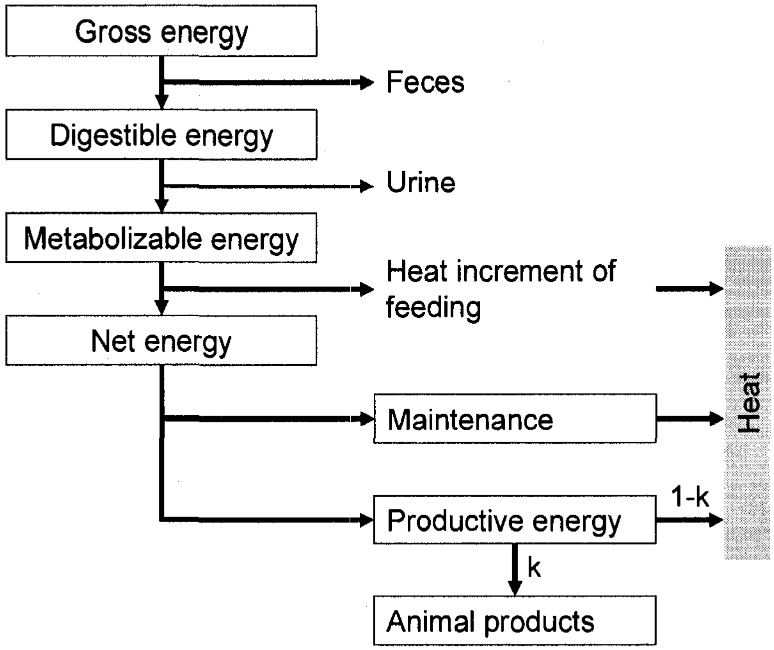

Figure 1-1. Animal energy partitioning model. Closed boxes represent components with potential to yield free energy within the animal organism. Source: modified from Leeson and Summers (2001).

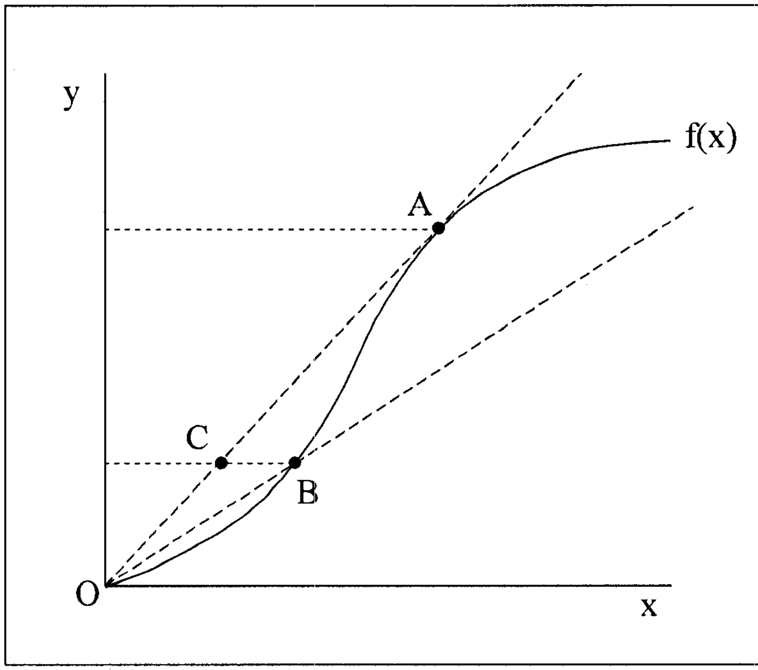

Figure 1-2. Production function frontier y=f(x). The slope of rays through points A and B provides a measure of productivity (y/x). Points A and B are technically efficient while point C is unfeasible. Source: modified from Coelli et al. (2005).

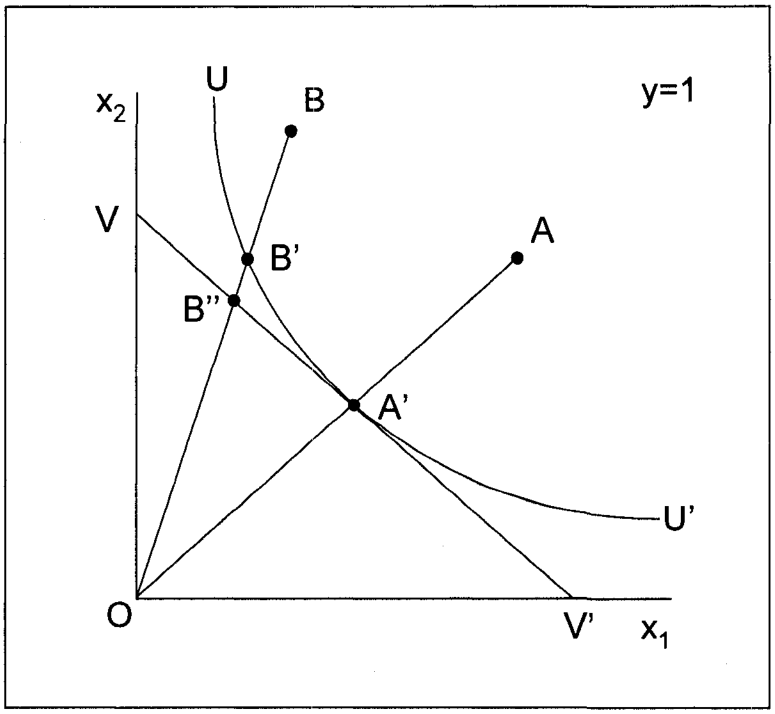

Figure 1-3. Unit frontier isoquant. Possible combinations of inputs x_1 and x_2 to produce a unit of output y. The tangency point between the isoquant UU' and the isocost VV' is the cost minimizing point A'. Source: modified from Farrell (1957).

Chapter 2. Effect of Reducing Body Weight Variability on the Sexual Maturation and Reproductive Performance of Broiler Breeder Females[1]

Abstract. A study was performed to assess the effect of reducing BW variability on sexual maturation and reproductive performance of broiler breeder hens. A total of 208 Ross-708 1 d old pullets were randomly assigned to one of two feed allocation treatments starting at 16 wk of age when all birds were placed in individual cages. A control treatment had feed allocated on a Group basis and followed the recommended BW target. A second treatment had feed allocated on an Individual bird basis. By design, the BW of Individual pullets converged at 20 wk. This design dictated that Individual birds had a lower BW variability and a higher feed intake variability than Group birds. Pullets were retrospectively classified in three initial (16 wk) BW categories: Low, Average, or High, using the mean ± 0.5 SD as threshold. After their first egg, 64 birds were dissected for determination of fleshing, fatness, and reproductive morphology. Egg production traits were analyzed to 60 wk, when the remaining birds were dissected.

Reducing BW variability did not reduce variability of age, follicle numbers, ovary and oviduct weight at sexual maturity. The Individual feed allocation accelerated the onset of production of Low BW birds, which increased total egg production (177 eggs) and average sequence length (3.9 d) with respect to Group x Low birds (163 eggs; 3.0 d). Individual x Low hens produced more eggs < 52 g than Group x Low hens (22 versus 8 eggs). The Individual treatment increased variability of ovary weight, LYF number, and LYF weight at 60 wk. Reducing BW variability increased variation in ovarian morphology at the end of production, which suggests that optimal BW for reproduction varied among birds. Correcting BW from 16 wk to reach the BW target primarily affected Low initial BW pullets, which entered lay sooner and produced more eggs, although many of the additional eggs weighed < 52 g.

2.1. Introduction

Maintaining a high uniformity is a major objective during the rearing period in broiler breeder pullets in order to more closely fulfill the nutritional requirements of the birds. Target BW are recommended by the breeding companies for each strain. Such standards are based on field results and supported by experimental observations (Renema et al., 2007a). The BW targets constitute the main criterion of feed allocation decisions, and deviations of the targets are thought

[1] A version of this paper has been submitted for publication in Poultry Science.

to diminish future production. The potential increment of flock productivity that can be obtained by reducing BW variation must be measured to develop strategies of feed allocation and BW management in commercial broiler breeder production.

It is often assumed that high uniformity causes a reduction of variability in age at sexual maturity and egg weight, as BW is considered a major determinant of both of those variables (Hocking, 2004; Wilson, 1991). However, the relationship between BW and reproduction is not a simple one in restricted broiler breeder females, since body composition plays a major role in the sexual maturation process (Bornstein et al., 1984), feed management during rearing may have long term effects on body composition and egg size (de Beer and Coon, 2007), and interactions between nutrition and genotype may affect sexual maturity age, ovarian morphology (Hocking and Robertson, 2000), egg size and reproductive performance (Joseph et al., 2002).

Cage feeding has been used to reduce feed intake variation in broiler breeder studies. Managing individual feed allocation to force each particular bird to a common target BW is a novel method to study the effect of reducing BW variability in broiler breeders and evaluate birds at equal BW. It was aimed to know how different birds in a broiler breeder population would perform if they all had the same BW. This study was designed to assess the effect of reducing BW variability of broiler breeder pullets on reproductive and carcass traits at sexual maturity and 60 wk of age, and reproductive performance to 60 wk of age.

2.2. Materials and Methods

2.2.1. Stocks and Management

A total of 600 Ross 708 (Aviagen Inc., Huntsville, AL) 1 d old pullets were individually identified by bar-coded neck tags (Heartland Animal Health, Fair Play, MO 65649) at housing and placed into two floor pens with 300 chicks per pen (23 chicks/m^2) in a light-tight facility. At 21 days of age, birds were split in two identical additional floor pens with 11 pullets/m^2 until 16 wk. Photoperiod was 23L:1D for the first 7 d and 8L:16D to 23 wk of age. At 23 wk, photophase was increased to 12L:12D, and one additional h/wk to 15L:9D at 26 wk. Feed was provided *ad libitum* for the first 14 d. At that age, feed intake was restricted and maintained on a daily basis until 4 wk when a skip-a-day program with 5 d of feed and 2 non-feed days per week was implemented until 16 wk of age. At 16 wk, 208 pullets were placed in individual laying cages. The rest of the pullets were used in other simultaneous experiments. Wheat and soy based mash diets (Appendix A) were supplied as follows: a Starter (2,900 kcal ME, 19% CP, 1.18% lys) from

0 to 3 wk; a Grower (2,900 kcal ME, 16.7% CP, 1% lys) from 3 to 25 wk; a Breeder 1 diet (2,870 kcal ME, 16% CP, 0.72% lys) from 25 to 49 wk; and a Breeder 2 diet (2,870 kcal ME, 15.5% CP, 0.70% lys) from 49 to 60 wk.

This research project was carried out in compliance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984) and was approved by a Faculty Policy and Welfare Committee.

2.2.2. Experimental Design

A completely randomized 2 x 3 factorial design was used to evaluate the effects of feed allocation treatment, initial (16 wk) BW and their interaction. Hen was the experimental unit. From the original population, a total of 208 birds were randomly assigned at hatch to one of two feed allocation treatments starting at 16 wks of age. A control treatment had feed allocated on a Group basis and followed the target BW recommended by the primary breeder; Group feed allocations decisions were based on the mean BW. Each Group hen received the same amount of feed on any given day. A second treatment had feed allocated on an Individual bird basis and followed the same BW target as Group, to which birds were planned to converge at 20 wk. Individual feed allocations decisions were unique for each particular hen. Pullets were retrospectively classified in one of three initial (16 wk) BW groups: Low, Average, or High, using the mean plus or minus 0.5 SD as the threshold (Figure 2-1). After their first egg, 64 birds were dissected for determination of fleshing, fatness, and reproductive morphology; the remaining 144 birds were kept for an egg production study and dissected at 60 wk of age.

2.2.3. Data Collection

Body weight was recorded bi-weekly to 32 wk and weekly thereafter. The day the first egg was laid was recorded as the age of sexual maturity. The morning after laying their first egg, each of the 64 birds were weighed and euthanatized by cervical dislocation. The breast, abdominal fat pad, liver, ovary, and oviduct were dissected from the carcass and weighed. From the ovary, large yellow follicle (LYF) number and weight (>10 mm , Renema et al. 2001a), small yellow follicle (SYF) number (4 to 10 mm), and large white follicle (LWF) number (2 to 4 mm) were recorded. At 60 wk, the remaining birds were dissected and breast, abdominal fat pad, liver, ovary, LYF and oviduct weights, and LYF number were recorded.

Eggs were individually weighed and coded according to shell integrity, shape and size. Small eggs were defined as those weighing < 52 g; normal eggs as total eggs minus deformed, membranous, soft shell, and double yolk eggs; and settable eggs as normal minus small eggs. Total egg mass was calculated as the sum of all egg weights for each hen. Average egg weight per hen was calculated to 60 wk. Average egg laying sequence length and prime sequence length were calculated as reported by Renema et al. (2001b). The proportion of follicles in multiple hierarchies was assessed as reported by Renema et al. (2007b).

2.2.4. Statistical Analysis

Differences among treatments were evaluated using generalized least squares (Proc Mixed; SAS Institute, Cary, NC) and a significance level of $P<0.05$. LS-mean separation was done through multiple t-tests. Differences in variability were evaluated using the Levene's test (Proc GLM; SAS Institute, Cary, NC) with a critical probability of $P<0.05$. As measures of variation, variances and CV are presented. For variables that presented heterogeneity of variances, heterogeneity in the variance-covariance structure of feed allocation treatments was specified in the model.

2.3. Results and Discussion

2.3.1. BW Profiles and Feed Intake

The initial (16 wk) BW did not differ between Individual and Group pullets ($P>0.05$). Due to the experimental design, an interaction between feed allocation and initial BW was evident by 20 wk. At photostimulation (23 wk), all initial BW categories of Individual converged with the average BW category of the Group treatment (Figures 2-1A and 2-1B). Since the Group hens had a common feed allocation, the BW of initial BW categories gradually converged as a result of variation in onset of lay and early demands of egg production. The BW interaction between feed allocation and initial BW disappeared by 30 wk of age. Variability in Individual BW rapidly decreased from 16 to 20 wk and remained lower (CV=1.9%) than for Group birds (CV=5.4%) until the end of the experiment (Figure 2-2). Supporting the rapid correction of Individual BW, different feed allocations were necessary among initial BW categories from 16 to 23 wk (Figure 2-3). Variation of Individual feed allocation was reduced after 23 wk (Figure 2-4), evidenced by similar feed intakes among initial BW categories until 44 wk. The experimental design not only created differences in BW variability, but also differences in Individual BW profiles and feed intakes, particularly from 16 to 23 wk of age.

2.3.2. Age, BW, Cumulative Feed Intake and Carcass Traits at Sexual Maturity

The Individual x Low birds responded strongly to the incremental management in feed allocation (Figure 2-3) by starting production 5 d ahead of the Group x Low birds (Table 2-1). In contrast, the Individual x High birds did not delay the onset of production although feed allocation and weight gains were decreased before 23 wk. Renema et al. (2007b) reduced feed allocation to high BW profile birds and increased feed allocation to low BW profile birds near 18 wk of age. In birds photostimulated at this time, the high profile birds entered lay 18 d more quickly than the low profile birds, on average. However, in birds photostimulated at 22 wk of age, after being on this altered feed allocation for longer, there was no difference in sexual maturation age (186 and 183 d in high and low profile birds, respectively), despite the high profile birds weighing 590 g more. Gous and Cherry (2004) reported that the onset of egg production was delayed by slowing down pullet growth before 20 wk. Although these studies demonstrate that BW alone is not the only determinant of sexual maturation age, the current study supports the thesis of a BW threshold for sexual maturity (Melnychuk et al., 2004).

At sexual maturity age, BW was not different between initial BW categories nor was the interaction between feed allocation and initial BW significant. Hocking (2004) reported a curvilinear relationship between BW and age at sexual maturity, in which greater BW had diminishing effects on the onset of production, and stated that energy intake was a limiting factor determining the onset of lay in severely restricted broiler breeders. Accordingly, Low hens consumed 8.6% more and High hens 4.4% less feed than Average initial BW hens from 16 wk to sexual maturity in the current study (Table 2-1). Presumably, Low hens had a limiting body mass to start egg production. In contrast, Renema et al. (1999) reported that a high and a low BW category based on BW at 20 wk consumed similar amounts of feed to sexual maturity but had different BW at first egg. Bartov and Wax (1998) found that birds with high BW at 18 wk had increased BW at first egg. The current study used a more modern high breast yield strain than those used by Renema et al. (1999) and Bartov and Wax (1998). The high potential for muscle development may have caused low BW birds to require greater intakes to deposit enough lipids to start reproduction in the current study. Renema et al. (1999) reported no differences in breast muscle percentage, fat pad percentage and carcass lipids percentage at sexual maturity among 20 wk BW categories. Similarly, breast and abdominal fat pad did not show differences at sexual maturity in the current study (Table 2-1), indicating that birds entered lay at a uniform composition.

2.3.3. Ovarian Morphology at Sexual Maturity and 60 Wk of Age

Neither follicle numbers nor weights of the ovary, oviduct or LYF at sexual maturity were affected by feed allocation or initial BW (Table 2-2). This demonstrates that High initial BW birds, even though were heavily restricted, maintained reproductive development at expense of BW mass when that restriction was applied before 20 wk. Moreover, instead of additional follicle development, the Individual x Low birds directed extra nutrients to muscle growth and fat storage as a compensatory response. Renema et al. (1999) reported that the number of recruited LYF at sexual maturity was stimulated by a very positive energy balance after photostimulation, and Hocking (2004) reported that LYF number and BW were linearly correlated. Results of the current study indicate that a steady feed allocation after photostimulation avoided such changes in LYF numbers within this BW range.

No effects of feed allocation, initial BW or interactions were detected in reproductive traits at 60 wk of age (Table 2-2). By this age, any residual effect of early production differences on the ovary had disappeared.

2.3.4. Egg Production and Egg Weight

Total eggs, settable eggs, and egg mass did not differ between Individual and Group birds (Table 2-3). Studies that have attempted to relate uniformity and production have not shown consistent results, in part because of methodological issues such as the use of non-randomized treatments (Hudson et al., 2001). The current results indicate that a fast reduction of BW variability after 16 wk did not affect egg production. However, the possibility that BW uniformity improvements at an earlier phase of development may affect egg production cannot be excluded. Pettite et al. (1982) reported that an improvement in uniformity through 4 wk BW segregation increased egg production during 10 wks following sexual maturity. An additional factor that should be considered is that the Group treatment had a greater uniformity than what is normally found in field conditions.

The Low initial BW category produced more total eggs in the Individual treatment (177.3 eggs; Table 2-3) than in the Group treatment (162.6 eggs). In addition to starting laying earlier, the Individual x Low hens had a prime sequence of 22.9 d versus 14.4 d of Group x Low hens (P=0.18; Table 2-3). Therefore, average sequence length was increased in the Individual x Low group (3.9 d versus 3.0 d in Group x Low). Accordingly, Individual x Low birds produced more normal eggs (173.6 eggs) than Group x Low birds (159.7 eggs). Nonetheless, the Individual x Low birds produced more small eggs (21.7 eggs) than the other sub-groups, which eliminated the

13.9 normal egg advantage compared to the Group x Low birds. As a result, production of eggs > 52 g (settable eggs) did not differ between Individual x Low (151.9 eggs) and Group x Low hens (151.4 eggs). In markets where eggs < 52 g are incubated, the 13.9 increase in normal egg production will be of great value. Corrections in BW profile of low BW birds before an advanced state of sexual development may increase flock productivity, especially if they are accompanied by strategies to improve egg weight of these birds.

The High initial BW hens consistently exhibited greater egg weights than Low and Average hens across feed allocation treatments. Interestingly, reducing the BW variability actually decreased the pooled egg weight by 1 g (P=0.07; Table 2-3), mostly because Individual x Low hens had lower egg weight (59.1 g) than the other sub-groups (60.3 to 62.7 g). Lewis and Gous (2006) reported that increasing the growth rate from 15 to 20 weeks did not have an effect on the mean egg weights. Similarly, Pettite et al. (1982) found that an early reduction in BW variability did not impact egg weight. However, Bornstein and Lev (1982) stated that egg size responded more readily than egg production to an increased energy intake during the pullet-layer transition period. Effects of changes on feed allocation and BW profile on egg weight may depend on whether or not they impact egg production.

2.3.5. Effects on Variability

Even though BW and fat pad proportion at sexual maturity were more variable in the Group than the Individual birds (Table 2-4), variability of sexual maturity age and ovarian morphology at sexual maturity were not affected by an improvement in BW uniformity. Variation in LYF number (Individual CV=16.9; Group CV=22.3%) and SYF number (Individual CV=47.4%; Group CV=56.7%) warrant further study. A greater difference in BW variability between feed allocation treatments could make this effect evident. In contrast with results at sexual maturity, ovary weight, LYF number and LYF weight had a greater variability in the Individual than Group hens at 60 wk (Table 2-4). It is possible that the optimal BW for reproduction differed among hens. Therefore, forcing hens to grow on a common target BW may have negatively affected the availability of nutrients for reproduction of hens with high breast yield and energetic demands for maintenance, although birds with lower maintenance requirements may have been benefited (Chapter 4). Although ovarian morphology appeared more variable in Individual than Group hens at the end of the experiment, reducing BW variability did not affect variability in egg production and egg weight (Table 2-4).

A reduction in BW variability at this age does not appear advantageous for settable egg production of the population, but may reduce egg weight and increase variation in the capacity to maintain a functional ovary until the end of production. However, correcting BW from 16 wk to reach the BW target affected positively Low initial BW pullets, which entered lay sooner and produced more eggs, although many of the additional eggs weighed < 52 g.

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Table 2-1. Age, body weight, cumulative feed intake, and breast, fat pad and liver relative weights at sexual maturity (first egg) for feed allocation treatments and initial BW categories

Feed allocation	Initial BW[1]	Age	BW	Cumulative feed intake[2]	Breast	Fat pad	Liver
		--- d ---	---------- g	----------	--------------	% BW	--------------
Individual[3]		186.2	2,990.8	6,555.9	21.2	1.60	1.57
Group[4]		186.2	3,000.6	6,673.9	20.6	1.67	1.65
SEM		0.6	18.7	199.5	0.3	0.10	0.04
	Low	187.8[a]	2,989.3	7,086.1[a]	20.3	1.60	1.68
	Average	185.5[b]	2,984.1	6,522.7[b]	21.2	1.74	1.58
	High	185.3[b]	3,013.6	6,235.9[c]	21.2	1.57	1.57
	SEM	0.8	23.4	210.2	0.4	0.13	0.05
Individual	Low	185.3[b]	2,965.1	6,965.5	20.7	1.47	1.65
Individual	Average	186.9[b]	3,010.4	6,662.6	21.2	1.83	1.54
Individual	High	186.2[b]	2,996.8	6,039.5	21.6	1.52	1.52
Group	Low	190.3[a]	3,013.4	7,206.7	19.9	1.74	1.72
Group	Average	184.1[b]	2,957.8	6,382.8	21.3	1.66	1.61
Group	High	184.3[b]	3,030.5	6,432.2	20.8	1.62	1.63
SEM		1.2	33.8	244.7	0.7	0.20	0.08
		--------------------------------		Probability	--------------------------------		
Source of variation							
Feeding allocation		0.94	0.71	0.33	0.28	0.62	0.12
Initial BW		0.035	0.63	<0.001	0.17	0.52	0.15
Feed allocation x initial BW		<0.001	0.24	0.06	0.63	0.38	0.96

[1] Birds were classified based on their 16 wk BW for analysis. The threshold was the mean BW ± 0.5 SD.
[2] Total feed intake from 113 d to first egg.
[3] Feed allocation decisions were made for each bird to maintain a BW target.
[4] Feed allocation decisions were made based on the mean BW. Birds had a common feed intake at any given day.
[a-c] LS-means within a column within effect with no common superscript differ (P<0.05).

Table 2-2. Ovarian morphology traits of feed allocation treatments and initial BW categories measured at sexual maturity and at 60 wk of age

Feed allocation	Initial BW[3]	Sexual maturity[1] Ovary weight	LYF[4] >11 mm	SYF[4] 5-10 mm	LWF[4] 2-4 mm	LYF[4] weight	F1 weight	Oviduct weight	60 wk[2] Ovary weight	LYF[4] >11 mm	LYF[4] weight	Oviduct weight
		--- g ---	--- # ---	--- # ---	--- # ---	--- g ---	--- g ---	--- g ---	--- g ---	--- # ---	--- g ---	--- g ---
Individual[6]		54.7	6.8	8.5	16.0	47.6	12.5	56.9	47.8	3.8	40.1	59.9
Group[7]		56.7	7.2	9.8	15.9	50.8	12.4	56.2	51.8	4.2	42.6	64.6
SEM		2.4	0.3	0.9	1.2	2.0	0.2	1.4	2.0	0.2	2.0	1.8
	Low	57.4	7.3	9.3	14.2	50.6	12.5	56.1	50.7	4.1	42.6	59.9
	Average	55.9	6.8	7.8	17.2	48.6	12.6	54.6	48.6	3.9	39.5	62.7
	High	53.8	6.8	10.4	16.5	48.5	12.2	58.9	50.1	4.1	42.0	64.0
	SEM	3.2	0.4	1.2	1.6	2.7	0.3	1.9	2.4	0.2	2.4	2.2
Source of variation												
Feed allocation		0.56	0.32	0.28	0.92	0.28	0.55	0.73	0.16	0.12	0.37	0.07
Initial BW		0.71	0.38	0.25	0.32	0.78	0.56	0.21	0.82	0.79	0.61	0.41
Feed allocation x Initial BW		0.53	0.65	0.42	0.67	0.41	0.67	0.98	0.97	0.97	0.86	0.59

[1] A subsample of 64 birds were euthanized and dissected the day after laying their first egg.
[2] The remaining birds were euthanized and dissected at the end of the experiment.
[3] Birds were classified based on their 16 wk BW for analysis. The threshold was the mean BW ± 0.5 SD.
[4] LYF= Large yellow follicles; SYF= Small yellow follicles; LWF= Large white follicles.
[5] The largest large yellow follicle.
[6] Feed allocation decisions were made for each bird to maintain a BW target.
[7] Feed allocation decisions were made based on the mean BW. Birds had a common feed intake at any given day.

Table 2-3. Production traits to 60 wk of age for feed allocation treatments and initial BW categories

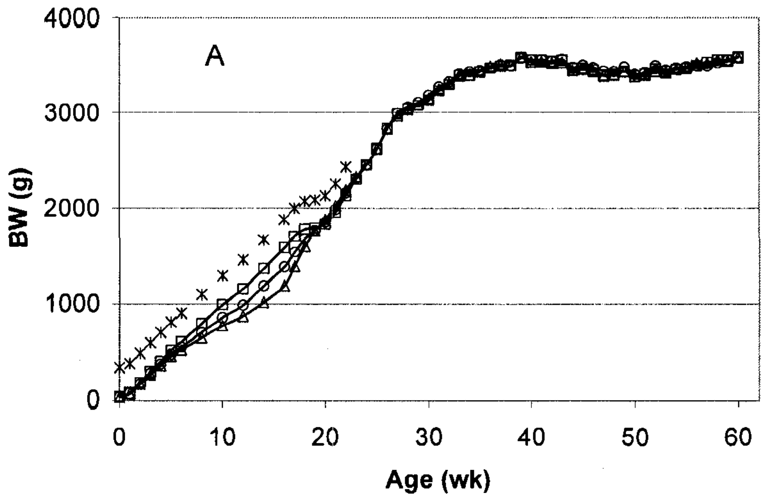
Feed allocation	Initial BW[1]	Total eggs	Normal eggs[2]	Small eggs[3]	Settable eggs[4]	Total egg mass	Egg weight	Prime sequence	Average sequence
		#				--- kg ---	--- g ---	d	
Individual[5]		169.4	165.2	12.7	152.4	10.2	60.5	18.5	3.5
Group[6]		168.1	164.3	8.9	155.4	10.3	61.5	16.5	3.2
SEM		2.7	2.6	1.5	2.6	0.2	0.4	2.0	0.1
	Low	170.0	166.7	15.0[a]	151.7	10.2	60.0[b]	18.6	3.5
	Average	167.6	163.7	10.1[ab]	153.7	10.1	60.6[b]	18.2	3.3
	High	168.8	163.8	7.3[b]	156.4	10.5	62.4[a]	15.6	3.3
	SEM	3.4	3.3	1.9	3.3	0.2	0.5	2.2	0.2
Individual	Low	177.3[a]	173.6[a]	21.7[a]	151.9	10.4	58.9	22.9	3.9[a]
Individual	Average	162.7[b]	158.3[b]	9.6[b]	148.6	9.8	60.6	17.6	3.1[ab]
Individual	High	168.3[ab]	163.6[ab]	6.9[b]	156.7	10.4	62.1	15.0	3.3[ab]
Group	Low	162.6[b]	159.7[b]	8.3[b]	151.4	9.9	61.1	14.4	3.0[b]
Group	Average	172.4[ab]	169.2[ab]	10.5[b]	158.7	10.5	60.7	18.8	3.4[ab]
Group	High	169.3[ab]	164.0[ab]	7.8[b]	156.1	10.6	62.8	16.3	3.3[ab]
SEM		4.8	4.7	2.7	4.7	0.3	0.7	4.1	0.3
Source of variation									
Feed allocation		0.72	0.81	0.07	0.42	0.60	0.07	0.41	0.22
Initial BW		0.88	0.77	0.017	0.57	0.27	0.002	0.46	0.73
Feed allocation x initial BW		0.034	0.027	0.010	0.40	0.11	0.34	0.18	0.048

[1] Birds were classified based on their 16 wk BW for analysis. The threshold was the mean BW ± 0.5 SD.
[2] Total eggs excluding double yolk, deform, soft shell, membranous and broken eggs. Value includes all sizes of eggs.
[3] Egg weights below 52 g.
[4] Normal minus small eggs.
[5] Feed allocation decisions were made for each bird to maintain a BW target.
[6] Feed allocation decisions were made based on the mean BW. Birds had a common feed intake at any given day.
[a-c] LS-means within a column within effect with no common superscript differ ($P<0.05$).

Table 2-4. Results of Levene's test to test homogeneity of variances for sexual maturity and 60 wk dissection traits between feed allocation treatments. Critical value was P=0.05. Variances and coefficients of variation (CV) are presented

Variable	Unit	Feed allocation effect	Variance		CV	
			Individual[1]	Group[2]	Individual	Group
Traits at sexual maturity		F probability			%	%
Age	d	0.38	40.2	48.8	3.4	3.7
BW	g	0.010	26,817.7[b]	44,120.9[a]	5.5	7.0
Fat pad	%BW	0.034	0.14[b]	0.39[a]	23.6	37.3
Breast	%BW	0.41	2.78	3.70	7.9	9.3
Liver	%BW	0.45	0.046	0.036	13.6	11.5
Ovary weight	g	0.97	162.1	165.2	23.2	22.8
LYF	#	0.14	1.34	2.53	16.9	22.3
LYF weight	g	0.82	123.3	110.8	23.2	20.8
Oviduct weight	g	0.49	65.0	47.6	14.3	12.3
Traits at 60 wk						
BW	g	0.0001	5,684.1[b]	58,825.9[a]	2.1	6.8
Fat pad	%BW	0.16	0.99	1.37	30.0	34.5
Breast	%BW	0.69	5.38	6.29	11.8	12.6
Liver	%BW	0.60	0.062	0.070	16.8	17.4
Ovary weight	g	0.003	362.1[a]	141.6[b]	39.8	22.8
LYF	#	0.012	2.24[a]	0.89[b]	38.9	22.4
LYF weight	g	0.054	308.0	181.1	43.6	31.3
Oviduct weight	g	0.067	296.6	126.2	28.7	17.4
Production traits						
Total eggs	#	0.99	678.4	677.9	15.5	15.9
Settable eggs	#	0.89	632.1	619.8	16.4	17.0
Total egg mass	kg	0.57	2.46	2.19	14.5	16.6
Egg weight	g	0.46	12.5	12.5	9.8	9.8

[1] Feed allocation decisions were made for each bird to maintain a BW target.
[2] Feed allocation decisions were made based on the mean BW. Birds had a common feed intake at any given day.
[a,b] Standard deviations (SD) with no common superscript differ (P<0.10).



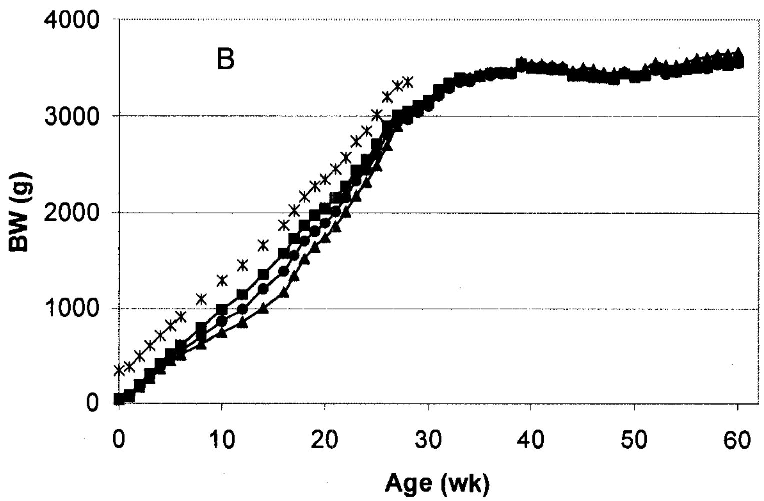


Figure 2-1. BW profiles of initial (16 wk) BW categories in the individual and the group-based feed allocation treatments. A. Low (△), Average (○) and High (□) 16 wk BW categories with the individual feed allocation. B. Low (▲), Average (●) and High (■) 16 wk BW categories with the group-based feed allocation. LS-mean differences were assessed with a critical *P*<0.05 (*).

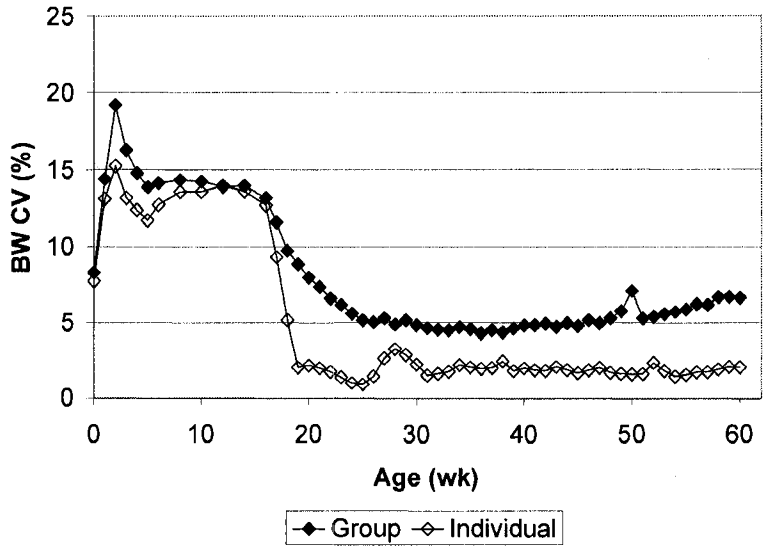


Figure 2-2. Weekly coefficient of variation (CV) of BW from broiler breeder females in Individual and Group-based feed allocation treatments starting at 16 wk of age.

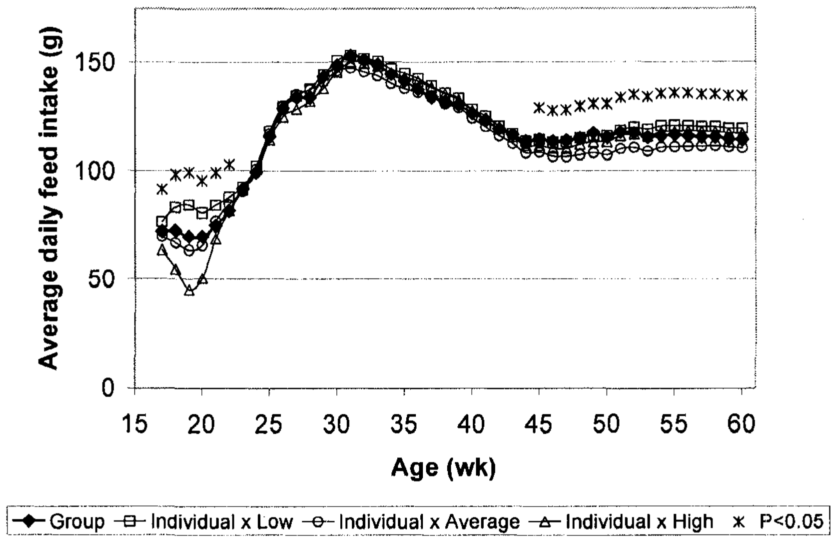


Figure 2-3. Average daily feed intake of the Group-based feed allocation treatment and initial (16 wk) BW categories within the Individual feed allocation treatment. LS-mean differences among BW categories of the Individual treatment were assessed with a critical $P<0.05$ (*).

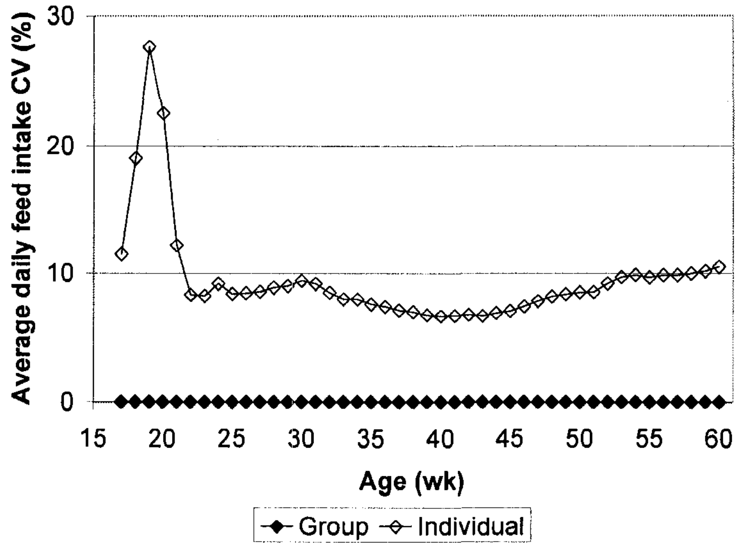


Figure 2-4. Coefficient of variation (CV) of average daily feed intake for the Group-based and Individual feed allocation treatments. Measurement error was assumed to be randomly distributed and independent of the feed intake, and was not accounted for in calculation of CVs.

Chapter 3. Evaluation of Empirical Models to Estimate Metabolizable Energy Intake in Broiler Breeder Females during the Production Phase[1]

Abstract. The ability of one linear and two nonlinear models to estimate ME intake (MEI) in broiler breeder hens from empirical data was evaluated from 20 to 60 wk of age. A total of 288 broiler breeder pullets were individually caged at 16 wk and assigned to one of four feed allocation groups. Three groups had feed allocated on a group basis with divergent target BW: Standard, High (Standard x 1.1), and Low (Standard x 0.9). The fourth group had Individual-based feed allocation and followed the Standard BW target. The linear model expressed MEI as a function of $BW^{0.75}$, average daily gain (ADG), egg mass (EM) and temperature. Nonlinear models used a normally distributed term associated with hen metabolic BW, and exponential terms of ADG and EM, or interactions with a Cobb-Douglas form. In nonlinear models, a second step regression measured the relationship between hen maintenance requirements and MEI level. Prediction equations of MEI were validated with an independent study that used broiler breeders of three strains assigned to four BW curves.

Estimation of energy partitioned towards maintenance and retention was in the range of reported values in the literature. However, a nonlinear model indicated that the ADG requirement increased by 0.60% and the EM requirement decreased by 2.07% for each 1% increment in BW. The simple linear model had the poorest fit (R^2=0.64) and underestimated MEI at greater feed intakes (slope bias =0.91). Nonlinear models improved fit (R^2=0.71 and 0.75) compared to linear models, but did not improve MEI predictions in the validation experiment when maintenance requirements were assumed constant. Using a system of two equations, one that defined the requirements for energy retention and one that defined the relationship between maintenance and MEI level, further improved fit (R^2=0.81 and R^2=0.88) and MEI predictions in the validation experiment (R^2=0.67 to 0.83 and R^2=0.78 to 0.90). This methodology could consistently predict MEI requirements and mathematically define energy-mass balance relationships in hens in a robust manner.

3.1. Introduction

Feed restriction has become a standard practice in modern broiler breeder operations as a result of sustained selection pressure for broiler growth, which has reduced the ability of commercial

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[1] A version of this paper has been submitted for publication in Poultry Science.

broilers to control their appetite (Bokkers and Koene, 2003). Broiler breeders fed *ad libitum* are unable to regulate their ovulatory cycle and present reproductive disorders that reduce settable egg and chick production compared to restricted hens (Yu et al., 1992; Renema and Robinson, 2004). Therefore, accurate estimation of energy intake requirements is an increasing necessity for successful broiler breeder management.

Linear models of energy balance have been widely used in animal science to estimate energy intake requirements. Respiration calorimetry and comparative slaughter (Spratt et al., 1990a; Rabello et al., 2006) have been the methods of choice to measure heat production and energy retention in bird models. However, the universality of prediction equations derived from NE or ME models using these techniques may be limited: the efficiency of retention is assumed to be a fixed value; the requirements for maintenance, growth and egg production are independently estimated considering a hierarchical order; and these methods present restrictions in the sample size or inability to perform repeated measures over long periods of time. Other methodological issues relative to indirect calculation of heat expenditure or retained energy have been demonstrated (Birkett and de Lange, 2001). Empirical ME models may lead to stronger inferences of energy partitioning than the current analytical methods since larger data sets and multiple sources of variation can be simultaneously analyzed. Furthermore, empirical models should confirm experimental observations from experiments assuming a NE system if the classic theory of energy partitioning (Armsby and Fries, 1915; Blaxter, 1989) holds true.

There has been a dichotomy between accepted theories of energy utilization in animals and the assumptions of equations for estimation of ME intake (MEI) in hens. For instance, feed intake prediction equations (NRC, 1987; Byerly et al., 1980) have often assumed constant energy requirements for energy retention and maintenance. However, the amount of energy partitioned for weight gain or egg production depends on the composition and efficiency of retention (Kielauowski, 1965; Chwalibog, A. 1992). Similarly, the energy partitioned for maintenance depends on the dietary thermogenesis and changes in metabolic rate, both of which are function of the energy intake level (Koh and MacLeod 1999; Richards and Proszkowiec-Weglarz, 2007). The performance of prediction equations of MEI may be improved by accounting for variation in the energy requirements for maintenance due to the energy balance and the heat increment of feeding.

The objective of this paper was to evaluate the use of three different models to estimate MEI in broiler breeder females from empirical data and then to validate the estimated parameters with an independent data set. This study attempted to correct logical flaws of traditional linear models and align model assumptions with accepted theories of energy utilization in animals. The study did not attempt to establish values of MEI requirements, but rather to establish a more dynamic model of energy-mass balance that can be used to improve MEI prediction equations and analyze energy partitioning in experimental and commercial applications.

3.2. Materials and Methods

3.2.1. Stocks and Management

Chicks were weighed on day of hatch and individually identified at housing by bar-coded neck tags (Heartland Animal Health, Fair Play MO 65649). Two floor pens with 300 chicks per pen (23 chicks/m^2) were used during the first 21 d, when birds were randomly split in two additional identical pens until 16 wk with a stocking density of 11 birds/m^2. Photoperiod was 23L:1D for the first 7 d followed by 8L:16D until photostimulation at 23 wk. At this time, day length was increased to 12L:12D, followed by 1 h/wk increments until 15L:9D at 26 wk. Feed was provided *ad libitum* for the first 14 d, then restricted on a daily basis until 4 wk, when a program with 5 d of feed 2 d non-feed days per week was implemented to 16 wk of age. At 16 wk, pullets were randomly assigned to individual cages in blocks of 12 cages to avoid confounding spatial effects. From 16 wk, feed was individually weighed and provided daily. Beginning at 30 wk of age, hens were inseminated weekly using 0.5 ml of pooled semen from 60 similar age Ross males (Aviagen Inc., Huntsville, AL).

Wheat and soy based mash diets (Appendix A) were supplied as follows: starter (2,900 kcal ME, 19% CP, 1.18% lys) from 0 to 3 wk; grower (2,900 kcal ME, 16.7% CP, 1% lys) from 3 to 25 wk; breeder 1 (2,870 kcal ME, 16% CP, 0.72% lys) from 25 to 49 wk; and breeder 2 (2,870 kcal ME, 15.5% CP, 0.70% lys) from 49 to 60 wk.

This research project was carried out in compliance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984) and was approved by the University of Alberta Faculty Animal Policy and Welfare Committee.

3.2.2. Experimental Design

A total of 288 Ross 708 (Aviagen Inc., Huntsville, AL) broiler breeders was selected randomly from a population of 600 birds, housed in individual laying cages at 16 wk, and randomly assigned to one of four feed allocation groups (Figure 3-1; 72 birds per group). Three groups of birds had feed allocated on a group basis with divergent BW targets achieved by 20 wk of age:

Standard, High (Standard x 1.1) and Low (Standard x 0.9). The standard BW target was the recommended by the primary breeder company (Aviagen, 2007). The fourth group had feed allocated on an Individual bird basis following the Standard BW target, to which birds converged at 20 wk. Three models used weekly individual hen BW, egg production, and egg weights data from 20 to 60 wks to estimate MEI. Measures of environmental temperature were additionally used in one of the models.

3.2.3. Data Collection

Body weight data were recorded semi-weekly until 32 wk, and weekly thereafter using an electronic balance (BW-1050, Weltech Agri Data, Charlotte, NC 28213). Average BW [(initial BW + final BW)/2] for each wk was considered for metabolic BW calculations. Average daily gain (ADG) was defined as the difference between initial and final BW for each wk divided by 7 d. Eggs were collected daily at 16:00 h, individually weighed and coded according to shell integrity (normal, membranous, soft shell, broken), shape (normal, deform) and size (normal, double yolk). The incidence of broken eggs was recorded and missing egg weight values were replaced by an estimate of egg weight per hen, fitting a nonlinear regression of egg weight as a function of the hen age (wk) in the form:

$$EggWt = a - b\left(\frac{1}{\ln(age)}\right)$$

Egg mass (EM) was defined as the sum of egg weights per wk divided by 7d. Samples of two eggs per hen were collected every 5 wk from 30 wk to measure yolk and shell weight. Sixteen temperature-humidity loggers with a resolution of 0.1 C and an accuracy of ±0.6 C (Microlog EC650, Fourier Systems, New Albany, IN 45150) were uniformly distributed in the barn. Temperature measurements were recorded every 4 h.

3.2.4. Design of Models

One linear and two mixed nonlinear models were evaluated (Table 3-1). Model *i* was a simple linear model of MEI as a function of metabolic BW, ADG and EM production (Byerly et al., 1980; Schulman et al., 1994). Metabolic BW was defined as $BW^{0.75}$ in this model to allow a direct comparison with other reports. Model *ii* allowed changes in the energy requirements for ADG and EM relative to the amount of each one of these variables by using exponential terms. The ADG values were divided in positive (ADG_P) and negative (ADG_N) as separate variables. Additionally, the scaling parameter of metabolic BW was allowed to fluctuate. Model *iii* included interactions between BW and ADG and EM using a Cobb-Douglas functional form (Griffin et al., 1987), under the hypothesis that requirements for EM and ADG may differ at different BW. The interaction between ADG_N and BW was included in a linear form. In both nonlinear models, a random term $u \sim N(0, Vu)$ associated with the coefficient of metabolic BW by hen was included to separate individual variation linked to maintenance from other sources of random variation. A second step linear regression was used after the nonlinear regressions to evaluate the effect of average MEI on the expected coefficient of maintenance (Table 3-1; $E(a+u)$) of the Low, Standard and High feed allocation groups. In addition, predicted MEI values were estimated by replacing the term $(a+u)$ with the linear equation calculated in the second step regression of models *ii* and *iii*, in which the requirement for maintenance was a function of the observed MEI (Table 3-1).

A pooled set of 11,567 valid weekly observations (ME intake, BW, ADG, and EM) from 20 to 60 wk was used. On weeks where hens presented depressed voluntary daily intake or compromised health status, data were excluded from the analysis. All reported energy values refer to calculated kcal of ME for poultry from a diet formulation software (Creative Formulation Concepts, Annapolis, MD). Variability in ME among hens was assumed to be part of the error term.

3.2.5. Statistical Analysis

Differences among feed allocation groups and LS-mean estimates of variables included in the models were evaluated using the Mixed Procedure of SAS (SAS Institute, Cary, NC) with a significance level of $P<0.05$. LS-mean separation was done through multiple t-tests. Hen was considered a random effect within feed allocation group. Pearson's correlation coefficients (the Corr Procedure, SAS Institute, Cary, NC) described relationships among dependent and independent variables.

The multiple linear regression was performed using the Mixed procedure of SAS (SAS Institute, Cary, NC), which used restricted maximum likelihood to fit the data. The assumed variance-covariance matrix was Compound-Symmetry with hen as subject. Nonlinear regressions were performed using the Nlmixed Procedure of SAS (SAS Institute, Cary, NC), which used maximum likelihood and allowed specifying a distribution of random effects, which were clustered by subject. All models had a zero intercept because energy intake requirements at zero metabolic BW and energy retention were assumed to be null. Systematic bias in model predictions was determined by evaluating the intercept and slope of regressing observed (y-variate) versus predicted (x-variate) MEI values as reported by Guiroy et al. (2001). The Bayesian Information Criterion (BIC) was used to evaluate the fit of the models; lower values mean a better fit. Mean squared errors (MSE) corrected by the overall bias of the model and R-squared values were also reported as fit statistics.

3.2.6. Validation Experiment

Data from an independent experiment (Robinson et al., 2007) carried out in the same facilities and with the same environmental conditions as the current study was used to evaluate the developed prediction equations. This data set included information from 288 hens of 3 strains (Hubbard Hi-Y, Ross 508, and Ross 708), which were randomly assigned to 4 BW curves diverging at 4 wk and converging at 32 wk of age (Low, Standard, Moderate, High). At 12 wk of age, the Low, Moderate and High BW curves were 75%, 150% and 200% of the Standard curve, respectively (Renema et al., 2007). Equations were validated with individual hen data from 18 to 58 wk of age within each interaction. R-squared values were reported as a measure of fit.

3.3. Results and Discussion

3.3.1. Feed Allocation Groups and Independent Variables

The BW profiles of Low and High feed allocation groups were 90% and 111% of the Standard profile (Table 3-2). The Individual BW profile was not significantly different than the Standard profile. The same was true for ADG, showing a proportional trend relative to BW. Low hens produced less EM than Individual, Standard and High hens, suggesting that egg production was limited by MEI for this group. The experimental design allowed an increased variability in the nutrient partitioning response among birds. A positive correlation between daily MEI and average BW (r=0.60; Table 3-3) was evident. However, ADG and EM were negatively correlated both among birds and among bird x wk observations (r=-0.40 and r=-0.65) and the correlation between ADG and ME intake was low (r=-0.08), which allowed modeling of more complex relationships among independent variables.

3.3.2. Model Regressions

Parameter estimates of model *i* are shown in Table 3-4. The variability of temperature (SD=1.12 C) was enough to be included in this model, but created instability in the more complex models. Additionally, no spatial differences in temperature were considered because the standard deviation among locations in the barn (0.44 C) was lower than the measuring error of the equipment (0.60 C at 21.5 C). Even with this low variability, model i showed a negative interaction between $BW^{0.75}$ and temperature (Table 3-4; -0.36 kcal/$kg^{0.75}$ x C) that had a lower absolute value than the linear relationships reported by Sakomura et al. (2003) in broiler breeder pullets (-1.88 to -1.94 kcal/$kg^{0.75}$ x C). The wider range of temperatures (15, 22 and 30 C) used by Sakomura et al., (2003) compared to the narrow range of temperatures used in the current study likely explain much of the difference between studies.

The coefficient associated with maintenance in model ***i*** (Table 3-4) was 112.0 kcal/kg, which corresponded to 104.4 kcal/kg when corrected by temperature at 21 C (112.0 kcal - 0.36 kcal x 21 C). This value was below the maintenance MEI requirement of 112.8 kcal/$kg^{0.75}$ reported by Rabello et al. (2006) for broiler breeders at 21 C. However, a lower coefficient was expected in the current study because Rabello et al. (2006) used floor pens instead of individual cages. Spratt et al. (1990a) and Johnson and Farrell (1983) reported even lower maintenance requirements (87.7 and 87.2 kcal/$kg^{0.75}$) for broiler breeders in metabolic cages, calculated as heat production at zero energy retention. The leaner strain used in this study was expected to have a greater maintenance requirement. Nonetheless, differences in the methodology, type of diet utilized, sample size, animal behaviour and the length of the experiments may have contributed to the discrepancy. The level of feed restriction level used may create slope changes in linear models; Johnson and Farrell (1983) reported a maintenance requirement of 101.8 kcal/$kg^{0.75}$ (increased by 14.6 kcal) when they added data from starvation heat production in the regressions.

The range of ME requirements for ADG reported in the literature for adult hens varies greatly possibly due differences in composition and efficiency of energy retention, although other methodological issues may be also responsible in the case of experiments in which egg production was halted through dietary or pharmacological means. Reports of MEI requirements for ADG in hens include Leeson et al. (1973), 4.80 kcal/g; Balnave et al. (1978), 2.06 kcal/g; Byerly et al. (1980), 8.38 kcal/g; and Rabello et al. (2006), 7.61 kcal/g. Sakomura (2004) reported age-related ADG requirements ranging from 2.83 to 7.62 kcal/g over the life of a broiler breeder hen. The coefficient of ADG in model *i* (3.36 kcal/g) was in this range, but it should be only considered as a mean slope of ADG since both composition and efficiency of energy retention may vary during the production cycle.

The coefficient of EM production in model ***i*** was 2.10 kcal/g EM, which was in agreement with reported values for laying and broiler breeder hens. Among other reports of MEI requirements for EM production are Leeson and Lewis (1973), 2.77 kcal/g; Byerly et al. (1980), 2.46 kcal/g; Chwalibog (1995), 2.00 to 2.98 kcal/g; and Rabello et al. (2006), 2.40 kcal/g. Sakomura (2004), based on the range of reported values for gross energy of eggs and efficiency of retention, suggested that it may range from 1.92 to 3.15 kcal/g of EM. Although reports of requirements for EM production are more consistent than those for ADG, their variability suggests that efficiency of energy retention in the eggs may differ due to genotype and physiologic state.

Tables 3-5 and 3-6 show the parameter estimates of models ***ii*** and ***iii*** respectively. In contrast with linear models where the slope was constant, requirements were expressed as a function in nonlinear models. The first derivative of the function estimated the change in the total requirement in response to a change in ADG_P, ADG_N or EM. The integral of that function estimated the area under the curve and represents the total ME requirement associated with each of those variables. That integral divided by ADG_P, ADG_N or EM estimated the average requirement. In all functions, the second derivative defined their curvature.

In model ***ii*** (Table 3-5), parameters were consistent with the assumption that requirements would change at different retention levels. The estimated requirement for ADG_P evaluated at the mean ADG_P (8.30 g/d) was 2.79 kcal/g, but the expected requirement increased with greater ADG_P as a greater deposition of fat was expected (Figure 3-2A). This relationship was confirmed by the second derivative, which had a positive value; therefore, the function was convex with respect to the origin (deflected upwards). Interestingly, the behaviour of the expected requirement of ADG_N showed a different relationship than that of positive gains. The energy yielding effect was greater at lower values of weight loss (5.77 kcal/g if ADG_N=1g) and it decreased at higher absolute ADG_N values (Figure 3-2A). Given the range in degree of restriction used in this study, this relationship was anticipated under the assumption that lipids constitute a primary source of energy when intake is close to equilibrium but oxidation of labile proteins increases when energy balance is more negative until a new equilibrium is reached (Hornick et al., 2000).

The expected requirement for EM was 2.37 kcal/g at the mean EM (43.4 g/d), but the requirement for EM was convex (deflected upwards; Figure 3-2B). This behaviour agreed with reports of increasing gross energy in the eggs during the first stages of production when EM production is increasing (Chwalibog, 1992). This observation may have been associated with a greater deposition of yolk, since the Pearson's coefficient between percentage of yolk in the eggs and EM production was high ($r=0.85$; $P<0.001$) in the current experiment.

Model ***iii*** (Table 3-6) accounted for the interactions of the ME requirements for ADG_P and EM with respect to BW using a Cobb-Douglas functional form. This type of function is widely used in production economics as it allows direct calculation of cross elasticities (Chambers, 1988). In the current application, the elasticity of the ME requirement for both ADG and EM with respect to BW corresponded to the exponent of BW in each of these terms. These elasticities estimated the percentage of change in the ME requirements in response to a 1% change in BW. The requirement of ADG_P evaluated at the mean BW and ADG_P values was 2.94 kcal/g, but the term cBW^dADG^e added flexibility by accounting for both an allometric relationship of the main chemical components of the carcass and the immediate metabolic state of the birds. Some of the relationships of chemical allometry in broilers have been described by Gous et al. (1999), who reported allometric exponents greater than one (1.23 to 1.24) for lipids and exponents lower than one (0.90 to 0.91) for water content with respect to total protein in broiler females. If these relationships are related to the expected changes in the energetic costs of ADG with respect to BW, an increment in the ME requirement for gain is expected at greater BW. Consistently, a change in 1% of BW caused a positive change of 0.60% in the requirement for ADG_P (Figure 3-3A).

The expected requirement for EM of model *iii* was 2.02 kcal/g at the mean EM and BW, which was in the range of reported requirement values. However, an increment in 1% in BW decreased the EM requirement by 2.07% (Figure 3-3B). Greater BW may reduce the requirement as a result of a greater efficiency of energy retention in the eggs, since a greater proportion of liver lipids may be available for deposition in the growing follicles. However, there were infeasible areas in the surface described in Figure 3-3B where BW was limiting for egg production. For instance, the lowest BW at which a hen produced eggs during the experiment was 2.3 kg. Other authors have suggested a BW threshold for egg production in broiler breeders, under which the neuro-endocrine system was not responsive to photostimulation (Melnychuk et al., 2004).

The scaling exponents of BW in models *ii* and *iii* were 0.47 and 0.54 respectively. In an extensive review of the variation in the scaling exponent of metabolic rate in animals, Glazier (2005) concluded that the accepted 0.75 power scaling law is universal neither within nor among species. It was argued that the maintenance conditions are not strictly met in organisms that are growing, reproducing or in constant activity. In laying hens, Luiting and Urff (1991) reported a reduction of the metabolic BW exponent with age during the production phase, ranging from 0.80 to 0.60, while Bordas and Mérat (1981) reported an exponent of 0.50.

Luiting (1990) concluded that the energy requirements for maintenance are the main cause of individual variation in the use of energy in hens. Based on this assumption, the random term $E(a+u)$ aimed to separate individual variation in the maintenance requirements from other variables affecting energetic efficiency. However, energy intake level affects this coefficient of maintenance in two different ways: 1) through the heat increment of feeding (Spratt et al., 1990b;

Koh and MacLeod, 1999), which is considered part of the maintenance coefficient in ME systems (Birkett and de Lange, 2001); and 2) through the self regulation of the metabolic rate, by which birds can modify their energy expenditure and maintain physiologic homeostasis (Richards and Proszkowiec-Weglarz, 2007). Thus, the assumed genetically identical High, Standard, and Low feed allocation groups constituted an appropriate model to separate the energy intake effect on the maintenance requirement through a second step regression. The relationships between *E(a+u)* and MEI for models *ii* and *iii* are shown in Figure 3-4. Model *ii* estimated that $E(a+u)_{iv}$ (kcal/$BW^{0.47}$) increased by 0.19 kcal/kcal of MEI whereas model *iii* estimated that $E(a+u)_{v}$ (kcal/$BW^{0.54}$) increased by 0.34 kcal/kcal of MEI. However, *E(a+u)* showed a stronger relationship with MEI in model *iii* (r^2=0.83) than model *ii* (r^2=0.52) as it accounted for the effect of BW on the requirements for ADG and EM. This relationship is assumed to be diet specific; inter-diet comparisons would require adjustments based on heat increment variables as those proposed by Emmans (1994) in the concept of effective energy.

3.3.3. Bias and Fit Statistics

In the regression of observed versus predicted MEI values, deviations from a slope of one and a zero intercept indicate systematic bias of the model (Table 3-7). All intercepts were different from zero. However, the intercept of model *i* was different than the others, which did not differ. Similarly, all slopes significantly differed from one, but model *i* showed a lower slope than the other models and a greater deviation from one. These results indicate that model *i* overestimated MEI at lower levels of intake and underestimated it at high levels. In contrast, models *ii* and *iii* reduced that bias in a similar fashion although a 2% slope bias in the MEI estimation was still present. This may be explained by a portion of the energy intake effect that is independent of changes metabolic BW.

Both nonlinear models (model *ii*, BIC=114,590; model *iii*, BIC=113,217), although more complex, had a better fit than a simple linear model (BIC=115,734; Table 3-8) using the same explanatory variables. Of these, model *iii* demonstrated the greatest reduction in the sum of squares (MSE=936) with respect to model *i* (MSE=1414). When the estimated coefficients of maintenance from models *ii* and *iii* were adjusted by the effect of energy intake level on the coefficient of maintenance, there was an improvement in the MEI prediction with an R^2=0.81 and 0.88, and MSE=720 and 431 kcal ME, respectively. In these two estimations, observed MEI values were used to calculate the maintenance requirement as they where experimentally controlled. In commercial production, predictions of MEI requirements using models ***ii*** and ***iii*** are possible by solving a system of two equations and two variables (MEI and maintenance requirement). For model *iii*, this system (Table 3-1) can be solved as follows:

$$MEI = \frac{iBW^{b} + cBW^{d}ADG_{P}^{e} + fBWADG_{N} + gBW^{h}EM^{i}}{1 - jBW^{b}}$$

3.3.4. Validation Experiment

The validity of the prediction equations (Table 3-1) that were evaluated in Table 3-8 was tested using data from an independent study. This study used a large range of feed intake levels during early production, when the High and Moderate BW curves were heavily feed restricted (Robinson et al., 2007). In general, the equation from model *iii* had the best fit at the Low and Standard BW curves whereas model *i* had the best fit at the Moderate and High curves. When a fixed coefficient of maintenance (141.0 kcal/kg$^{0.54}$) was assumed in the equation from model *iii*, the maintenance requirement may have been overestimated, particularly at low levels of feed intake. However, when the coefficient of maintenance was a function of the energy intake level, model *iii* exhibited consistent estimations across strains and BW curves (R^2=0.78 to 0.90), which underscores the robustness of the model. Since there was theoretical support for this approach and the regression methods were considered appropriate, improvements of fit were not considered a tautological artifact.

The main advantage of using mixed nonlinear models was the ability to isolate the relationship between maintenance requirements and the energy intake level, which mutually affect each other in a dynamic fashion to achieve homeostasis. Based on this relationship, a system of two equations, one that defines the requirements for energy retention and one that defines the relationship between maintenance and energy intake level and/or energy balance, appears to be a consistent method to mathematically define energy-mass balance relationships in birds. Through this approach, the MEI requirements of broiler breeders were accurately estimated by using the same explanatory variables as simple linear models in a more flexible manner. Consideration of activity and temperature effects should be made when applying these models for MEI estimation in commercial stocks.

3.4. References

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Table 3-1. Functional specifications of evaluated models of energy-mass balance

Model	Function Specification[1]
i	$MEI_d = BW^{0.75}(a - bT) + cADG + dEM + \varepsilon$
ii[2]	$MEI_d = (a+u)BW^b + cADG_P^d + eADG_N^f + gEM^h + \varepsilon$;
	$u \sim N(0,V_u)$, $MEI_d \sim N(\mu,V)$
	$E(a+u) = i + jMEI_a$
iii[2,3]	$MEI_d = (a+u)BW^b + cBW^d ADG_P^e + fBWADG_N + gBW^h EM^i + \varepsilon$;
	$u \sim N(0,V_u)$, $MEI_d \sim N(\mu,V)$
	$E(a+u) = j + kMEI_a$
ii adjusted maintenance[4]	$MEI = (i + jMEI_d)BW^b + cADG_P^d + eADG_N^f + gEM^h$
iii adjusted maintenance[4]	$MEI = (j + kMEI_d)BW^b + cBW^d ADG_P^e + fBWADG_N + gBW^h EM^i$

MEI_d= Daily ME Intake (kcal/day)
MEI_a= Average ME Intake (kcal/day) from 20 to 60 wk
BW=Body Weight (kg)
T=Temperature (C)
ADG=Average Daily Gain (g/d)
ADG_P=Positive ADG (g/d)
ADG_N=Negative ADG (-g/d)
EM=Egg Mass (g/d)
u=Hen related random term
ε=Residual error
[1] Estimated parameters are lower case letters
[2] The error term *u* was associated with each hen; variance parameters V and V_u were estimated in the regressions. Linear regressions were performed in a second step to relate the estimated maintenance requirement [*E(a+u)*] to MEI_a of Low, Standard and High hens
[3] Interactions between BW and ADG_P or EM had a Cobb Douglas functional form specification
[4] Based on the parameters estimated in models *ii* and *iii*, the coefficient associated with BW^b was expressed as a function of the observed MEI

Table 3-2. Body weights, average daily gain and egg mass of hens from Individual, Low, Standard and High feed allocation groups from 20 to 60 wk

Effect	BW[1]	ADG[2]	EM[3]	Non-zero EM[4]
	-------g-------	-----------------------g/d-----------------------		
Feed allocation group[5]				
Individual	3,227.7[b]	6.4[b]	35.6[a]	43.5[a]
Low	2,888.1[c]	5.9[c]	32.8[b]	41.3[b]
Standard	3,216.9[b]	6.3[b]	35.8[a]	44.1[a]
High	3,556.6[a]	7.1[a]	37.1[a]	44.5[a]
SEM	15.6	0.1	0.5	0.6
Source of variation	--------------------------- Probability ---------------------------			
Feed allocation	<0.0001	<0.0001	<0.0001	0.0002

[1] Body weight (kg)
[2] Average daily gain (g/d)
[3] Egg mass (g/d)
[4] Values of zero egg mass were excluded
[5] Standard, High (Standard+10%), and Low (Standard-10%) differed in their BW target. Individual followed the standard BW target and had feed allocated on an individual bird basis
[a,c] LS-means within a column with no common superscript differ (P<0.05).

Table 3-3. Pearson's correlation matrix of the main variables included in the models

Variable	Daily ME intake	Average BW	Average daily gain	Egg mass production
	------- Pearson's coefficient / (Probability)[1] -------			
Daily ME intake	1.00	0.60	-0.08	0.60
		(<0.001)	(<0.001)	(<0.001)
Average BW	0.75	1.00	0.49	0.66
	(<0.001)		(<0.001)	(<0.001)
Average daily gain	0.30	0.25	1.00	-0.65
	(<0.001)	(<0.001)		(<0.001)
Egg mass production	0.42	0.22	-0.40	1.00
	(<0.001)	(<0.001)	(<0.001)	

[1] Correlations above the main diagonal correspond to bird x wk observations whereas correlations below the diagonal correspond to mean bird observations from 20 to 60 wk of age

Table 3-4. Model *i*. Regression coefficients of ME intake from a basic linear model including metabolic BW, temperature, average daily gain and egg mass production. R^2=0.64; BIC=115,734

Parameter[1]	Estimate	Standard error	t-value	P>t
$BW^{0.75}$	111.95	2.696	41.53	<0.0001
$BW^{0.75}$x $T^{(2)}$	-0.36	0.120	-3.00	0.0026
ADG	3.36	0.037	91.98	<0.0001
EM	2.10	0.027	77.60	<0.0001
Estimated equation	$MEI_d = BW^{0.75}(111.95 - 0.36T) + 3.36ADG + 2.10EM$			

[1] $BW^{0.75}$=Metabolic BW; T=Temperature (C); ADG=Average Daily Gain (g/d); EM=Egg Mass (g/d)
[2] Mean temperature was 21.5°C with a standard deviation of 1.12°C during the experiment

Table 3-5. Model *ii*. Regression coefficients of ME intake from a nonlinear model including exponential terms associated with ADG and EM; and average ME requirements for ADG_P, ADG_N, and EM. R^2=0.71; BIC= 114,590

Parameter	Estimate	Standard error	t-value	P>t
a	142.58	2.152	66.25	<0.0001
b	0.47	0.012	37.60	<0.0001
c	2.03	0.202	10.05	<0.0001
d	1.15	0.027	41.99	<0.0001
e	-5.77	0.914	6.32	<0.0001
f	0.60	0.057	10.38	<0.0001
g	1.51	0.170	8.90	<0.0001
h	1.12	0.027	41.89	<0.0001
V	1,109.97	14.805	74.97	<0.0001
V_u	71.55	7.844	9.12	<0.0001

Evaluated function[1] $MEI_d = (a+u)BW^b + cADG_P^d + eADG_N^f + gEM^h;$
$u \sim N(0, V_u)$

Average requirement

ADG_P $\frac{\partial MEI_d}{\partial ADG_P} = 2.33ADG_P^{0.15}$; then $\frac{\int 2.33ADG_P^{0.15}}{ADG_P} = 2.03ADG_P^{0.15}$

ADG_N $\frac{\partial MEI_d}{\partial ADG_N} = -3.46ADG_N^{-0.4}$; then $\frac{\int -3.46ADG_N^{-0.4}}{ADG_N} = -5.77ADG_N^{-0.4}$

EM $\frac{\partial MEI_d}{\partial EM} = 1.69EM^{0.12}$; then $\frac{\int 1.69EM^{0.12}}{EM} = 1.51EM^{0.12}$

[1] BW^b=Metabolic BW; T=Temperature (C); ADG_P=Positive Average Daily Gain (g/d); ADG_N=Negative Average Daily Gain (g/d);EM=Egg Mass (g/d)

Table 3-6. Model ***iii***. Regression coefficients of ME intake from a nonlinear model including interactions of ADG_P and EM with BW using a Cobb-Douglas functional form; average ME requirements for ADG_P, ADG_N and EM; and elasticities of ADG_P, and EM with respect to BW. R^2=0.75; BIC= 113,217

Parameter	Estimate	Standard error	t-value	P>t
a	141.00	2.533	55.67	<0.0001
b	0.54	0.014	37.69	<0.0001
c	1.18	0.144	8.21	<0.0001
d	0.60	0.059	10.26	<0.0001
e	1.10	0.025	44.48	<0.0001
f	-0.46	0.030	15.56	<0.0001
g	4.99	0.724	6.89	<0.0001
h	-2.07	0.074	-28.02	<0.0001
i	1.40	0.036	39.30	<0.0001
V	1,110.00	17.472	63.53	<0.0001
Vu	72.00	5.741	12.54	<0.0001

Evaluated function[1] $MEI_d = (a+u)BW^b + cBW^d ADG_P^e + fBWADG_N + gBW^h EM^i$; $u \sim N(0, V_u)$

Average requirement

ADG_P $$\frac{\partial MEI_d}{\partial ADG_P} = 1.30BW^{0.60}ADG_P^{0.10}; \quad \frac{\int 1.30BW^{0.60}ADG_P^{0.10}}{ADG_P} = 1.18BW^{0.60}ADG_P^{0.10}$$

ADG_N[(2)] $$\frac{\partial MEI_d}{\partial ADG_N} = -0.46BW$$

EM $$\frac{\partial MEI_d}{\partial EM} = 6.29BW^{-2.07}EM^{0.40}; \quad \frac{\int 6.29BW^{-2.07}EM^{0.40}}{EM} = 4.99BW^{-2.07}EM^{0.40}$$

Cross elasticities with respect to BW[(3)]

ADG_P $$e_{BW}^{ADG_P} = \frac{\partial\left(\frac{\partial MEI_d}{\partial ADG_P}\right)}{\partial BW} \cdot \frac{BW}{\left(\frac{\partial MEI_d}{\partial ADG_P}\right)} = 0.60$$

EM $$e_{BW}^{EM} = \frac{\partial\left(\frac{\partial MEI_d}{\partial EM}\right)}{\partial BW} \cdot \frac{BW}{\left(\frac{\partial MEI_d}{\partial EM}\right)} = -2.07$$

[1] BW^b=Metabolic BW; T=Temperature (C); ADG_P=Positive Average Daily Gain (g/d); ADG_N=Negative Average Daily Gain (g/d);EM=Egg Mass (g/d)

[2] A linear term was used because of a low number of negative gains in the data set

[3] Percentage change in the requirement by a 1% change in BW

Table 3-7. Linear regression of observed (y-variate) vs. predicted (x-variate) daily ME intake

Model	Parameter	Estimate	Standard Error	P>t
Model ***i***	Intercept	35.33	2.26	<0.0001
	Slope	0.91	0.006	<0.0001
Model ***ii***	Intercept	-6.63	2.15	<0.0001
	Slope	1.02	0.006	<0.0001
Model ***iii***	Intercept	-8.83	1.95	<0.0001
	Slope	1.02	0.006	<0.0001

Table 3-8. Fit statistics of the evaluated models

Model	Type	BIC[(1)]	MSE[(2)]	R^2
i	Linear	115,734	1,414	0.64
ii	Nonlinear	114,590	1,084	0.71
iii	Nonlinear	113,217	936	0.75
ii – adjusted maintenance [(3)]	Nonlinear	---	720	0.81
iii – adjusted maintenance [(3)]	Nonlinear	---	431	0.88

[1] Bayesian Information Criterion; smaller values mean a better fit of the model
[2] Mean Square Error corrected by the overall bias of the model
[3] The coefficient associated with metabolic BW was a function of MEI

Table 3-9. R-squared values of predicted versus observed MEI from a validation experiment with 3 strains and 4 BW curves, using the prediction equations developed in the current study

Treatment[1]						
Strain	BW curve	Model *i*	Model *ii*	Model *iii*	Model *ii* adjusted maintenance	Model *iii* adjusted maintenance
Hubbard Hi-Y	Low	0.75	0.70	0.75	0.82	0.90
	Standard	0.53	0.49	0.56	0.67	0.82
	Moderate	0.60	0.61	0.54	0.77	0.84
	High	0.57	0.56	0.43	0.75	0.82
Ross 508	Low	0.68	0.69	0.71	0.81	0.88
	Standard	0.69	0.68	0.70	0.79	0.87
	Moderate	0.57	0.56	0.46	0.71	0.78
	High	0.55	0.52	0.39	0.72	0.80
Ross 708	Low	0.68	0.71	0.75	0.83	0.90
	Standard	0.56	0.59	0.62	0.73	0.84
	Moderate	0.60	0.59	0.50	0.72	0.78
	High	0.48	0.46	0.37	0.67	0.78

[1] Prediction equations of individual ME intake were validated within treatment interactions from a previous independent experiment (Robinson et al., 2007) performed at the same facilities and environmental conditions as the current study. The data set consisted of repeated measures of 288 hens from 19 to 58 wk of age

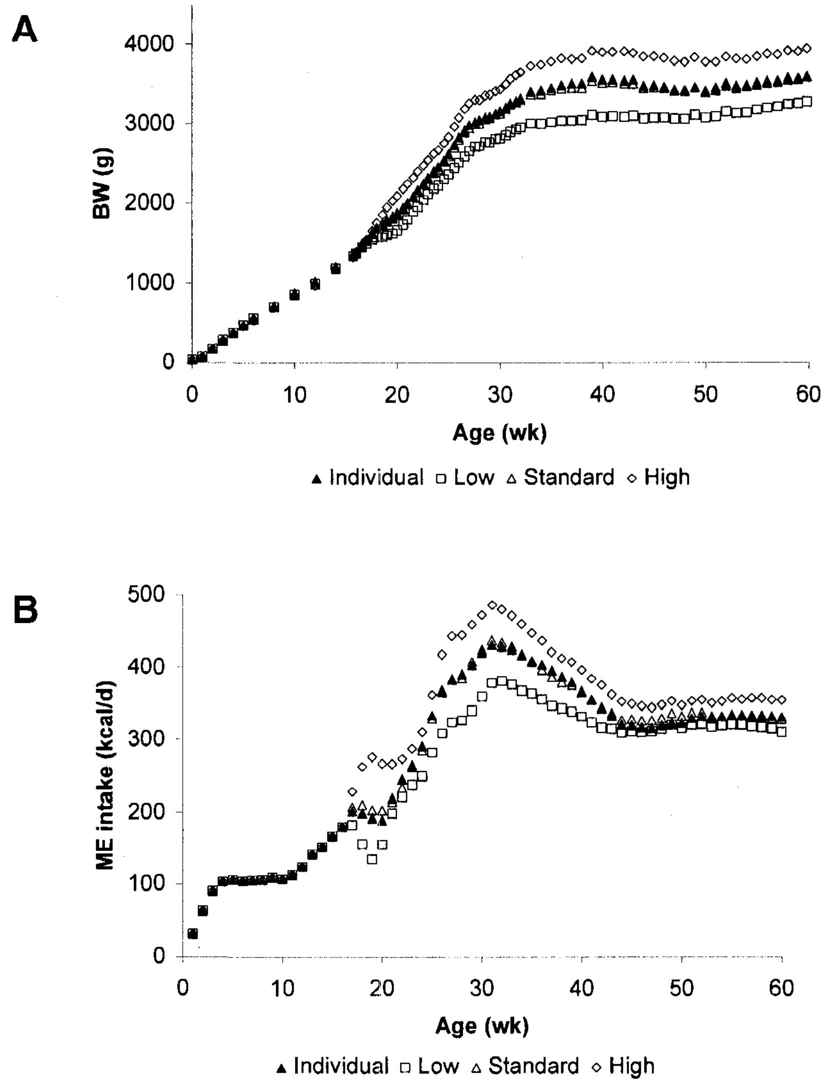


Figure 3-1. Broiler breeder body weight profiles (A) and average daily ME intake (B) of feed allocation groups between 0 and 60 wk of age.

A

B

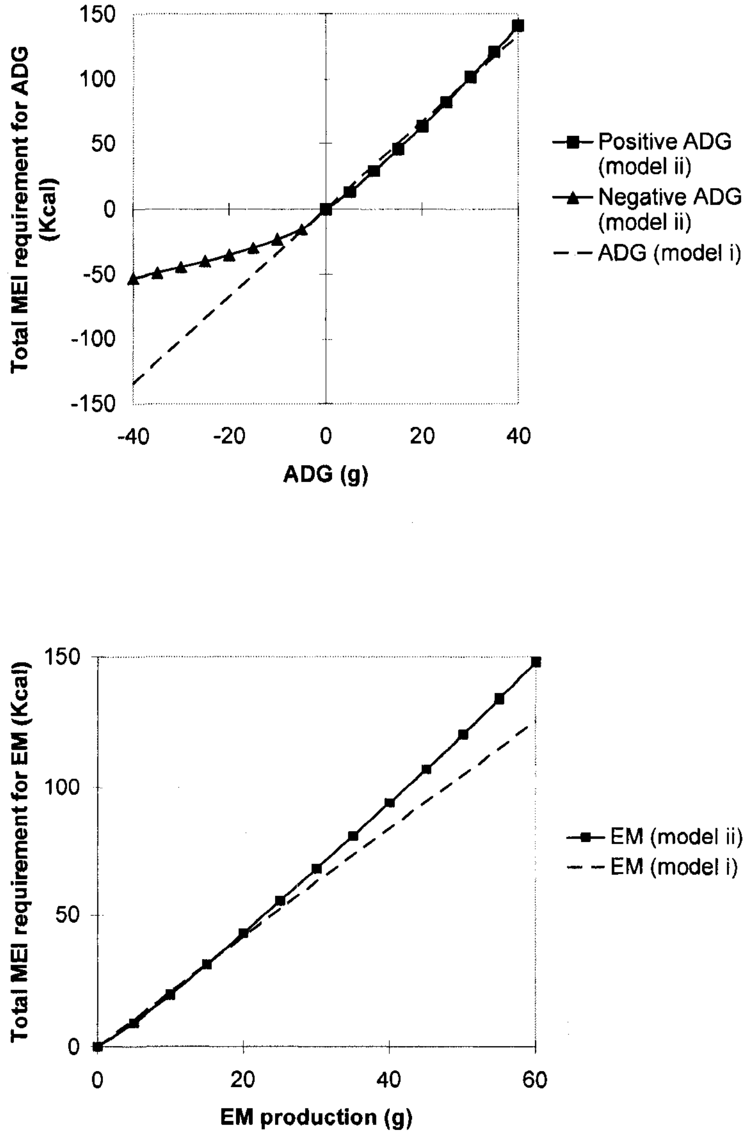
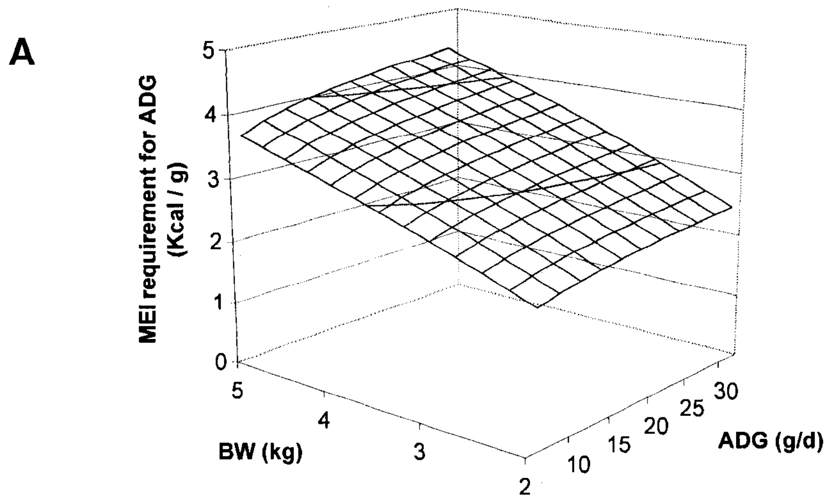


Figure 3-2. Estimated total MEI requirements for average daily gain (ADG) as a function of the ADG level (A) and for egg mass (EM) as a function of daily EM production (B) as derived from model *i* compared to those of model *ii*.



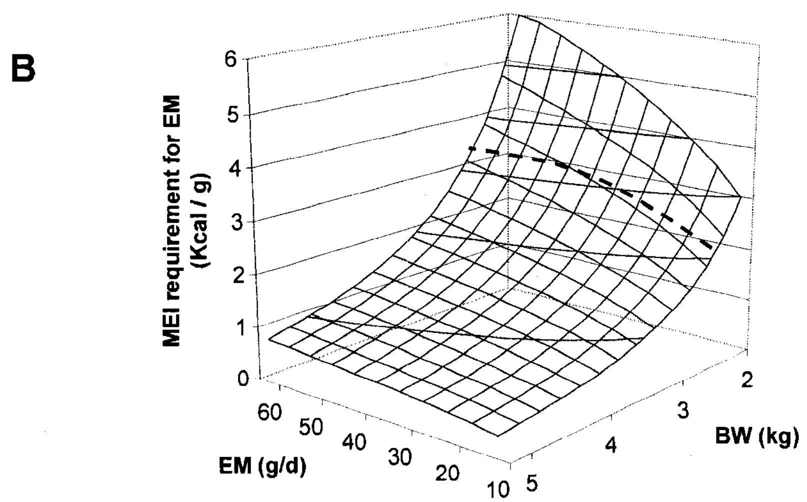


Figure 3-3. Estimated average MEI requirement for average daily gain (ADG) as a function of BW and ADG level (A) and average MEI requirement for egg mass (EM) as a function of BW and EM production (B). The surface above the broken line (3B) was outside the range of values in the regressions and may not be feasible.

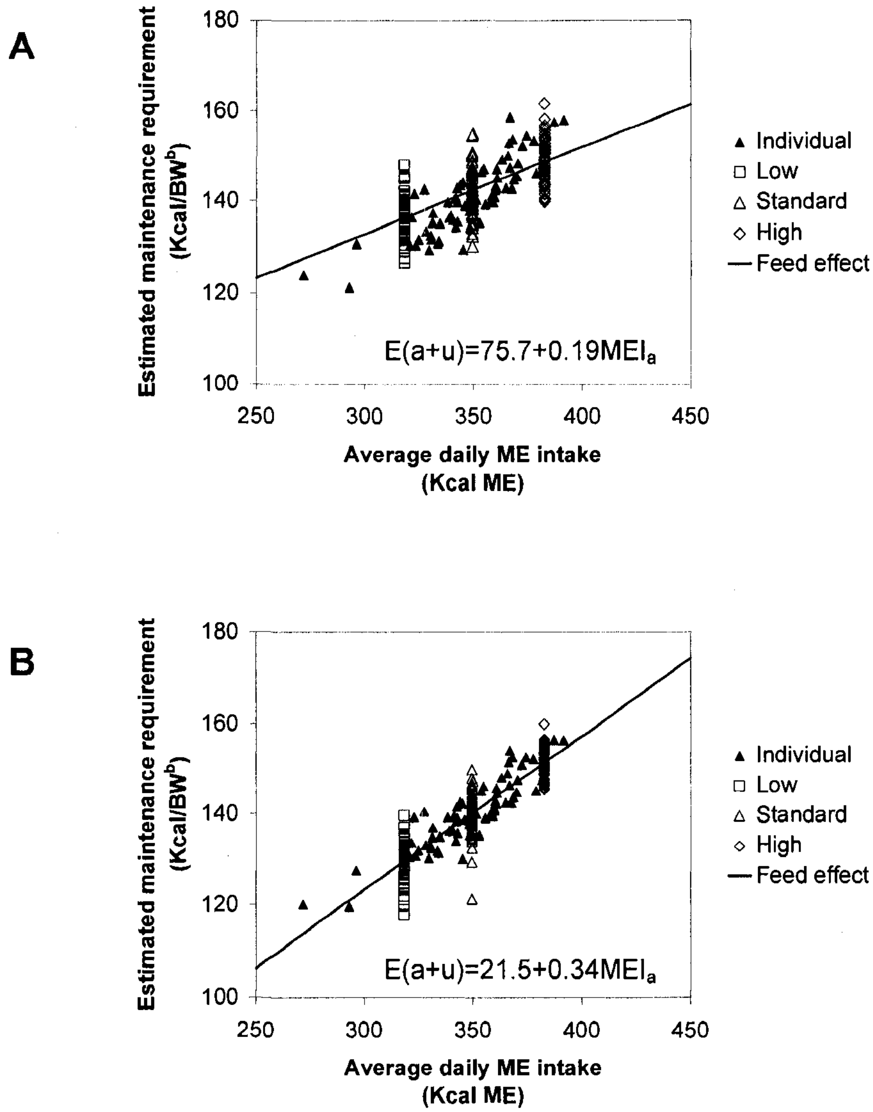


Figure 3-4. Estimates of the random terms associated with hen [E(a+u)] relative to average ME intake of feed allocation groups in model *ii* (r^2=0.52) (A) and model *iii* (r^2=0.83) (B).

Chapter 4. Characterization of Energetic Efficiency in Adult Broiler Breeder Hens[1]

Abstract. This trial characterized residual feed intake (RFI) and residual maintenance ME requirement (RME_m) as measures of energetic efficiency in broiler breeder hens. The RFI was defined as the difference between observed and expected ME intake and the RME_m as the difference between observed and expected maintenance requirement. A total of 600 Ross-708 1 d old pullets were placed in floor pens. At 16 wk, hens were caged and randomly assigned to one of two feed allocation treatments (72 birds each). A control treatment had feed allocated on a Group basis following the standard BW target. A second treatment had feed allocated on an Individual bird basis and followed the same BW target as Group. Sexual maturity age, egg and chick production, and several feed conversion ratios were correlated to standardized efficiency indices of RFI (SRFI) and RME_m ($SRME_m$) in each treatment. Greater SRFI and $SRME_m$ values described a greater energetic efficiency.

RFI was more variable in Individual than Group hens (P<0.001). The variability of RME_m did not differ between treatments (P=0.14). The SRFI was positively correlated to egg production in the Group hens (r=0.31), but negatively correlated in Individual hens (r=-0.40), and was correlated to feed conversion per chick only in the Group based feed allocation (r=-0.44). The $SRME_m$ correlated strongly to egg production (r=0.64), chick production (r=0.64) and feed conversion per chick (r=-0.59) in both feed allocation treatments. Feed intake confounded the RFI calculation, which limits the value of RFI as a selection criterion in meat-producing animals. The independence of RME_m from feed intake is desirable for energetic efficiency assessment in selection programs as consistent values can be obtained across different management schemes. Hens with lower maintenance requirements (greater RME_m efficiency) partitioned more energy towards reproduction than high maintenance hens. The RME_m methodology provided an unbiased estimate of energetic efficiency by adjusting the maintenance requirement for the effect of dietary thermogenesis.

4.1. Introduction

Feed efficiency has been defined as an input-output ratio in broilers (Skinner-Noble and Teeter, 2004; Lassiter et al., 2006), layers (Flock, 1998), and broiler breeders (de Beer and Coon, 2007).

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[1] A version of this paper has been submitted for publication in Poultry Science.

However, simple input-output ratios (feed intake per egg or chick) are affected by management. Therefore, breeder companies wishing to identify the genetically heritable fraction of feed efficiency require more accurate efficiency measures. Residual feed intake (RFI) is defined as the portion of ME intake not explained by metabolic BW, average daily gain (ADG), and egg mass (EM) production. RFI has been used to select indirectly for feed efficiency in laying hens (Flock, 1998; Van Eerden et al., 2004). Divergent selection for RFI has allowed a complete characterization of that measurement in laying hens as well as some of its mechanisms and correlated responses (Bordas and Mérat, 1981; Luiting and Urff, 1991a).

Selection for RFI in laying hens is possible as this trait presents high phenotypic variability (Luiting, 1990) and intermediate heritability (h^2=0.46, Schulman et al, 1994; h^2=0.42 to 0.62, Luiting and Urff, 1991b). In broiler breeders, hen energetic efficiency has not been widely used as a selection trait because growth rate, yield and feed conversion are the primary focus of broiler selection programs (Pollock, 1999). However, heavy selection for those traits has intensified the need to manage female parent stocks to achieve an acceptable reproductive performance (Siegel and Wolford, 2003). Selection for energetic efficiency will increase broiler supply chain productivity if reproductive performance, growth, and yield are not reduced.

Maintenance requirement has been proposed to compare the energetic efficiency of cattle (DiCostanzo et al., 1991). This approach may be particularly valuable for broiler breeder and laying hens where the maintenance requirement is the main cause of variation in energetic efficiency (Luiting, 1990). A nonlinear model to estimate ME intake in broiler breeder hens was proposed (Chapter 3; Table 3-6; Figure 3-4B). Such model estimated a hen based coefficient of the maintenance requirement. From that work, the concept of residual maintenance ME requirement (RME_m) was developed. RME_m is the residual of the linear relationship between maintenance energy requirement and energy intake. RME_m aims to measure energetic efficiency without being confounded by feed intake. It was hypothesized that RME_m would provide a more consistent estimation of individual energetic efficiency across different management schemes than RFI.

The objectives of the current study were 1) to compare RFI and RME_m as measures of energetic efficiency in broiler breeder hens, 2) to characterize the relationship between feed intake and energetic efficiency, and 3) to correlate RFI and RME_m with reproductive performance and several feed conversion ratios.

4.2. Materials and Methods

4.2.1. Stocks and Management

A total of 600 Ross-708 (Aviagen Inc., Huntsville, AL) 1 d old female chicks were identified by bar-coded neck tags (Heartland Animal Health, Fair Play MO 65649) and reared in floor pens in a light-tight facility (11 pullets/m^2) until 16 wk. Feed was provided *ad libitum* for the first 14 d, and on a daily basis to 4 wk. A 3/1/2/1 skip a day program was implemented to 16 wk. At that age, pullets were moved to laying cages and individually fed daily. Temperature was set at 21 C. Photoperiod was 23L:1D for the first 7 d and 8L:16D to 23 wk of age. Birds were photostimulated at 23 wk with an increase to 12L:12D followed by weekly 1 h increases until 15L:9D at 26 wk. Beginning at 30 wk of age, hens were inseminated weekly using 0.5 ml of pooled semen collected from 60 caged Ross (Aviagen Inc., Huntsville, AL) roosters. Eggs were stored at 16 C and set for incubation weekly in a commercial facility using the same machine and control set up. Average storage time of hatching eggs prior to incubation was 4.5 d. The trial was completed when breeders reached 60 wk of age.

Wheat and soy based mash diets (Appendix A) were supplied as follows: starter (2,900 kcal ME, 19% CP, 1.18% lys) from 0 to 3 wk; grower (2,900 kcal ME, 16.7% CP, 1% lys) from 3 to 25 wk; breeder 1 (2,870 kcal ME, 16% CP, 0.72% lys) from 25 to 49 wk; and breeder 2 (2,870 kcal ME, 15.5% CP, 0.70% lys) from 49 to 60 wk.

This research project was carried out in compliance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984) and was approved by the University of Alberta Faculty Animal Policy and Welfare Committee.

4.2.2. Experimental Design

At 16 wk of age, 144 birds were randomly assigned to one of two feed allocation treatments. A control treatment had feed allocated on a Group basis following the standard BW target. Each Group hen received the same amount of feed on any given day. A second treatment had feed allocated on an Individual bird basis following the same BW target as the Group treatment. The experiment compared the relationship (Pearson's correlation) between standardized energetic efficiency indices of RFI and RME_m (SRFI and $SRME_m$) and different performance traits to 60 wk of age for the two feed allocation treatments. Each broiler breeder hen was considered an experimental unit.

A simultaneous experiment with 144 birds was performed, in which two additional group based feed allocation treatments had target BW 10% greater (High) or 10% lower (Low) than Group (72 birds per treatment; Chapter 3). Data from these birds were only used to estimate the effect of energy intake level on maintenance requirements for the RME_m calculation.

4.2.3. Data Collection

Body weight was recorded twice weekly until 32 wk, and weekly thereafter. The age at the first egg was recorded for every pullet. Eggs were collected daily, individually weighed, and coded according to shell integrity (membranous, soft shell, broken), shape (deform) and size (double yolk). Normal eggs were calculated as total eggs minus eggs with shell problems, double yolk and deforms. Settable eggs were the normal eggs minus small eggs (< 52 g). Average egg laying sequence length and prime sequence length (Renema et al., 2001) were determined.

Unhatched eggs were separated from the hatch residue and recorded to determine hatchability (Renema et al., 2001). Results from five hatches were excluded from the analysis as they were performed in a different facility. For the excluded hatches, hatchability was estimated using logistic regression with age as direct effect (Catmod Procedure; SAS Institute, Cary, NC). Unique feed conversion ratios were defined, relating cumulative feed intake (0 to 60 wk) to five different outputs: total egg mass, total eggs, normal eggs, settable eggs, and total chicks.

4.2.4. Energetic Efficiency Measures

Predicted ME intake was calculated weekly (20 to 60 wk) using a linear model (Byerly et al., 1980; Schulman et al., 1994). For every hen, a single RFI value was calculated as the mean difference between observed and predicted ME intake. The following ME intake prediction equation (Chapter 3; Table 3-4) was used:

$$MEI_d = BW^{0.75}(111.95 - 0.36T) + 3.36ADG + 2.10EM$$

Where MEI_d was the average daily ME intake; BW was body weight; T was temperature; ADG was average daily gain; and EM was egg mass production.

A nonlinear mixed model was used to estimate hen maintenance ME requirements (Chapter 3; Table 3-6):

$$MEI_d = (a+u)BW^{0.54} + 1.18BW^{0.60}ADG_P^{1.10} - 0.46BWADG_N + 4.99BW^{-2.07}EM^{1.40} + \varepsilon$$

Where MEI_d was the average daily ME intake; ADG_p was a positive and ADG_N a negative ADG; and a was estimated as 141.0 kcal of ME. Each hen was considered a subject associated to a random term $u \sim N(0, V_u)$ such that each hen was assigned a unique maintenance ME requirement. A linear regression between individual hen maintenance ME requirement ($a+u$; ME_m) and ME intake was performed for the Group, High and Low birds (Chapter 3; Figure 3-4B):

$$ME_m = 21.5 + 0.34MEI + \varepsilon$$

RME_m was the residual of the relationship between hen maintenance requirement and ME intake. RME_m values are represented by the vertical distances between every point and the regression line in Figure 4-1.

In a preliminary analysis, RFI was calculated using the linear and the nonlinear models above. Because the inferences from linear and nonlinear RFI models were similar, it was chosen to contrast RME_m with the traditional linear RFI model reported in the literature. Standardized efficiency indices of RFI (SRFI) and RME_m ($SRME_m$) were defined as the probability at the right hand side of the correspondent Z value for each treatment. That approach avoided confounding effects of differences in variability between RFI and RME_m. Greater SRFI and $SRME_m$ values indicated a greater energetic efficiency to be consistent with the concept of efficiency in other fields.

4.2.5. Statistical Analysis

Linear regressions used the Mixed Procedure, and nonlinear regressions used the Nlmixed Procedure of SAS (SAS Institute, Cary, NC). Analyses of variance were performed using the Mixed Procedure of SAS with a critical value of $P<0.05$. Homogeneity of variances was assessed with the Levene's test of the GLM procedure of SAS (SAS Institute, Cary, NC) with a critical value of $P<0.05$. Pearson's correlation coefficients were calculated using the Corr Procedure of SAS (SAS Institute, Cary, NC).

4.3. Results and Discussion

4.3.1. Feed Allocation Treatments and Energetic Efficiency Measurements

Consistent with the experimental design, the Individual hens were characterized by a low BW variability (CV=1.8% to 2.0%) and a variable feed intake (CV=7.1% to 10.6%) whereas the Group hens had a higher BW variability (CV=4.6% to 6.1%) and a null feed intake variability (Table 4-1). Mean BW did not differ in any period between Individual and Group hens (Chapter 2).

The mean RFI did not differ between Individual and Group hens (Table 4-2; P=0.33). Nonetheless, RFI variance was greater for Individual (256.2 $kcal^2$) than Group hens (91.3 $kcal^2$; Table 4-3). Luiting (1990) reviewed RFI variability in laying hens and reported CVs (SD RFI/$\bar{x}$ ME intake) between 4 and 12%. Interestingly, the RFI CV of Individual hens (CV=4.6%) was in that range, but the one of Group hens was below 4% (CV=2.7%) since their feed intake did not vary. Swennen et al. (2007) reported that the decreased efficiency of a positive RFI strain of laying hens was related to a greater feed intake and a greater absolute postprandial thermogenesis, which highlights the heat increment of feeding as an important factor affecting the RFI estimation.

The current estimates of ME_m could not be directly compared to ME_m reported in the literature because the exponential term of metabolic BW ($BW^{0.54}$; Chapter 3) was different than the commonly assumed $BW^{0.75}$. Considering the BW range reported in Table 4-1, ME_m would vary between 107.6 and 115.6 kcal/$BW^{0.75}$, which coincided with the value of 112.8 kcal/$kg^{0.75}$ reported by Rabello et al. (2006) for broiler breeders in floor pens, but was greater than reports for broiler breeders in metabolic cages, such as those of Spratt et al. (1990; 87.7 kcal/$kg^{0.75}$) and Johnson and Farrell (1983; 87.2 kcal/$kg^{0.75}$). Similar to RFI, ME_m variance was greater for Individual (58.3 $(kcal/kg^{0.54})^2$) than Group hens (21.3 $(kcal/kg^{0.54})^2$; Table 4-3). Luiting (1990) reviewed CVs of ME_m between 4 and 12% in studies using *ad libitum* fed laying hens. The CV of ME_m in the current study was 5.5% for Individual and 3.3% for Group hens. Again, differences in feed intake variability were reflected.

In contrast with RFI and ME_m, neither RME_m mean (P=0.88) nor RME_m variance (P=0.14) differed between feed allocation treatments. A positive relationship between feed intake level and energy expenditure is accepted in chickens (Koh and MacLeod, 1999), and other species (Birkelo et al., 1991). Williams and Jenkins (2003) proposed a model to calculate maintenance requirements in cattle assuming a linear relationship between maintenance heat production and feed intake. Similarly, RME_m accounted for the fact that ME_m depended on the plane of nutrition. The relationship between ME_m and feed intake corrects maintenance requirement for the effect of dietary thermogenesis. In order to have an unbiased estimation of that relationship (Figure 4-1), comparable populations should be evaluated. The Individual birds were excluded from the current regression because correlation between individual hen efficiency and feed intake level was possible. For instance, Gabarrou et al. (1998) reported that the slope of the relationship between ME intake and dietary thermogenesis was greater for an inefficient strain of layers.

4.3.2. Adult Body Weights and Feed Intake

In the experimental design, Individual BW was controlled whereas Individual ME intake was allowed to fluctuate. In contrast, Group BW was allowed to fluctuate whereas Group ME intake was controlled. Hence, Individual ME intake and Group BW were the variables of interest to correlate with energetic efficiency estimates. As expected, SRFI had a strong negative correlation with ME intake in the Individual hens (Figure 4-2A). Bordas et al. (1992) and Schulman et al. (1994) also reported that in laying hens divergently selected for RFI, efficient hens had a lower intake than inefficient hens. In the Group treatment (Figure 4-2B), where ME intake did not vary among birds, SRFI-efficient birds were heavier, especially from 29 to 52 wk of age (r>0.50). In *ad libitum* fed laying hens, Bordas et al. (1992) found the opposite relationship between efficiency and BW, where an inefficient strain became heavier than an efficient strain over 5 generations of selection for RFI. This was probably due to the fact that RFI-inefficient birds had a higher feed intake.

The correlation between $SRME_m$ and ME intake was negative in Individual hens from 25 to 28 wk (r=-0.24 to -0.26), and positive from 43 to 60 wk (r=0.21 to 0.39; Figure 4-3A). Consistently, when ME intake was Group-based (Figure 4-3B), $SRME_m$ was positively correlated to BW from 20 to 26 wk (r=0.23 to 0.27) and negatively correlated from 52 to 60 wk of age (r=-0.25 to -0.31). This was likely due to a greater persistence of egg production of $SRME_m$-efficient hens.

4.3.3. Egg and Chick Production

The SRFI was correlated with age at sexual maturity only in the Individual treatment (r=0.27; Table 4-4). Bordas et al. (1992) observed no significant correlated responses of RFI selection on age at first egg, and Schulman et al. (1994) found that RFI-efficient hens had lower voluntary feed intakes and took longer to reach sexual maturity. The relationship between RFI efficiency and sexual maturity age in Individual hens may be an artifact due to a lower feed intake of RFI-efficient birds. In contrast, a negative correlation of $SRME_m$ and age at sexual maturity was found only in the Group treatment (r=-0.35), probably because of a positive correlation with BW at photostimulation (Figure 4-2B). Accordingly, prime sequence length had a negative relationship with SRFI in the Individual treatment (r=-0.40) and a positive relationship with $SRME_m$ in the Group treatment (r=0.59).

Total eggs, normal eggs, and egg mass were negatively correlated to SRFI in the Individual treatment (r=-0.40, r=-0.38 and r=-0.36; Table 4-4), but positively correlated in the Group treatment (r=0.31, r=0.26 and r=0.45). SRFI-efficient hens from the Individual treatment had lower feed intakes and lower egg production. In contrast, SRFI-efficient hens in the Group treatment had higher egg production than inefficient hens. These opposite relationships agreed with the lack of relationship between RFI and egg mass production reported by Luiting and Urff (1991a) in layers, where neither BW nor ME intakes were experimentally controlled. Bordas et al. (1992) and Schulman et al. (1994) also reported no significant responses of RFI selection on egg production and egg weight. Katle and Kolstad (1991) reported that selection of RFI-inefficient laying hens reduced egg mass production, which resembled the positive relationship between SRFI and egg mass production of Group hens in the current study.

In contrast to SRFI, $SRME_m$ was positively correlated with average sequence length (r=0.52), total egg number (r=0.64), normal eggs (r=0.60), settable eggs (r=0.74), total egg mass production (r=0.80), egg weight (r=0.27), and total chick number (r=0.64) in both the Individual and the Group treatments (Table 4-4). It was hypothesized that $SRME_m$-efficient hens had a lower requirement for maintenance, and therefore a greater proportion of nutrients available for reproduction than $SRME_m$-inefficient (high maintenance) hens, irrespective of feed intake. The RME_m methodology eliminates the effect of dietary thermogenesis as a factor in energetic efficiency estimations. Therefore, animal performance can be more clearly related with mechanisms determining efficiency at the organism, tissue and cellular levels. Factors such as the relative development of supply and demand organs (Konarzewski et al., 2000), activity level (Gabarrou et al., 1998), feather coverage (Peguri and Coon, 1993) and differences in mitochondrial function (Bottje et al., 2002) affect energetic efficiency through changes in maintenance energy expenditure. However, for proper scientific interpretation, it is important that estimated maintenance energy expenditure is not confounded by feed intake and the resulting dietary thermogenesis. RME_m provides a consistent measure of energetic efficiency, unaffected by feed intake.

4.3.4. Feed Conversion Ratios

The SRFI was not correlated with feed conversion ratios in the Individual treatment (Table 4-5), although was negatively correlated with feed per egg mass (r=-0.43), per total egg (r=-0.27), per settable egg (r=-0.36) and per chick (r=-0.44) in the Group treatment. The Individual birds with lower feed intake appeared more efficient and had a lower reproductive output. Thus, SRFI was not consistently related to productivity. Bordas et al. (1992) and Katle (1991) observed that selection for RFI improved feed conversion (egg mass/feed intake) in *ad libitum* fed laying hens. They also observed that voluntary feed intake was positively correlated to RFI. Presumably, voluntary intake was an important factor determining feed efficiency and was confounded with other feed efficiency traits. Despite possible increments in productivity, a correlated response reducing voluntary intake is not desirable in meat producing animals and constitutes a weakness of RFI as a phenotypic selection criterion.

The $SRME_m$ index was negatively correlated with feed per egg mass (r=-0.83), per total egg (-0.67), per normal egg (-0.62), per settable egg (r=-0.71), and per chick (r=-0.59) in both Individual and Group hens. The $SRME_m$ was independent of feed intake. In meat cattle, Shuey et al. (1993) attempted to relate individual maintenance requirements to heifer productivity. However, fasting heat production and ME_m were not correlated to feed conversion ratios. They attributed this result to a high plane of nutrition and the physiological state of the animals during metabolism measurements, even though confounding effects of feed intake on energy expenditure were possible. Even calorimetric estimations may not be meaningful if the assumptions of the energy balance model are flawed. Feed intake level is a critical factor affecting animal metabolic rate (Richards and Proszkowiec-Weglarz, 2007). The RME_m methodology, based on a mathematical calculation of energy partitioned for BW gain, EM production and maintenance corrected for feed intake, is an improvement on existing energetic efficiency models.

The SRFI efficiency index was a good indicator of productivity only at common feed intake levels. In contrast, the $SRME_m$ efficiency index was consistently related with broiler breeder productivity across feed management treatments. Such independence is highly desirable for phenotypic selection in commercial meat production, where high levels of variation in feed intake occur. Further studies on heritability of RME_m and its relationship to broiler productivity traits are required before including RME_m in commercial selection programs.

In conclusion, hens with lower maintenance requirements (greater RME_m efficiency) partitioned more energy towards chick production than hens with high maintenance requirements. The RME_m methodology provided an unbiased estimate of energetic efficiency by adjusting the maintenance requirement for the effect of dietary thermogenesis and related consistently to broiler breeder productivity.

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Table 4-1. Descriptive statistics of BW and metabolizable energy (ME) intake for Individual and Group feed allocation treatments in periods of 10 wk from 20 to 60 wk of age

Variable – period[3]	Individual[1]		Group[2]	
	Mean	CV[4]	Mean	CV[4]
Body weight (g)				
20 – 30 wk	2,535.1	1.95	2,516.9	5.91
30 – 40 wk	3,409.1	1.97	3,374.8	4.56
40 – 50 wk	3,490.4	1.87	3,468.0	5.02
50 – 60 wk	3,491.0	1.82	3,512.7	6.11
ME intake (kcal/d)				
20 – 30 wk	310.2	10.60	308.5	0.0
30 – 40 wk	414.1	7.72	413.0	0.0
40 – 50 wk	334.3	7.05	341.3	0.0
50 – 60 wk	334.6	9.43	336.3	0.0

[1] Feed allocation was individually-based to maintain a BW target.
[2] Feed allocation was group-based to maintain a BW target. Each bird had the same feed allocation on any given day.
[3] Only birds that finished the experiment (60 wk) were included.
[4] Average weekly CV during each period.

Table 4-2. Energetic efficiency estimates of Individual and Group feed allocation treatments

Effect	RFI[1]	ME_m[2]	RME_m[3]
Feed Allocation	kcal ME	---------- kcal ME/kg$^{0.54}$ ----------	
Individual	1.21	139.88	0.28
Group	3.38	140.30	0.17
SEM	1.59	0.76	0.49
Source of variation	-------------------- Probability --------------------		
Feed Allocation	0.33	0.70	0.88

[1] Residual feed intake. Observed minus predicted ME intake (MEI) for each hen from 20 to 60 wk of age calculated as: $MEI = BW^{0.75}(111.95 - 0.36T) + 3.36ADG + 2.10EM$; T=temperature; ADG=average daily gain; EM=egg mass production.

[2] Expected maintenance requirement (a+u); where u~N(0,V_u) associated with each hen was estimated from the following equation from 20 to 60 wk of age:
$MEI = (a+u)BW^{0.54} + 1.18BW^{0.60}ADG_P^{1.10} - 0.46BWADG_N + 4.99BW^{-2.07}EM^{1.40}$; ADG_P=positive average daily gain; ADG_N=negative average daily gain; EM=egg mass production.

[3] Residual maintenance ME requirement. Residual of the regression between ME_m and MEI for each hen: $ME_m = 21.5 + 0.34MEI$; ME_m=predicted maintenance ME requirement; MEI=average ME intake from 20 to 60 wk of age.

Table 4-3. Variances[1] of the energetic efficiency estimates of Individual and Group feed allocation treatments

Effect	RFI[(2)]	ME_m[(3)]	RME_m[(4)]
	(kcal ME)^2	-------- (kcal ME/kg$^{0.54}$)^2 --------	
Individual[5]	256.2[a]	58.3[a]	12.3
Group[6]	91.3[b]	21.3[b]	21.2
Pooled	174.2	39.7	16.6
Levene's test	--------------------- Probability ---------------------		
Feed Allocation	0.0003	0.002	0.14

[1] Variances within a column lacking a common superscript differ ($P<0.05$).

[2] Residual feed intake. Observed minus predicted ME intake (MEI) for each hen from 20 to 60 wk of age calculated as:

$MEI = BW^{0.75}(111.95 - 0.36T) + 3.36ADG + 2.10EM$; T=temperature; ADG=average daily gain; EM=egg mass production.

[3] Expected maintenance requirement (a+u); where $u \sim N(0, V_u)$ associated with each hen was estimated from the following equation from 20 to 60 wk of age:

$MEI = (a+u)BW^{0.54} + 1.18BW^{0.60}ADG_P^{1.10} - 0.46BWADG_N + 4.99BW^{-2.07}EM^{1.40}$; ADG_P=positive average daily gain; ADG_N=negative average daily gain; EM=egg mass production.

[4] Residual maintenance ME requirement. Residual of the regression between ME_m and MEI for each hen: $ME_m = 21.5 + 0.34MEI$; ME_m=predicted maintenance ME requirement; MEI=average ME intake from 20 to 60 wk of age.

[5] Feed allocation was individually-based to maintain a BW target.

[6] Feed allocation was group-based to maintain a BW target. Each bird received the same feed allocation on a given day.

Table 4-4. Pearson's correlation coefficients between efficiency indices (SRFI and $SRME_m$) and age at first egg, prime egg sequence, average sequence, total eggs, normal eggs, settable eggs, total egg mass, average egg weight, hatch rate and total chick number of Individual, Group, and pooled hens; and LS-means and standard errors of the Individual and Group feed allocation treatments

	SRFI[1]			$SRME_m$[2]			LS-mean[3]		SEM	
Variable	Individual[4]	Group[5]	Pooled[6]	Individual	Group	Pooled	Individual	Group	Individual	Group
	------------------- Pearson's coefficient / (Probability) -------------------									
Age at first egg (d)	0.27 (0.022)	-0.03 (0.82)	0.12 (0.16)	0.14 (0.24)	-0.35 (0.003)	-0.11 (0.22)	185.6	186.5	0.74	0.75
Prime sequence (d)	-0.40 (0.001)	0.17 (0.17)	-0.16 (0.058)	0.12 (0.31)	0.59 (<0.0001)	0.31 (0.0002)	18.5	16.6	1.68	1.70
Average sequence (d)	-0.39 (0.001)	0.13 (0.30)	-0.15 (0.08)	0.41 (0.0004)	0.66 (<0.0001)	0.52 (<0.0001)	3.48	3.25	0.14	0.14
Total eggs (#)	-0.40 (<0.0001)	0.31 (0.010)	-0.10 (0.27)	0.55 (<0.0001)	0.77 (<0.0001)	0.64 (<0.0001)	169.3	168.2	2.66	2.72
Normal eggs[7] (#)	-0.38 (0.001)	0.26 (0.034)	-0.11 (0.19)	0.52 (<0.0001)	0.72 (<0.0001)	0.60 (<0.0001)	164.9	164.4	2.61	2.67
Settable eggs[8] (#)	-0.20 (0.10)	0.38 (0.001)	0.05 (0.55)	0.71 (<0.0001)	0.79 (<0.0001)	0.74 (<0.0001)	152.9	155.5	2.56	2.62
Egg mass (kg)	-0.36 (0.003)	0.45 (0.0001)	0.01 (0.88)	0.72 (<0.0001)	0.89 (<0.0001)	0.80 (<0.0001)	10.23	10.33	0.16	0.16
Egg weight (g)	0.20 (0.09)	0.33 (0.006)	0.26 (0.002)	0.25 (0.036)	0.30 (0.013)	0.27 (0.002)	60.6	61.5	0.41	0.42
Hatch rate (%)	-0.10 (0.41)	0.21 (0.08)	0.05 (0.55)	0.06 (0.61)	0.11 (0.39)	0.08 (0.32)	87.6	86.7	0.88	0.90
Total chicks (#)	-0.19 (0.11)	0.43 (0.0002)	0.08 (0.38)	0.59 (<0.0001)	0.72 (<0.0001)	0.64 (<0.0001)	134.3	134.9	2.81	2.87

[1] Standardized residual feed intake index. Higher SRFI values indicate a greater energetic efficiency.
[2] Standardized residual maintenance ME requirement index. Higher $SRME_m$ values indicate a greater energetic efficiency.
[3] LS-means with different superscripts differ.
[4] Feed allocation was individually-based to maintain a BW target.
[5] Feed allocation was group-based to maintain a BW target. Each bird received the same feed allocation on a given day.
[6] Pooled Individual and Group birds.
[7] Total minus eggs with shell problems, double yolk and deforms.
[8] Normal minus small eggs (<52 g).

Table 4-5. Pearson's correlation coefficients between efficiency indices (SRFI and $SRME_m$) and grams of feed per total egg, per settable egg, per gram of egg mass and per chick of Individual, Group, and pooled hens; and LS-means and standard errors of the Individual and Group feed allocation treatments

	SRFI[1]			$SRME_m$[2]			LS-mean[3]		SEM	
Variable[4]	Individual[5]	Group[6]	Pooled[7]	Individual	Group	Pooled	Individual	Group	Individual	Group
	---------- Pearson coefficient / Probability ----------									
Feed per egg mass	0.09	-0.43	-0.14	-0.79	-0.91	-0.83				
(g/g egg)	(0.46)	(0.0003)	(0.12)	(<0.0001)	(<0.0001)	(<0.0001)	4.00	3.96	0.06	0.06
Feed per total egg	0.17	-0.27	-0.01	-0.61	-0.77	-0.67				
(g/egg)	(0.16)	(0.029)	(0.95)	(<0.0001)	(<0.0001)	(<0.0001)	242.8	243.3	3.92	4.01
Feed per normal egg	0.16	-0.21	0.01	-0.58	-0.72	-0.62				
(g/egg)	(0.19)	(0.08)	(0.87)	(<0.0001)	(<0.0001)	(<0.0001)	249.5	248.7	4.08	4.17
Feed per settable egg	-0.05	-0.36	-0.16	-0.68	-0.82	-0.71				
(g/egg)	(0.67)	(0.0027)	(0.06)	(<0.0001)	(<0.0001)	(<0.0001)	270.6	263.4	4.96	5.07
Feed per chick	0.01	-0.44	-0.14	-0.55	-0.72	-0.59				
(g/chick)	(0.91)	(0.0002)	(0.09)	(<0.0001)	(<0.0001)	(<0.0001)	313.3	306.2	7.66	7.83

[1] Standardized residual feed intake index. Higher SRFI values indicate a greater energetic efficiency.
[2] Standardized residual maintenance ME requirement index. Higher $SRME_m$ values indicate a greater energetic efficiency.
[3] LS-means with different superscripts differ.
[4] Cumulative feed intake and production were calculated from d 1 to 420 of age.
[5] Feed allocation was individually-based to maintain a BW target.
[6] Feed allocation was group-based to maintain a BW target. Each bird received the same feed allocation on a given day.
[7] Pooled Individual and Group birds.

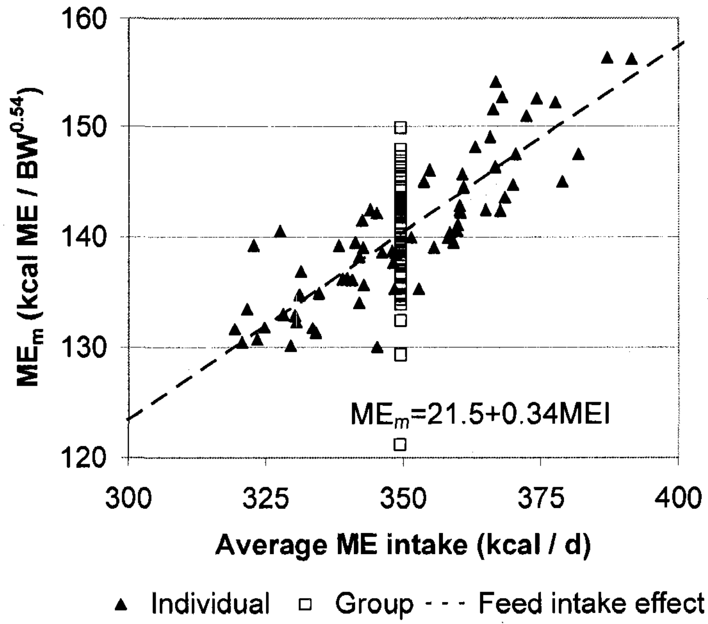

Figure 4-1. Estimates of the maintenance requirement (ME_m) for Individual and Group hens with respect to average daily ME intake from 20 to 60 wk of age. The ME_m was the expected value of the term (a+u); where a is the mean ME_m for the population and u~N(0,V_u), associated with each hen, estimates deviation of individuals from the mean, calculated as:

$$MEI = (a+u)BW^{0.54} + 1.18BW^{0.60}ADG_P^{1.10} - 0.46BWADG_N + 4.99BW^{-2.07}EM^{1.40};$$

ADG_P=positive average daily gain; ADG_N=negative average daily gain; EM=egg mass production.

The regression of ME_m and ME intake included the Group birds and two contemporaneous treatments with target BW 10% greater or lower than the Group treatment. The vertical distance between every point and the regression line corresponded to the residual maintenance ME requirement (RME_m) value.

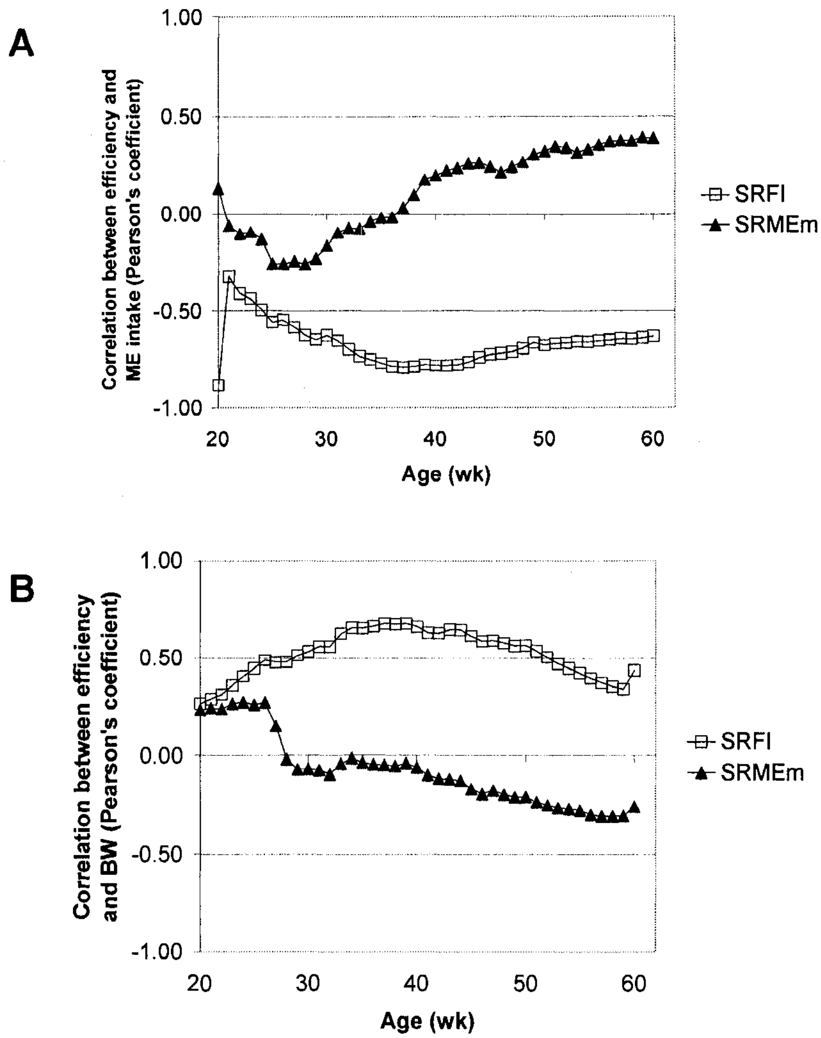

Figure 4-2. Weekly Pearson's correlation coefficients between standardized residual feed intake (SRFI) and standardized residual maintenance ME requirement ($SRME_m$) indices, and feed intake and body weights from 20 to 60 wk of age. A. Correlations with ME intake for the Individual hens. The SRFI negatively correlated to ME intake from 20 to 60 wk (P<0.001). The $SRME_m$ correlated negatively from 25 to 28 wk (P<0.05) and positively from 43 to 60 wk (P<0.05). B. Correlations with BW for the Group hens. The SRFI positively correlated to BW from 20 to 60 wk (P<0.01). The $SRME_m$ correlated positively to 26 wk (P<0.05) and negatively from 52 to 60 wk (P<0.05).

Chapter 5. Effects of Maternal Energetic Efficiency on Egg Traits, Chick Traits, Broiler Growth, Yield and Meat Quality[1]

Abstract. This study assessed egg traits, chick traits, growth, yield and meat quality characteristics of the offspring from broiler breeders classified by two measurements of energetic efficiency: residual feed intake (RFI), defined as the difference between observed and expected ME intake; and residual maintenance ME requirement (RME_m), defined as the residual of the relationship between hen maintenance requirement and feed intake. A group of 72 pullets were placed in laying cages from 16 to 60 wk of age. Individual hen-based feed allocation was provided following a standard BW target. At 41wk, eggs from 8 d of production were collected and pedigree-hatched. Chicks were assigned to one of three maternal RFI (RFI_{mat}) categories: Low, Average and High. A total of 366 chicks were placed in 36 floor pens, 6 per Sex x RFI_{mat} interaction, and raised to 38 d. At the end of the breeder experiment (60 wk), broilers were retrospectively assigned to a Low or High maternal RME_m (RME_{mmat}) category.

Low RFI_{mat} broilers had greater 38 d BW than Average and High RFI_{mat} broilers. That was achieved through a greater BW gain and feed intake of Low RFI_{mat} broilers from 21 to 28 d. RFI_{mat} had no effect on feed conversion, yield or meat quality characteristics. Low RME_m hens produced heavier eggs (62.3 g) and chicks (42.5 g) than High RME_m hens (60.0 g; 41.0 g), but RME_{mmat} did not affect broiler 38 d BW. High RME_{mmat} broilers had greater breast yield (29.5 %) and lower breast shear force (4.7 kgf/g) than Low RME_{mmat} broilers (28.5 %; 5.6 kgf/g). The Low RFI_{mat} x High RME_{mmat} broilers had the greatest growth to 38 d. RFI_{mat} was inversely related to broiler growth, particularly when RME_{mmat} was high. Although low maintenance requirements may be desirable for egg and chick production, hens with a high maintenance requirement produced broilers with greater breast yield and tenderness. Minimizing maintenance requirements may not be compatible with maximizing broiler performance and meat yield.

5.1. Introduction

Feed efficiency is enhanced by nutrient partitioning towards marketable outputs. Because of differences in production objectives, mechanisms affecting feed efficiency in parent stocks may differ from those controlling broiler efficiency, growth and development. Understanding these

[1] A version of this paper has been submitted for publication in Poultry Science.

relationships is important for continued improvements in broiler productivity without causing productivity losses in parent stocks.

Maintenance energy requirements are the most important factor affecting feed efficiency in laying hens (Luiting, 1990). It may be possible to separate variation in maintenance requirements of hens from other sources of variation in energetic efficiency. Residual feed intake (RFI), which is defined as the difference between the observed and expected ME intake after accounting for metabolic BW, BW gain and egg mass production (Bordas et al., 1992), has been used as a measure of energetic efficiency in hens (Flock, 1998). Previously, the RFI methodology was refined to obtain a more specific estimate of hen maintenance (Chapter 4). The residual maintenance ME requirement (RME_m) was described as the residual of the relationship between hen maintenance requirement and feed intake. In Chapter 4, it was concluded that low maintenance requirements in broiler breeders were related to high productivity. It is not clear whether high broiler breeder energetic efficiency has a positive effect on broiler production.

Energetic efficiency of broiler breeders may affect growth and development of their progeny in two main ways: first, through heritable factors affecting efficiency; and second, through egg size and composition. The size and metabolic activity of visceral organs and muscle mass are the main variables that affect breeder metabolic rate (Spratt et al., 1990) and broiler growth and development (Konarzewski et al., 2000). Variability in those traits may be captured in the calculation of breeder RME_m, and may impact broiler growth and development. Variation in the composition of both eggs and BW gain can also be captured in the calculation of hen RFI (Luiting, 1990), and may affect broiler growth potential. Additional phenotypic effects affecting broiler growth are relationships between egg size and early muscle development (Sklan et al., 2003); and albumen proportion and embryonic growth (Enting et al., 2007).

The objective of this study was to assess egg traits, chick traits, growth, yield and meat quality characteristics of high breast yield broilers produced from broiler breeder hens classified by two measures of energetic efficiency: RFI and RME_m. It was hypothesized that, within a commercial high breast yield population, low RFI breeders would contribute efficiency-related traits that improve broiler performance, but breeders with low maintenance requirements would produce broilers with a lower proportion of high energy demand tissues such as breast muscle. This was an exploratory study to relate maternal energetic efficiency with a number of egg and broiler variables.

5.2. Materials and Methods

5.2.1. Stocks and Management

A total of 600 Ross 708 broiler breeder pullets (Aviagen Inc., Huntsville, AL) were raised in floor pens to 16 wk of age. Seventy two pullets were randomly selected and placed in laying cages to 60 wk. A more detailed description of the broiler breeder experiment was reported in Chapter 2. Unique feed allocations were provided to individual hens, following the standard BW target for the strain. Artificial insemination was performed weekly from 30 wk of age. At 40 wk, eggs from 3 d of production were collected for analysis of egg traits. At 41 wk, eggs were collected for 8 d, identified by hen and date, stored at 16 C and set into single stage incubators with a randomized location. At 19 d of incubation, eggs were transferred to pedigree hatching trays with a newly randomized tray position in the hatcher. At hatch, chicks were feather-sexed and identified with bar-coded neck tags (Heartland Animal Health, Fair Play MO 65649). Chicks were placed in floor pens (1.7 x 2.1 m) at 32 C. Temperature was decreased by 1 C each 3 d to 22 C. Photoperiod was 23L:1D for the entire experiment. Pelleted wheat-soybean based diets were provided *ad libitum* as follows (Appendix B): starter (3,068 kcal ME/kg; 23% CP; 1.4% lys) from 0 to 11 d; grower (3,152 kcal ME/kg; 20% CP; 1.1% lys) from 11 to 21 d; and finisher (3,196 kcal ME/kg; 10% CP; 1.0% lys) from 21 to 38 d. At 39 d, birds were processed in a federally-inspected facility. Duplicate bar-coded wing bands identified birds during processing. The fasting and water withdrawal period prior to slaughter was 10 h.

This research project was carried out in compliance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984) and was approved by the University of Alberta Faculty Animal Policy and Welfare Committee.

5.2.2. Maternal Energetic Efficiency

Hen RFI was calculated from 35 to 41 wk using individual BW, average daily gain (ADG) and egg mass production (EM) data as reported by Luiting and Urff (1991). Additional data from 216 broiler breeders from the experiment described in Chapter 3 were included in the regression. RFI was calculated for each hen as the observed minus the predicted ME intake as follows:

$$MEI_d = BW^{0.75}(147.44 - 0.85T) + 0.97ADG + 1.14EM$$

Where MEI_d was the ME intake (kcal/d); $BW^{0.75}$ was the metabolic BW ($kg^{0.75}$); ADG and EM were expressed in g/d; and T was temperature (C).

Hen RME_m was calculated from 20 to 60 wk of age using the methodology reported in Chapter 4. Briefly, a nonlinear mixed regression model included a random variable that described the deviation of each hen from the mean maintenance requirement. This enabled a unique maintenance requirement estimate for every hen. RME_m was defined as the residual of the linear regression of maintenance requirement and average ME intake. The following equations were calculated (Chapter 3).

$$MEI_d = (a+u)BW^{0.54} + 1.18BW^{0.60}ADG_P^{1.10} - 0.46BWADG_N + 4.99BW^{-2.07}EM^{1.40}$$

$$E(a+u) = 21.5 + 0.34MEI$$

Where ADG_P was a positive and ADG_N a negative ADG (g/d); *E(a+u)* was the expected maintenance requirement per hen (kcal/kg$^{0.54}$); *E(a)* was the mean maintenance requirement and was estimated as 141 kcal/kg$^{0.54}$; and $u \sim N(0,72)$ was a random variable that described the deviation of each hen from the mean maintenance requirement. The residual of *E(a+u)* as a function of MEI was the RME_m value.

Three maternal RFI (RFI_{mat}) categories were delimited by the 33.3 and 66.6 percentiles. Two maternal RME_m (RME_{mmat}) categories corresponded to values above or below the mean. Figure 5-1 shows the distribution of RFI and RME_m values for individual hens. Since RFI and RME_m values were residuals, lower values indicated greater efficiency. The number of hens in each RFI category was balanced since RFI was known before the broiler experiment. Offspring from 3 hens were excluded since they died before 60 wk. Hen number in each RME_m category was not balanced within RFI (Table 5-1). The number of broilers within each interaction is reported in Table 5-2.

5.2.3. Experimental Design

A total of 138 eggs were analyzed for composition and quality traits with a 3 x 2 factorial design with 3 levels of RFI (Low, Average and High) and 2 levels of RME_m (Low and High), where hen was a random term.

In the broiler experiment, chicks were assigned to one of three RFI_{mat} categories at hatch (Low, Average and High). A total of 366 chicks were placed in 36 floor pens, 6 per each Sex x RFI_{mat} interaction. At 60 wk of age, RME_{mmat} was calculated and broilers were retrospectively assigned to a Low or High RME_{mmat} category. To analyze set eggs and newly hatched chick characteristics, the design was a 3 x 2 factorial with 3 levels of RFI_{mat} and 2 levels of RME_{mmat}, where each egg or chick was an independent experimental unit. For growth analysis, the design was a split plot with Sex as the main plot, and RFI_{mat} category, pen and RME_{mmat} category as sub-plots. Pen nested within Sex x RFI_{mat}, and pen x RME_{mmat} nested within Sex x RFI_{mat} were declared as random effects. Analysis of feed intake and feed conversion was only possible for RFI_{mat} and Sex using a 3 x 2 factorial design with pen as experimental unit. A 2 x 3 x 2 factorial with 2 Sex, 3 RFI_{mat} and 2 RME_{mmat} levels was used for yield and meat quality, where each carcass was an independent experimental unit. A total of 338 carcasses were analyzed. Breast sample weight was included as a covariate in cooking loss analysis.

To ensure random fertilization, hens were inseminated using 0.5 ml of pooled semen from 60 Ross roosters (Aviagen Inc., Huntsville, AL). This approach allowed study of variation due to female efficiency categories and vertical analysis of maternal factors such as egg composition. Therefore, sire efficiency was assumed to be randomly distributed and independent from dam efficiency.

5.2.4. Data Collection

Yolk weight, dried shell weight and albumen height were measured as described by Wolanski et al. (2007). Equatorial shell thickness was recorded. Albumen weight was estimated as the egg weight minus yolk and shell weights. To assess albumen quality, Haugh units (HU; Kemps et al., 2006) were calculated as follows:

$$HU = 100 \log_{10} (h - 1.7\, w^{0.37} + 7.6)$$

Where h was albumen height (mm), and w was egg weight (g).

Incubated eggs were weighed at collection and transfer. At hatch, chicks were weighed, and the length from the beak to the toe, excluding the nail, was measured. Chick yield was the chick weight as a proportion of the fresh egg weigh. Individual weights were recorded at 11, 21, 28 and 38 d and the daily weight gains calculated between weighing periods. Breast pH was measured approximately 15 min after slaughter using a 10 mm incision in the ventral side of the right *pectoralis major*. Distilled water was added before inserting a pH probe (HI 98240, Hanna Instruments, Woonsocket, RI 02895). Breast temperature was immediately recorded by inserting a temperature probe at the cranial end of the breast to the highest temperature point. Carcasses were cut up by trained personnel approximately 5 h post-mortem, after reaching an internal breast temperature of 4 C (maximum). Weights of the whole carcass, *p. major*, *p. minor*, thighs, drums and wings were recorded.

The right *p. major* was stored to measure pH and color 24 h after processing. Breast color was measured in three different points at the dorsal side of the *p. major*, using a Chroma-meter CR-400 (Konica Minolta, Mississauga, Ontario). Color measurement was based on the L*a*b* three dimensional color space, with one dimension for lightness (L*) and two for color (a*: green to red; b*: blue to yellow; Zhang and Barbut, 2005). A 25 x 50 mm core, cut in the same direction as the muscle fibres, was taken at the thickest part of the left *p. major* from one male and one female per broiler breeder for cooking loss and shear force measurements. Samples were weighed and stored at 2 C in trays with absorbent pads within plastic bags until 24 h after slaughter. After weighing, samples were placed in parchment paper lined trays, and cooked at 200 C to an internal temperature of 80 C using an electric convection oven and individual temperature probes (92000, Digi-sense, Vernon Hills, IL 60061). Cooking loss was calculated as the weight difference after cooling down the sample at room temperature. An Instron 411 (Instron, Norwood, MA 02062) with an Allo-Kramer blade set (10-blades; Cavitt et al., 2005) was employed to asses shear force. Shear force was defined as the peak force in kg force (kgf) per g of sample.

5.2.5. Statistical Analysis

Analyses of variance were performed using the Mixed procedure of SAS (SAS Institute, Cary, NC). Data are presented as LS-mean ± SEM. Significant differences between LS-means were determined using a Tukey-Kramer adjustment for unbalanced data. Unless specified otherwise, statements of significance are based on testing at $P \leq 0.05$.

5.3. Results and Discussion

5.3.1. Egg and Chick Characteristics

The proportion of albumen was greater in eggs from Low RME_m hens (61.0%) than in those from High RME_m hens (60.0%; Table 5-3). This was the only evident effect of efficiency categories on egg composition and quality. Consistent with the hypothesis that hens with a lower requirement for maintenance had more nutrients available for reproduction, Low RME_m hens had greater egg weights (62.3 g) than High RME_m hens (60.0 g; Table 5-4). However, that difference was not found in Low RFI hens where feed intake was lower (Chapter 4). Enting et al. (2007) stated that a greater egg weight and a greater proportion of albumen gave broilers advantages for embryonic growth. In contrast, the greater albumen proportion and egg weight of Low RME_m hens neither affected chick yield nor chick length, considered an indicator of development at hatch (Wolanski et al. 2004).

Chick yield was greater for High RFI_{mat} than Low and Average RFI_{mat} broilers. This difference may have been caused by differences in embryo metabolism among RFI categories because chick yield was neither a reflection of egg weights (Table 5-4) nor shell quality (Table 5-3). Tona et al. (2004) found a lower weight loss and heat production for an experimental broiler strain with a lower egg weight compared to a commercial broiler strain, and Lourens et al. (2006) reported greater heat production during incubation for large eggs compared to small eggs. Although differences in transfer and chick BW were detected among RFI_{mat} categories, no differences in chick length were found.

5.3.2. Broiler Growth, Yield and Feed Conversion

Differences in chick weight were no longer evident by 11 d (Table 5-5). From 21 to 28 d, the Low RFI_{mat} broilers exhibited a greater BW gain (77.7 g/d) than High (73.6 g/d) RFI_{mat} broilers. Additionally, Low RFI_{mat} broilers had a greater feed intake (128.0 g/d) compared to the Average RFI_{mat} category (118.7 g/d; Table 5-6) during that period. These two factors contributed to the greater BW of Low RFI_{mat} broilers at 28 d and 38 d (1,297 g and 2,255 g, respectively) compared to High RFI_{mat} broilers (1,234 g and 2,144 g, respectively), and compared to Average RFI_{mat} broilers (2,151 g) at 38 d. Notably, the effect of RFI_{mat} on BW gain occurred at a BW before the rate of energy retention as fat and protein are maximum (Lopez et al., 2007), so RFI_{mat} may have affected the shape of the energy retention pattern. Inter-breeder variation in BW gain composition was expected to be captured by RFI_{mat}, and may be involved in determining differences in broiler growth.

The High RME_{mmat} broilers gained more weight (94.1 g/d) than the Low RME_{mmat} broilers (90.7 g/d) from 28 to 38 d. Hens with greater maintenance requirements produced broilers with a greater growth rate during the last part of the experimental growth period. Interestingly, the interaction between RFI_{mat} and RME_{mmat} indicated that only Low RFI_{mat} x High RME_{mmat} broilers had a greater 38 d BW (2,335 g) than the other sub-groups. It was therefore hypothesized that RFI_{mat} captured feed efficiency characteristics in breeders that affected broiler growth, especially in birds with a higher metabolic rate (High RME_{mmat}). Tona et al. (2004), based on a calorimetric study, suggested that faster-growing broiler strains have greater metabolic rates beginning during the final stage of incubation. In contrast, Malan et al. (2003) compared the total heat production (measured by comparative slaughter) of chicken genotypes differing in growth rate and reported that fast-growing strains had a lower heat production per $kg^{0.75}$ than slow-growing strains. It is possible that differences in development among strains at the time of the trial as well as the assumption of $BW^{0.75}$ as scaling metabolic BW (Lopez and Leeson, 2005) may have affected their conclusions.

Interspecies work (Ricklefs et al., 1996) has shown that the relationship between basal metabolism and total energy expenditure is very weak in birds compared to mammals, which suggests that in birds, independent mechanisms may affect nutrient partitioning at periods of high metabolic demand, as is the case in fast-growing broilers. Konarzewski et al. (2000) reported that a fast-growing line of chickens had a lower or equal resting metabolic rate than a slow-growing line. However, the fast-growing line had a greater peak metabolic rate when subjected to a cold stress, which was explained by a larger relative muscle mass. In the current study, differences between Low RME_{mmat} and High RME_{mmat} broilers in breast weight (386.6 g vs. 406.5 g, respectively) and breast yield (28.5% vs. 29.5%, respectively; Table 5-7) were observed. This difference was not the result of differences in BW because the interaction was not significant; which supported the hypothesis that low maintenance breeders produce less muscular broilers. A high metabolic rate is required to support rapid growth because of energetic demands for maintenance of muscle and supply organs (Konarzewski et al., 2000).

No differences in carcass yield or abdominal fat pad percentage were evident among RME_{mmat} categories (Table 5-7). Abdominal fat pad weight was greater for Low RFI_{mat} (1.84 %) than Average RFI_{mat} broilers (1.63 %), even though carcass yield and breast proportion did not differ. Evidently, the nutrient partitioning of these two subgroups was different, but the mechanisms are unknown. Early differences in egg and chick weight between High and Average RFI_{mat} categories suggest that phenotypic maternal effects may be involved. Additionally, voluntary intake (Table 5-6) may have played a role, as the Low RFI_{mat} broilers had a greater intake than Average and High RFI_{mat} broilers (P=0.08).

No significant differences were found in FCR among RFI_{mat} categories. Phenotypic selection for low RFI reduced feed conversion (Bordas et al, 1992; Katle 1991) and voluntary ME intake (Swennen et al., 2007) in Leghorns. In restricted broiler breeders, feed intake strongly influences RFI, probably because of differences in dietary thermogenesis (Chapter 4). In the current breeder experiment, feed intake was experimentally controlled to obtain a common BW. Feed intake may have affected reproductive performance. Therefore, RFI was confounded by an interaction between feed intake and reproductive performance. Selection for RFI may not cause consistent improvements on broiler feed conversion because of these confounding effects.

The split-plot design of the current broiler experiment did not allow calculation of feed conversion for RME_{mmat} because pens contained both RME_{mmat} categories. However, maintenance requirements may affect feed conversion in older broilers when maintenance accounts for a greater proportion of total energetic costs. Repeated attempts to relate basal metabolic rate to feed conversion have not yielded consistent results in broilers (Skinner-Noble et al., 2003a). This is likely due to the multifactorial nature of the maintenance requirement (Emmerson, 1997). Even though a low maintenance requirement would be expected to improve feed efficiency, some factors may increase both maintenance requirements and feed efficiency. For instance, Skinner-Noble et al. (2003b) found that more active broilers had higher feed efficiency than less active birds.

5.3.3. Meat Quality

A greater breast weight of High RME_{mmat} broilers resulted in a greater internal breast temperature at 15 min post-mortem (37.6C; Table 5-8) than Low RME_{mmat} broilers (36.9 C; P=0.07), but ultimate pH was not affected (5.93 vs. 5.96; P=0.32). High RME_{mmat} broilers had breast meat with lower shear force (4.7 kgf/g) than Low RME_{mmat} broilers (5.6 kgf/g). Based on the regression equations between sensory evaluation and shear force developed by Cavitt et al. (2005), this shear force difference is undetectable by consumers. Increased breast weight and yield has been associated with reduced muscle glycolytic potential and reduced lactate content at 15 min post-mortem (Berri et al., 2007). If High RME_{mmat} broilers indeed had a lower glycolytic potential, development of rigor mortis may have been faster, which could have affected shear force at this post-slaughter cooling period as reported by Alvarado and Sams (2000).

Despite growth differences, no differences in meat functional properties were detected among RFI_{mat} categories. Nonetheless, in High RME_{mmat} broilers, a greater a* value was observed in High RFI_{mat} broilers (8.94) than in Average RFI_{mat} (8.12) broilers. Such a* difference may not be noticeable for consumers, as Fletcher (1999) reported that fillets selected as darker than normal by visual assessment had an a* value that was 1.6 units greater than normal fillets. Hens that were inefficient based on both measures of efficiency may have produced broilers with unique muscle characteristics, such as higher myoglobin (Boulianne and King, 1998) or lower fat content (Jaturasitha et al., 2008). Breast muscle lightness (L*) was greater in Low RFI_{mat} birds (61.2, 60.7 and 60.5 for Low, Average and High RFI_{mat} broilers, respectively; P=0.08). Light breast muscles have been associated with lower pH and poorer water holding capacity in chickens (Zhang and Barbut, 2005) as an unintended effect of selection for growth and muscle mass (Dransfield and Sosnicki, 1999). Cooking loss did not differ among RFI_{mat} (P=0.19) nor RME_{mmat} (P=0.36) categories. Although a negative correlation between ultimate pH and lightness was present (r=-

0.21; $P<0.0001$), these results do not support the idea that broilers from breeders of any efficiency category were more susceptible to PSE type problems.

Overall, low RFI_{mat} values were related with increased broiler growth to 38 d, although no substantial effects of RFI_{mat} on feed conversion, parts yield or meat quality characteristics were detected. Low maintenance requirements are advantageous for egg and chick production; however, high maintenance hens produced broilers with desirable traits such as greater breast yield and tenderness. Maximizing economic efficiency in the chicken meat supply chain depends on strategic decisions of energy partitioning; minimizing maintenance requirements may not be compatible with maximizing broiler performance and meat yield.

5.4. References

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Table 5-1. Mean hen energetic efficiency measurements. Broiler offspring from these broiler breeders were assigned to experimental treatments based on these measures

RFI[1] category	n hens	RME_m[2] category	n hens	Hen RFI (kcal/d)	Hen RME_m ($kcal/kg^{0.54}$)
Low	22	Low	15	-30.4	-1.8
		High	7	-32.0	4.8
Average	24	Low	16	0.6	-2.3
		High	8	4.0	3.5
High	23	Low	9	27.4	-2.7
		High	14	29.9	3.2

[1] Residual feed intake. Observed minus predicted ME intake calculated from 35 to 41 wk of age. Lower values indicated greater energetic efficiency because feed intake was lower than predicted.
[2] Residual maintenance ME requirement. Residual of the relationship between hen maintenance requirement and feed intake calculated from 20 to 60 wk of age. Lower values indicated greater energetic efficiency because maintenance requirement was lower than predicted.

Table 5-2. Experimental design. Numbers of broilers placed from each Sex, RFI_{mat}[1] and RME_{mmat}[2] category. A split plot design with Sex as main plot, and RFI_{mat}, pen and RME_{mmat} as sub-plots was used for the broiler growth trial

Sex	n	RFI_{mat}	n	RME_{mmat}	n
Female	173	Low	47	Low	33
				High	14
		Average	64	Low	44
				High	20
		High	62	Low	24
				High	38
Male	193	Low	61	Low	46
				High	15
		Average	66	Low	40
				High	26
		High	66	Low	21
				High	45

[1] Maternal residual feed intake. Observed minus predicted ME intake calculated from 35 to 41 wk of age.
[2] Maternal residual maintenance ME requirement. Residual of the relationship between hen maintenance requirement and feed intake calculated from 20 to 60 wk of age.

Table 5-3. Characteristics of eggs collected for 3 d prior to collection of eggs incubated for the broiler experiment. Breeders were classified in three RFI[1] and two RME_m[2] categories

RFI	RME_m	Albumen	Yolk	Shell	Albumen quality	Shell thickness
		------------- % of egg weight		-------------	--- HU[3] ---	---- µm----
Low		61.1	30.3	8.55	78.8	281.5
Average		60.0	31.4	8.63	77.1	284.6
High		60.5	31.2	8.24	76.5	274.3
SEM		0.4	0.4	0.17	0.8	6.9
	Low	61.0[a]	30.6	8.31	76.4	276.6
	High	60.0[b]	31.3	8.63	78.5	283.7
	SEM	0.4	0.4	0.14	1.4	5.6
Source of variation		------------------	------------------	Probability	------------------	------------------
RFI		0.14	0.13	0.14	0.60	0.43
RME_m		0.031	0.13	0.08	0.25	0.32
RFI x RME_m		0.84	0.73	0.12	0.47	0.35

[1] Hen residual feed intake calculated from 35 to 41 wk of age.
[2] Hen residual maintenance ME requirement calculated from 20 to 60 wk of age.
[3] Haugh Units. HU = 100 $\log_{10}(h - 1.7 w^{0.37} + 7.6)$; h= albumen height, w= egg weight.
[a,b] LS-means within a column within effect with no common superscript differ (P<0.05).

Table 5-4. Egg weight, transfer egg weight, chick weight, chick yield and chick length at hatch of eggs and chicks classified in three RFI_{mat}[1] and two RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Egg weight	Transfer egg weight	Chick BW	Chick yield[3]	Chick length[4]
		---------- g	----------	----------	--- % ---	-- mm --
Low		61.6	52.3^{ab}	41.7^{ab}	67.4^{b}	181.7
Average		60.2	51.2^{b}	40.9^{b}	67.8^{b}	182.8
High		61.7	53.0^{a}	42.7^{a}	68.9^{a}	181.9
SEM		0.6	0.4	0.3	0.3	0.6
	Low	62.3^{a}	52.9^{a}	42.5^{a}	68.2	182.5
	High	60.0^{b}	51.4^{b}	41.0^{b}	67.8	181.8
	SEM	0.5	0.3	0.3	0.3	0.5
Low	Low	61.2^{ab}	52.0^{a}	41.6^{b}	67.9	181.5
Low	High	62.0^{ab}	52.5^{a}	41.8^{ab}	67.0	181.9
Average	Low	62.5^{ab}	52.7^{a}	42.5^{ab}	67.9	183.5
Average	High	57.9^{c}	49.6^{b}	39.2^{c}	67.6	182.0
High	Low	63.2^{a}	53.9^{a}	43.5^{a}	69.0	182.3
High	High	60.2^{bc}	52.1^{a}	41.9^{ab}	68.8	181.5
SEM		1.0	0.7	0.6	0.5	1.0
Source of variation		----------	----------	Probability	----------	----------
RFI_{mat}		0.039	0.0005	<0.0001	0.0002	0.33
RME_{mmat}		0.0001	0.0006	<0.0001	0.18	0.29
RFI_{mat} x RME_{mmat}		0.001	0.003	0.0005	0.64	0.45

[1] Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to one of three RFI_{mat} categories before hatching.
[2] Maternal residual maintenance ME requirement. Calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to one of two RME_{mmat} categories.
[3] Chick weight as percentage of fresh egg weight.
[4] Measured from the beak to the toe, excluding the nail.
[a-c] LS-means within a column within effect with no common superscript differ (P<0.05).

Table 5-5. Body weight at 11, 21, 28 and 38 d, and BW gains between weighing periods from broilers classified in three RFI_{mat}[1] and two RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Sex	BW				BW gain			
			11 d	21 d	28 d	38 d	0-11 d	11-21 d	21-28 d	28-38 d
			g				g/d			
Low			252.7	749.5	1,297.2[a]	2,255.4[a]	19.2	48.9	77.7[a]	95.1
Average			240.4	726.2	1,242.7[ab]	2,151.0[b]	18.1	49.2	74.0[ab]	91.0
High			241.7	720.4	1,234.1[b]	2,144.4[b]	18.1	48.3	73.6[b]	91.2
SEM			5.8	16.4	20.2	31.2	0.5	2.6	1.3	1.6
	Low		242.2	727.2	1,253.7	2,159.8	18.2	48.7	75.0	90.7[b]
	High		247.7	736.9	1,262.3	2,207.5	18.5	48.9	75.2	94.1[a]
	SEM		4.5	12.9	16.0	24.7	0.4	1.6	1.0	1.3
		Female	250.6	722.9	1,214.3[b]	2,068.6[b]	19.0	47.5	70.3[b]	85.0[b]
		Male	239.3	741.2	1,301.8[a]	2,298.7[a]	17.9	50.2	79.9[a]	99.9[a]
		SEM	4.3	12.5	14.8	22.7	0.4	2.2	1.0	1.2
Low	Low		239.5	722.6	1,258.4	2,175.9[b]	18.0	47.5	75.6	91.7
Low	High		266.0	776.4	1,336.1	2,335.0[a]	20.4	50.3	79.8	98.4
Average	Low		242.8	730.9	1,249.9	2,139.9[b]	18.2	49.5	74.6	89.5
Average	High		238.1	721.5	1,235.5	2,162.1[b]	18.1	49.0	73.4	92.6
High	Low		244.4	728.1	1,252.8	2,163.5[b]	18.3	49.0	74.7	91.1
High	High		239.1	712.7	1,215.4	2,125.3[b]	17.9	47.6	72.5	91.3
SEM			9.2	25.9	34.1	53.0	0.8	3.0	2.2	2.8
Source of variation			Probability							
RFI_{mat}			0.33	0.46	0.041	0.012	0.31	0.96	0.041	0.12
RME_{mmat}			0.42	0.61	0.68	0.14	0.30	0.82	0.84	0.045
Sex			0.16	0.37	<0.0001	<0.0001	0.14	0.51	<0.0001	<0.0001
RFI_{mat} x RME_{mmat}			0.19	0.33	0.08	0.049	0.20	0.42	0.14	0.31

[1] Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to one of three RFI_{mat} categories before hatching.

[2] Maternal residual maintenance ME requirement calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to one of two RME_{mmat} categories.

[a,b] LS-means within a column within effect with no common superscript differ (P<0.05).

Table 5-6. Partial and total feed intakes and feed conversion ratios from male and female broilers classified in three RFI_{mat}[1] categories

		Feed intake[2]					FCR[2]				
RFI_{mat}	Sex	0-11 d	11-21 d	21-28 d	28-38 d	Total	0-11 d	11-21 d	21-28 d	28-38 d	Total
		g/d				g	g feed/g BW				
Low		27.7	77.2	128.0[a]	172.9	3,701.7	1.46	1.56	1.67	1.86	1.70
Average		26.5	74.1	118.7[b]	161.7	3,480.5	1.47	1.53	1.60	1.81	1.66
High		26.3	73.3	122.1[ab]	170.6	3,583.4	1.48	1.54	1.67	1.88	1.71
SEM		0.5	1.5	2.6	4.5	67.9	0.04	0.03	0.03	0.06	0.03
	Female	27.9	75.7	120.7	167.0	3,578.3	1.47	1.60[a]	1.71[a]	1.99[a]	1.77[a]
	Male	25.7	74.1	125.2	169.8	3,598.8	1.47	1.49[b]	1.59[b]	1.71[b]	1.61[b]
	SEM	0.4	1.2	2.1	3.6	54.6	0.03	0.02	0.02	0.05	0.03
Source of variation		Probability									
RFI_{mat}		0.10	0.15	0.05	0.17	0.08	0.93	0.68	0.13	0.66	0.39
Sex		0.001	0.33	0.13	0.58	0.79	0.99	0.001	0.001	0.0003	0.0001
RFI_{mat} x Sex		0.016	0.07	0.79	0.80	0.74	0.011	0.08	0.41	0.97	0.83

[1] Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to one of three RFI_{mat} categories before hatching.
[2] LS-mean values were calculated for 36 pens used in the experiment.
[a,b] LS-means within a column within effect with no common superscript differ ($P<0.05$).

Table 5-7. Carcass weight, carcass yield, abdominal fat pad weight as proportion of the live BW, and breast, thighs, drums and wings weights as proportion of the carcass weight from broilers classified in three RFI_{mat}[1] and two RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Sex	Carcass weight	Carcass yield	Abdom. fat pad	Breast	Thighs	Drums	Wings
			--- g ---	------ % BW ------		---------------- % carcass ----------------			
Low			1,397.6	62.5	1.84^{a}	29.2	17.1	14.9	11.9
Average			1,340.7	62.0	1.63^{b}	28.9	17.1	14.6	12.1
High			1,352.6	62.3	1.74^{ab}	28.9	17.0	14.8	12.1
SEM			22.0	0.2	0.05	0.5	0.2	0.1	0.1
	Low		1,352.9	62.1	1.72	28.5^{b}	17.2	14.8	12.1
	High		1,374.3	62.4	1.75	29.5^{a}	17.0	14.7	12.0
	SEM		17.2	0.2	0.04	0.4	0.1	0.1	0.1
		Female	1,283.8^{b}	62.3	1.87^{a}	29.6^{a}	17.0	14.4^{a}	12.1
		Male	1,443.5^{a}	62.2	1.60^{b}	28.4^{b}	17.2	15.1^{b}	11.9
		SEM	15.8	0.2	0.03	0.3	0.1	0.1	0.1
Low	Low		1,357.7	62.1	1.76^{ab}	28.8	17.4	14.9	11.9
Low	High		1,437.5	62.8	1.92^{a}	29.7	16.9	14.8	11.9
Average	Low		1,329.7	62.0	1.60^{b}	28.6	17.2	14.7	12.2
Average	High		1,351.7	62.0	1.67^{ab}	29.3	17.0	14.6	12.0
High	Low		1,371.3	62.3	1.80^{ab}	28.1	16.9	14.8	12.0
High	High		1,333.9	62.2	1.68^{ab}	29.6	17.1	14.7	12.1
SEM			37.0	0.4	0.08	0.8	0.3	0.2	0.2
Source of variation			---------------- Probability ----------------						
RFI_{mat}			0.12	0.31	0.003	0.84	0.80	0.35	0.49
RME_{mmat}			0.35	0.38	0.44	0.028	0.32	0.50	0.62
Sex			<0.0001	0.52	<0.0001	0.008	0.40	<0.0001	0.16
RFI_{mat} x RME_{mmat}			0.12	0.29	0.045	0.79	0.23	0.90	0.68

[1] Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to one of three RFI_{mat} categories before hatching.
[2] Maternal residual maintenance ME requirement. Calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to one of two RME_{mmat} categories.
[a,b] LS-means within a column within effect with no common superscript differ (P<0.05).

Table 5-8. Meat quality characteristics of broilers classified in three RFI_{mat}[1] and two RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Sex	Temp. 15 min[3]	pH 15 min[4]	pH 24 h[5]	Color[6] L*	Color[6] a*	Color[6] b*	Cook loss[7]	Shear force[8]
			C						%	kgf/g
Low			37.7	6.91	5.93	61.2	8.44	5.54	17.8	5.30
Average			37.3	6.92	5.93	60.7	8.34	5.16	18.4	5.03
High			36.7	6.88	5.96	60.5	8.59	5.20	17.5	5.19
SEM			0.4	0.03	0.03	0.3	0.17	0.21	0.4	0.22
	Low		36.9	6.87	5.93	60.8	8.51	5.42	18.1	5.60[a]
	High		37.6	6.93	5.96	60.8	8.40	5.19	17.7	4.75[b]
	SEM		0.3	0.02	0.02	0.2	0.13	0.16	0.3	0.19
		Female	37.0	6.88	5.97[a]	61.1[a]	8.56	5.46	18.0	5.02
		Male	37.5	6.93	5.92[b]	60.5[b]	8.36	5.14	17.9	5.32
		SEM	0.3	0.02	0.02	0.2	0.12	0.15	0.3	0.2
Low	Low		36.9	6.86	5.90	61.2	8.73[ab]	5.61	18.8	5.83
Low	High		38.5	6.96	5.96	61.3	8.15[ab]	5.48	16.9	4.77
Average	Low		37.1	6.93	5.91	60.6	8.57[ab]	5.22	18.1	5.48
Average	High		37.5	6.91	5.96	60.8	8.12[b]	5.10	18.8	4.59
High	Low		36.7	6.84	5.97	60.6	8.24[ab]	5.42	17.5	5.49
High	High		36.7	6.92	5.95	60.3	8.94[a]	4.99	17.4	4.89
SEM			0.6	0.05	0.04	0.4	0.28	0.34	0.8	0.36
Source of variation			---------- Probability ----------							
RFI_{mat}			0.58	0.12	0.56	0.08	0.48	0.32	0.19	0.69
RME_{mmat}			0.07	0.07	0.32	0.97	0.53	0.29	0.36	0.001
Sex			0.11	0.20	0.035	0.010	0.21	0.12	0.81	0.20
RFI_{mat} x RME_{mmat}			0.20	0.23	0.37	0.69	0.004	0.78	0.10	0.75

[1] Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to one of three RFI_{mat} categories before hatching.
[2] Maternal residual maintenance ME requirement calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to one of two RME_{mmat} categories.
[3] A temperature probe was inserted 15 min post-mortem at the highest temperature point of the *p. major*.
[4] Measured in an incision made 15 min post-mortem at ventral side of the *p. major*.
[5] Measured in an incision made 24 h post-mortem at ventral side of the *p. major*.
[6] Mean of three measures at the dorsal side of the *p. major*. Based on the L*a*b* three dimensional color space. A Chroma-meter CR-400 (Konica Minolta, Mississauga, Ontario) was used. L*: lightness; a*: green to red; b*: blue to yellow.
[7] Weight loss after cooking the samples at 200 C to an internal temperature of 80 C.
[8] Shear force from an Instron 411 (Instron, Norwood, MA 02062) with an Allo-Kramer blade set (10 blades) measured as kg force (kgf) corrected to kgf/g. Sample area was standardized to 25 mm x 55 mm.
[a,b] LS-means within a column within effect with no common superscript differ ($P<0.05$).

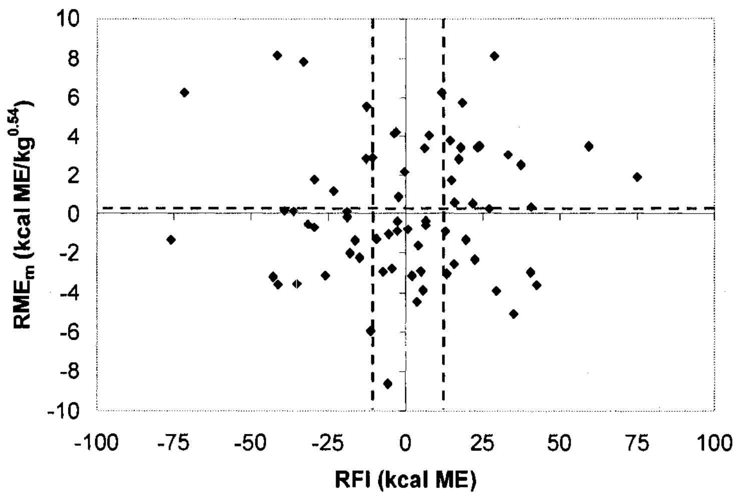

Figure 5-1. Residual feed intake (RFI) and residual maintenance ME requirement (RME_m) values of 69 Ross-708 dams, source of the broilers used in the current study. The RFI was defined as the difference between expected and observed ME intake and was measured from 35 to 41 wk of age. The RME_m was defined as the residual of the relationship between the hen maintenance requirement and feed intake, and was calculated from 20 to 60 wk of age. Broken lines indicate the borders of RFI_{mat} and RME_{mmat} categories.

Chapter 6. Effects of Maternal Energetic Efficiency on Broiler Feed Conversion, Residual Feed Intake and Residual Maintenance ME Requirement

Abstract. This study investigated the effect of maternal residual feed intake (RFI_{mat}) and maternal residual maintenance ME requirement (RME_{mmat}) on feed conversion ratio (FCR), residual feed intake (RFI) and residual maintenance ME requirement (RME_m) of broiler offspring from 7 to 40 d of age. RFI was calculated as the difference between observed and predicted ME intake. RME_m was calculated as the difference between observed and predicted maintenance requirements, considering the ME intake. A total of 600 Ross-708 broiler breeder pullets were raised in floor pens. At 16 wk, 144 birds were placed in individual laying cages. Hens with the greatest RFI (n=32) and lowest RFI (n=32) values from 20 to 56 wk of age were selected. At 59 wk, eggs were collected for 8 d and hatched in individual baskets. A total of 338 broilers classified by dam and sex were raised to 40 d in 128 cages. Selected hens were retrospectively assigned to a High or Low RME_m category. The design was a 2 x 2 x 2 factorial with 2 levels of RFI_{mat}, 2 levels of RME_{mmat}, and 2 sexes.

Neither RFI_{mat} nor RME_{mmat} category affected broiler BW or total FCR. The High RFI_{mat} x Low RME_{mmat} broilers exhibited reduced growth to 40 d. From 14 to 21 d, the Low RFI_{mat} x Low RME_{mmat} broilers presented the lowest FCR (P=0.08). From 34 to 40 d, Low RME_{mmat} broilers had greater FCR than High RME_{mmat} broilers (P=0.08). Low RFI_{mat} x Low RME_{mmat} broilers had a lower RME_m (-5.93 kcal ME/kg$^{0.60}$.d) and RFI (-0.86 kcal ME/d) than High RFI_{mat} x Low RME_{mmat} broilers (RME_m= 1.70 kcal ME/kg$^{0.60}$.d; RFI=0.38 kcal ME/d). Overall, hens with low maintenance requirements (Low RME_m) produced more efficient broilers when other efficiency related traits were present (Low RFI). Exclusion of High RFI x Low RME_m hens from selection programs may improve energetic efficiency at the broiler level. The RME_m methodology is an alternative to evaluate energetic efficiency in broilers because it avoids confounding environmental effects and allows measurement standardization.

6.1. Introduction

A strong selection pressure for growth rate and yield (Havenstein et al., 2003) has caused enormous increments in broiler productivity. However, further selection for these variables might present increasing collateral effects that reduce productivity at the parent stock level (Yu et al., 1992; Bilcik et al., 2005). Although selection for feed conversion rations (FCR) has been practiced from the 1970s, a great part of the obtained increment in feed efficiency has been indirectly caused by accelerated growth and higher feed intake (Emmerson, 1997). The correlation among these three variables determines that selection for FCR does not necessarily improve productivity of broiler breeders. It is possible that selection for specific components of energetic efficiency may simultaneously have a positive impact on productivity of broilers and broiler breeders.

The traditional measure of energetic efficiency in broilers has been FCR (Skinner-Noble and Teeter, 2004; Orejano-Dirain, 2004). The difference between feed intake and body weight gain is primarily made up of energy losses in form of heat and feces. Therefore, FCR accounts for variability in metabolizable energy, gain composition, efficiency of energy retention, heat increment of feeding and maintenance energy expenditure. Most of these factors have an important environmental component; therefore, capturing the heritable component of feed efficiency using FCR has been difficult (Emmerson, 1997).

Standardization of energetic efficiency measurement may be achieved by recognizing metabolic BW as a scaling factor that determines part of the heat expenditure. This is particularly important in animals in which maintenance requirements have a high share of the total energy expenditure, such as in broiler breeders (Spratt et al., 1990). However, energetic efficiency measurement in broilers may also benefit from this recognition. The residual feed intake (RFI) methodology (Bordas and Merat, 1981) was refined (Chapter 4) to separate broiler breeder energetic efficiency into two components: 1) systematic sources of variation related to hen maintenance, and 2) the residual, which captures all other sources of variation in energetic efficiency. These components were defined as the residual maintenance ME requirement (RME_m) and the RFI, respectively. RME_m was the residual of estimated maintenance requirement as a function of energy intake, and RFI was the residual of predicted ME intake.

The main objective of the current study was to assess the relationship between hen energetic efficiency, and feed and energy efficiency of broilers. The effects of maternal RFI (RFI_{mat}) and maternal RME_m (RME_{mmat}) on broiler FCR, RFI and RME_m were determined. It was hypothesized that the most efficient hens would produce the most efficient broilers. Additionally, this study aimed to apply and evaluate the RME_m methodology in broiler research as an alternative to the traditional measure of FCR.

6.2. Materials and Methods

6.2.1. Stocks and Management

A total of 600 Ross-708 broiler breeder pullets (Aviagen Inc., Huntsville, AL) were raised in floor pens to 16 wk. At this age, 144 birds were placed in individual laying cages until 60 wk. Seventy two birds received feed allocated on an individual basis and 72 birds received feed allocated on a group basis following the standard BW target for the strain (Chapter 2). Starting at 30 wk, hens were inseminated weekly using 0.5 ml of pooled semen from 60 Ross roosters (Aviagen Inc., Huntsville, AL). At 59 wk, eggs were collected for 8 d from 64 selected hens. These eggs were identified by hen and date, stored at 16 C and set into single stage incubators with a randomized location. At 19 d of incubation, eggs were transferred to individual chick hatching compartments with a newly randomized tray position.

At hatch, chicks were feather-sexed, weighed and identified with bar-coded neck tags (Heartland Animal Health, Fair Play MO 65649). A total of 338 chicks were placed in group cages (20 chicks/cage) until 7 d of age. At 7 d, chicks were classified by dam and Sex, and raised in 128 laying cages to 40 d. Initial temperature was 32 C; then, temperature was decreased by 1 C each 3 d to 22 C. Photoperiod was 23L:1D for the entire broiler experiment. Pelleted wheat-corn-soybean based diets (Appendix B) were provided *ad libitum* as follows: starter (3,068 kcal ME/kg; 23% CP; 1.4% lys) from 0 to 11 d; grower (3,152 kcal ME/kg; 20% CP; 1.1% lys) from 11 to 21 d; and finisher (3,196 kcal ME/kg; 10% CP; 1.0% lys) from 21 to 40 d. At 41 d, birds were processed in a federally-inspected facility.

This research project was carried out in compliance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984) and was approved by the University of Alberta Faculty Animal Policy and Welfare Committee.

6.2.2. Maternal Energetic Efficiency

RFI was defined as the difference between observed and predicted ME intake; lower RFI values indicated a greater energetic efficiency. RME_m was defined as the difference between observed and predicted maintenance requirements based on the ME intake level; lower RME_m values indicated a greater energetic efficiency for maintenance. Broiler breeder RFI was calculated from 20 to 56 wk of age as reported in Chapter 4. The 64 hens with the greatest RFI (High RFI; n=32) and lowest RFI (Low RFI; n=32) values were selected for egg collection. At the termination of the broiler breeder trial, broiler breeder RME_m was calculated from 20 to 60 wk of age (Chapter

4). The 64 selected hens were retrospectively assigned to a High or Low RME_m category with respect to the mean RME_m.

6.2.3. Experimental Design

The experimental design was a 2 x 2 x 2 factorial with 2 levels of RFI_{mat} (Low and High), 2 levels of RME_{mmat} (Low and High), and 2 sexes. All interactions were included in the model. A total of 128 cages representing 64 dams and either Sex were the experimental units. Balanced blocks of 8 cages were considered in the model, based on the location in the barn. Broiler FCR was independently analyzed for 4 periods (1-14 d, 14-21 d, 21-34 d and 34-40 d), and the total 7 to 40 d period. Broiler RFI and RME_m were assessed for the 7 to 40 d period.

6.2.4. Data Collection

Broiler individual BW was recorded at 0, 7, 14, 21, 28, 34 and 40 d of age. Feeders were refilled daily and feed consumption was recorded from 7 to 40 d, and between intervals of 7, 11, 14, 21, 34 and 40 d of age. Sixteen temperature loggers with a resolution of 0.1°C and an accuracy of ±0.6°C (Microlog EC650, Fourier Systems, New Albany, IN 45150) were uniformly distributed in the barn. Each sensor recorded temperature for 8 surrounding cages. Temperature measurements were recorded every 1 h, and mean temperatures for each time interval (1-14 d, 14-21 d, 21-34 d and 34-40 d) were calculated.

6.2.5. Broiler Energetic Efficiency

Based on models of energy partitioning developed in Chapter 3, an energy balance function was selected to fit the broiler data using the Nlmixed Procedure of SAS (SAS Institute, Cary, NC 27513). The function specification was the following:

$$MEI_d = (a+u)BW^b + cT.BW^b + dADG + eADG.SEX;$$

$$MEI_d \sim N(\mu, V); \;\; u \sim N(0, V_u)$$

Where MEI_d was ME intake (kcal ME/d); T was average daily environmental temperature (C); ADG was average daily BW gain (g/d); and Sex was a dummy variable (1 if male; 0 if female). A normally distributed random term *u* was associated with the coefficient of maintenance *a*.

After the expected maintenance requirement (E(a+u)) was estimated for each experimental unit (broilers with same Sex and parent hen), a second stage linear regression (the Reg Procedure, SAS Institute, Cary, NC 27513) was used to relate estimated maintenance requirement and ME intake as follows:

$$E(a+u) = b + c(MEI / BW^{0.60})$$

Where MEI was the average ME intake from 7 to 40 d for each experimental unit. The ME intake relative to metabolic BW was preferred than absolute intake because of the high growth rate of broilers during the experimental period. The residual of this regression corresponded to the broiler RME_m value.

6.2.6. Statistical Analysis

Analyses of variance were performed using the Mixed procedure of SAS (SAS Institute, Cary, NC). Data are presented as LS-mean ± SEM. Significant differences between LS-means were determined using multiple t-tests. Unless specified otherwise, statements of significance are based on testing at $P \leq 0.05$.

6.3. Results and Discussion

6.3.1. Body Weights and Feed Conversion Ratios

In Chapter 4, it was concluded that the hen RFI calculation was confounded by feed intake and the effect of dietary thermogenesis. However, based on extensive RFI work in laying hens and other species (Bordas and Merat, 1981; Johnson et al., 1999; Herd et al., 2003), it was assumed that RFI also captured heritable efficiency traits. Supporting this assumption, low maternal RFI values appeared to be related with increased broiler growth to 38 d in the study reported in Chapter 5. However, no effects of RFI_{mat} category on BW were evident in the current study (Table 6-1).

Neither the current (Table 6-1) nor the previous study (Chapter 5) indicated growth differences between RME_{mmat} categories. However, the previous study (Chapter 5) found an increased growth of Low RFI_{mat} x High RME_{mmat} broilers to 38 d of age. In the current study, the High RFI_{mat} x Low RME_{mmat} broilers exhibited lower BW at 40 d (1,966 g) than the other RFI_{mat} x RME_{mmat} interactions (2,056 g to 2,125 g; Table 6-1). As hens with different feed allocation strategies were included in the current study, effects of RFI_{mat} on broiler efficiency should be less attached to feeding strategy than in the previous experiment (Chapter 5). Nonetheless, both experiments supported the hypothesis that low RFI_{mat} and high RME_{mmat} may be advantageous for broiler growth and, conversely, high RFI_{mat} and low RME_{mmat} may be disadvantageous.

Greater values for FCR were found from 7 to 14 d than in the 14 to 21 d period (Table 6-2). This may have been a reflection of the fact that birds were divided into smaller groups per cage at 7 d of age, which may have affected their ability to conserve energy through physical contact with other chicks. Alternatively, this may have caused behavioural feeding issues. It is also possible that marginal increments in enzymatic activity in the gut (Sklan and Noy, 2000) had been obtained beyond the second week. Overall, no significant FCR differences were found between RFI_{mat} or RME_{mmat} categories (Table 6-2). However, patterns of FCR among maternal efficiency categories are noteworthy (Figure 6-1). From 14 to 21 d of age, the FCR of Low RFI_{mat} x Low RME_{mmat} broilers was 1.43 g/g compared to 1.49 to 1.57 g/g for the other RFI_{mat} x RME_{mmat} interactions (P=0.08). From 34 to 40 d of age, Low RME_{mmat} broilers had a FCR of 1.92 g/g compared to 1.83 g/g of High RME_{mmat} broilers (P=0.08). Even though FCR of broiler RME_{mmat} categories was not measured in Chapter 5, it was reported that High RME_{mmat} broilers had a greater BW gain than Low RME_{mmat} only during the 28 to 38 d period. These results suggest that a high maternal metabolic rate may be related with greater broiler growth and efficiency at the end of this growing period. Conversely, broilers from the most efficient hens (Low RFI_{mat} x Low RME_{mmat}), may have had an advantage in feed efficiency at the beginning of the growing period.

6.3.2. Energy Balance Model

The energy balance model used for broiler RFI and RME_m estimation (Table 6-3) was consistent with the broiler breeder model proposed in Chapter 3 with regard to the assumption of variability in maintenance requirements among birds. In the current study, these maintenance estimates were assumed to be dependent of the relative feed intake (Table 6-4). Several models were evaluated in order to choose a broiler energy balance model. Since the interaction between metabolic BW and ADG was not significant, and the exponential term of ADG was not different from 1 (P>0.05), the current model did not include these features (Table 6-3) that were used in Chapter 3 in broiler breeders. Additionally, instead of assuming a fixed metabolic BW exponent (e. g. 0.75), it was estimated as 0.60. This model feature avoided systematic bias in ME intake estimation. Lopez and Leeson (2005) reported that assuming scaling exponents of 0.60 or 0.75 significantly affected estimation of energy partitioning and efficiencies of protein and fat retention in broilers.

Some reports of ME requirements for maintenance in broilers are presented in Table 6-5. Considering the average weight of males in the current study (890 g) and a temperature of 22 C, estimations of ME requirements for maintenance from Table 6-5 would be 180.7 (Hurwitz et al., 1978), 130.7 to 150.3 (Robbins and Ballew, 1984), 112.9 (Sakomura et al., 2004, 2005), and

155.0 (Lopez and Leeson, 2005) kcal ME/kg$^{0.60}$. Buyse et al. (1998) reported fasting heat production for two strains of broilers that would correspond to values from 154.3 to 173.0 kcal /kg$^{0.60}$. The average maintenance requirement from this study was 348.0 kcal ME/kg$^{0.60}$ (590.1 kcal - 11kcal x 22 C; Table 6-3), which was high with respect to other reports. The high correlation between metabolic BW and ADG (r=0.96) may have interfered with the ability to discern between variation in maintenance and other sources of variation in energetic efficiency (i.e. ADG composition).

Considering the assumption of the relationship between maintenance and relative ME intake (Table 6-4), the maintenance requirement at a zero ME intake (368.1 kcal - 11kcal x 22 C) was estimated as 126.1 kcal ME/kg$^{0.60}$. This value was low compared with the values of fasting heat production reported by Buyse et al. (1998). However, the relationship between maintenance requirements and relative ME intake (Figure 6-2) may not be linear beyond the broiler ME intakes of this study and cannot be compared with reported values of fasting metabolic rate.

Since maintenance requirements may have been overestimated, requirements for ADG (1.15 kcal ME/g for females and 1.41 kcal ME/g for males; Table 6-3) may have been underestimated. Reported values of requirements for ADG (Table 6-5) vary from 2.05 to 4.21 kcal ME/g. If part of the variation in ME intake due to ADG was actually captured by the maintenance coefficient, factors such as gain composition may have not been effectively separated to calculate RME_m.

The second stage regression between estimated maintenance requirements and relative ME intake (Table 6-4; Figure 6-2) indicated that maintenance requirements increased by 0.65 kcal ME/kg$^{0.60}$ per 1 kcal increment of ME intake/kg$^{0.60}$. Therefore, 65% of the ME intake would be lost as heat increment of feeding. In laying type cockerels, Gabarrou et al. (1998) reported values from 30% to 48% of dietary thermogenesis as a proportion of ME intake. As maintenance requirements may have been overestimated in the current study, dietary thermogenesis may have been overestimated as well. Therefore, this value may also have included heat losses involved in tissue synthesis. Evidence supports the thesis of "partitioned pathways" between basal and normal metabolism in birds (Ricklefs et al., 1996). However, nutrient absorption, breakdown and transport, tissue maintenance and energy retention are simultaneous interrelated processes, especially in fast-growing animals where completely basal or maintenance (zero retention) metabolism does not occur. For instance, amino acid absorption, non-essential amino acid synthesis in liver, and protein turnover and synthesis in muscle are interrelated and part of feeding increment, maintenance and retention energy expenditures. An accurate determination of energy losses related to heat increment of feeding, maintenance, and energy retention in *ad libitum* fed broilers appears to be difficult. Most methodologies used to model energy utilization in animals are based on predetermined assumptions of maintenance requirements (Lopez and Leeson, 2005) or efficiency of retention (Rabello et al., 2006) to achieve this objective, which presents analytical and conceptual problems (Birkett and de Lange, 2001). The current methodology could be improved just by using a greater variability in ME intakes. Although RFI and RME_m estimates in the current study measured energetic efficiency, separation of maintenance requirements may not be complete and RME_m may also comprehend some variability in energy retention efficiency or composition.

6.3.3. Broiler RFI and RME_m

Broilers did not display differences in RFI due to Sex (Table 6-6), but RME_m was greater for females (5.44 kcal ME/$kg^{0.60}$) than males (-8.34 kcal ME/$kg^{0.60}$). Since different ADG requirements of males and females were considered in the energy balance model (Table 6-3), energy retention factors affecting RFI were accounted for. The RME_m difference between Sex was likely due to a difference in maintenance requirements. Females develop their breast muscle earlier than males (Gous et al., 1999), which may increase their mean requirements for maintenance as compared to males of similar age.

Interactions between RFI_{mat} and RME_{mmat} on broiler RFI and RME_m were detected (Table 6-6). However, both broiler RFI and RME_m exhibited similar patterns in relation to maternal efficiency categories, which may be another indication of the difficulty to separate variation of maintenance requirements in *ad libitum* broilers. High RME_{mmat} broilers had intermediate RFI and RME_m values regardless of the RFI_{mat}. In contrast, broilers from the most efficient broiler breeders (Low RFI_{mat} x Low RME_{mmat}) had a lower RME_m (-5.93 kcal ME/$kg^{0.60}$.d) and RFI (-0.86 kcal ME/d) than High RFI_{mat} x Low RME_{mmat} broilers (RME_m= 1.70 kcal ME/$kg^{0.60}$.d; RFI=0.38 kcal ME/d). Mechanisms of variability in broiler maintenance (RME_m) may include individual bird differences in dietary thermogenesis (Gabarrou et al., 1997; Orejano-Dirain et al., 2004), development of visceral organs and muscle mass (Konarzewski et al., 2000), activity levels (Skinner-Noble et al., 2003; Rabello et al., 2004) and thermal isolation (Bordas and Minvielle; 1999 ; Neme et al., 2005). Additionally, mechanisms of total variability in hen energetic efficiency (RFI) may include bird differences in ME (Maisonnier et al., 2001), BW gain and egg composition (Luiting, 1990), efficiency of retention (Kielauowski, 1965), and feed intake (Swennen et al., 2007).

Overall, it is hypothesized that hens with low maintenance requirements (low RME_m) will produce more efficient broilers when other efficiency related traits (low RFI) are present. In contrast, these results suggest that exclusion of High RFI x Low RME_m hens from pedigree selection programs may improve energetic efficiency at the broiler level. However, studies of genetic variability of RFI and RME_m in meat type chickens are needed. The RME_m methodology proved to be a plausible alternative to evaluate energetic efficiency in broilers. Increasing variability on ME intake may improve the ability of RME_m to separate variation in maintenance from other sources of variation in energetic efficiency. The RME_m methodology avoids confounding environmental effects such as temperature, body size and dietary thermogenesis, and may give more accurate and consistent estimates of efficiency than FCR.

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Table 6-1. Body weight at 0, 14, 21, 28, 34 and 40 d of broilers classified in two RFI_{mat}[1] and two RME_{mmat}[2] categories

			BW					
RFI_{mat}	RME_{mmat}	Sex	0 d	14 d	21 d	28 d	34 d	40 d
			g					
Low			43.2	318	645	1,097	1,546	2,090
High			43.9	310	628	1,054	1,498	2,037
SEM			0.5	7	11	18	21	26
	Low		42.5[b]	313	633	1,077	1,516	2,045
	High		44.5[a]	315	640	1,074	1,528	2,081
	SEM		0.5	7	12	18	21	27
		Female	42.6[b]	321	641	1,058	1,470[b]	1,961[b]
		Male	44.4[a]	307	631	1,093	1,573[a]	2,166[a]
		SEM	0.4	6	10	17	19	24
Low	Low		42.4	325	659[a]	1,123[a]	1,576[a]	2,125[a]
Low	High		43.9	311	630[ab]	1,072[a]	1,516[a]	2,056[a]
High	Low		42.6	301	606[b]	1,031[b]	1,455[b]	1,966[b]
High	High		45.1	319	649[a]	1,076[ab]	1,540[a]	2,107[a]
SEM			0.9	12	21	34	39	49
Source of variation			Probability					
RFI_{mat}			0.25	0.32	0.25	0.06	0.07	0.11
RME_{mmat}			0.001	0.87	0.64	0.91	0.65	0.28
RFI_{mat} x RME_{mmat}			0.37	0.06	0.014	0.041	0.007	0.002
Sex			0.003	0.10	0.47	0.13	<0.001	<0.001
RFI_{mat} x Sex			0.39	0.76	0.53	0.81	0.66	0.33
RME_{mmat} x Sex			0.003	0.28	0.15	0.66	0.59	0.92
RFI_{mat} x RME_{mmat} x Sex			0.15	0.14	0.22	0.13	0.041	0.015

[1] Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to one of three RFI_{mat} categories before hatching.
[2] Maternal residual maintenance ME requirement calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to one of two RME_{mmat} categories.
[a,b] LS-means within a column within effect with no common superscript differ (P<0.05).

Table 6-2. Feed conversion ratios and feed intake of broilers classified in two RFI_{mat}[1] and two RME_{mmat}[2] categories

			Feed conversion ratio					Feed intake
RFI_{mat}	RME_{mmat}	Sex	7-14 d	14-21 d	21-34 d	34-40 d	7-40 d	7-40 d
			g/g					g/d
Low			1.61	1.49	1.70	1.90	1.70	98.8
High			1.65	1.53	1.74	1.84	1.71	98.9
SEM			0.05	0.04	0.04	0.04	0.03	1.8
	Low		1.62	1.50	1.73	1.92	1.71	97.4
	High		1.63	1.52	1.72	1.83	1.70	100.3
	SEM		0.05	0.04	0.04	0.04	0.03	1.8
		Female	1.58	1.52	1.75	1.92[a]	1.73	94.7[b]
		Male	1.68	1.50	1.69	1.82[b]	1.69	103.0[a]
		SEM	0.05	0.04	0.04	0.04	0.03	1.7
Low	Low		1.57	1.43	1.68	1.96	1.69	97.3
Low	High		1.65	1.55	1.72	1.85	1.72	100.2
High	Low		1.68	1.57	1.77	1.88	1.74	97.4
High	High		1.61	1.49	1.72	1.81	1.69	100.5
SEM			0.10	0.08	0.07	0.08	0.05	3.3
Low		Female	1.58	1.54	1.77	2.00	1.76[a]	95.1
Low		Male	1.64	1.44	1.64	1.81	1.65[b]	102.4
High		Female	1.58	1.49	1.74	1.85	1.70[ab]	94.3
High		Male	1.71	1.57	1.75	1.84	1.73[ab]	103.5
SEM			0.08	0.06	0.06	0.06	0.04	2.7
Source of variation			Probability					
RFI_{mat}			0.58	0.45	0.40	0.26	0.78	0.95
RME_{mmat}			0.91	0.66	0.91	0.08	0.69	0.19
RFI_{mat} x RME_{mmat}			0.28	0.08	0.34	0.64	0.25	0.96
Sex			0.15	0.84	0.17	0.05	0.28	<0.001
RFI_{mat} x Sex			0.56	0.10	0.11	0.09	0.042	0.66
RME_{mmat} x Sex			0.42	0.77	0.82	0.15	0.39	0.62
RFI_{mat} x RME_{mmat} x Sex			0.37	0.34	0.05	0.37	0.07	0.45

[1] Maternal residual feed intake calculated from 35 to 56 wk of age. Broilers were assigned to one of two RFI_{mat} categories before hatching.
[2] Maternal residual maintenance ME requirement calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to one of two RME_{mmat} categories.
[a,b] LS-means within a column within effect with no common superscript differ ($P<0.05$).

Table 6-3. Parameter estimates of energy balance function to estimate broiler RFI[1]. r^2=0.99

Parameter	Estimate	Standard error	t-value	P>t
a	590.1	58.3	10.1	<0.0001
b	0.60	0.02	38.0	<0.0001
c	-11.0	2.1	-5.3	<0.0001
d	1.15	0.26	4.5	<0.0001
e	0.26	0.05	4.7	<0.0001
V	60	41	1.5	0.14
Vu	1,300	124	10.5	<0.0001

Evaluated function[2]

$$MEI_d = (a+u)BW^b + cT.BW^b + dADG + eADG.SEX;$$
$$MEI_d \sim N(\mu, V); u \sim N(0, V_u)$$

[1] Residual feed intake
[2] MEI_d=daily ME intake (g/d); T=average daily environmental temperature (C); ADG=average daily gain (g/d); Sex=1 if male, Sex=0 if female

Table 6-4. Parameter estimates of maintenance requirements as function of ME intake per $kg^{0.60}$, used to estimate broiler RME_m[1]. r^2=0.73

Parameter	Estimate	Standard error	t-value	P>t
b	368.1	12.13	30.35	<0.0001
c	0.65	0.04	18.34	<0.0001
Evaluated function[2]	$E(a+u) = b + c.(MEI / BW^{0.60})$			

[1] Residual maintenance ME requirement
[2] E(a+u)= estimated broiler maintenance requirement; MEI=average ME intake (g/d)

Table 6-5. Summary of reports of estimated metabolizable energy requirements for broiler maintenance and growth

Author	Maintenance	Growth	Method
Hurwitz et al. (1978)	182 kcal/$BW^{0.66}$	2.05 kcal/g	Linear regression
Robbins and Ballew (1984)	133 to 153 kcal/$kg^{0.75}$	N/A	Comparative slaughter
Sakomura et al. (2004, 2005)	$(308-15.6T+0.31T^2)$kcal/ $kg^{0.75}$	3.72 to 4.21 kcal/g	Comparative slaughter
Lopez and Leeson (2005)	155.3 kcal/$kg^{0.60}$	N/A	Comparative slaughter

Table 6-6. RFI and RME_m from broilers classified in two RFI_{mat}[1] and two RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Sex	RFI	RME_m
			kcal ME/d	kcalME/kg$^{0.6}$.d
Low			-0.37	-2.90
High			0.04	0.00
SEM			0.29	1.72
	Low		-0.24	-2.11
	High		-0.09	-0.79
	SEM		0.29	1.75
		Female	-0.13	5.44[a]
		Male	-0.20	-8.34[b]
		SEM	0.27	1.63
Low	Low		-0.86[b]	-5.93[b]
Low	High		0.12[ab]	0.12[ab]
High	Low		0.38[a]	1.70[a]
High	High		-0.30[ab]	-1.70[ab]
SEM			0.53	3.16
Source of variation			---------- Probability ----------	
RFI_{mat}			0.27	0.19
RME_{mmat}			0.68	0.55
RFI_{mat} x RME_{mmat}			0.026	0.034
Sex			0.84	<0.001
RFI_{mat} x Sex			0.23	0.46
RME_{mmat} x Sex			0.22	0.25
RFI_{mat} x RME_{mmat} x Sex			0.44	0.56

[1] Maternal residual feed intake calculated from 35 to 56 wk of age. Broilers were assigned to one of two RFI_{mat} categories before hatching.
[2] Maternal residual maintenance ME requirement calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to one of two RME_{mmat} categories.
[a,b] LS-means within a column within effect with no common superscript differ (P<0.05).

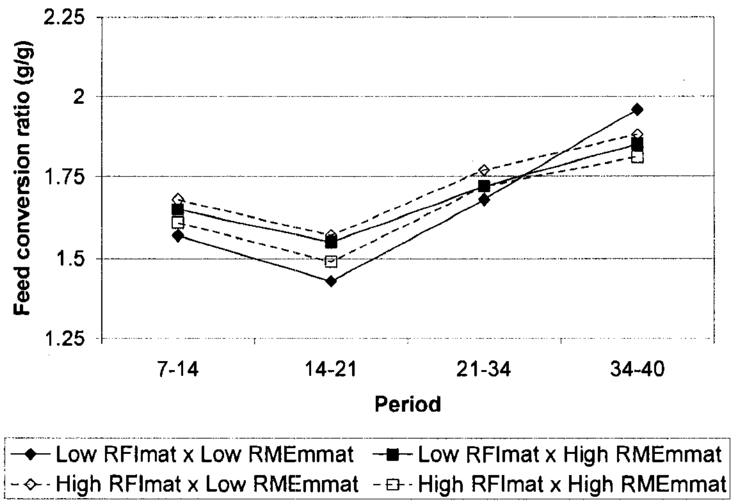

Figure 6-1. Feed conversion ratios of broilers classified in two maternal RFI (RFI_{mat}) and two maternal RME_m (RME_{mmat}) categories. RFI was defined as the difference between observed and expected ME intake and RME_m as the difference between observed and expected maintenance requirement based on the fed intake level.

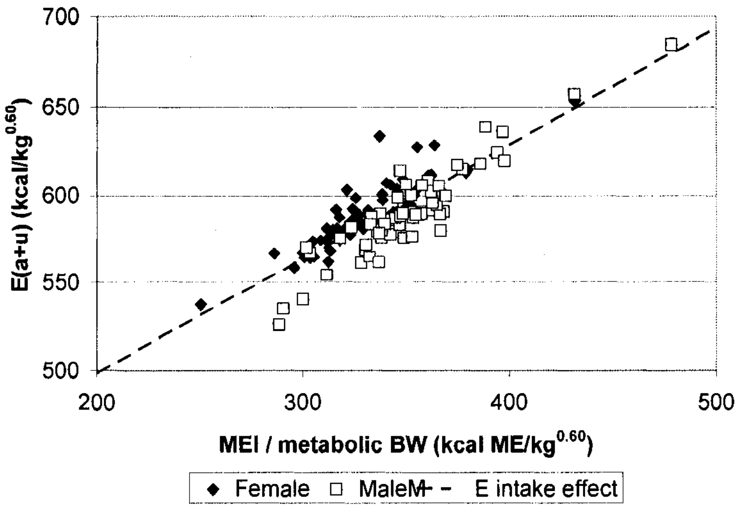

Figure 6-2. Relationship between individual coefficients of maintenance (E(a+u)) and relative ME intake for broiler males and females. The vertical distance between each point and the ME intake effect line (r^2=0.73) corresponds to the residual maintenance ME requirement (RME_m) value.

Chapter 7. Effects of Maternal Energetic Efficiency on Myofibre Number of *Biceps Femoris* Muscle of One Day Old Chicks

Abstract. This preliminary study evaluated the effect of maternal energetic efficiency, measured as residual maintenance ME requirement (RME_m), and residual feed intake (RFI), on weight and total fibre numbers (TFN) of *biceps femoris* muscles of 1 d old chicks. The experimental design was a 2 x 2 factorial with 2 levels of maternal RFI (RFI_{mat}; Low and High) and 2 levels of maternal RME_m (RME_{mmat}; Low and High). Egg weight and chick weight were investigated in 214 chicks hatched from 32 selected 59-wk old hens. *Biceps femoris* muscle weights were assessed for 32 chicks, one from each hen. Myofibre number was assessed for one *biceps femoris* muscle of 16 of these chicks, which were selected from hens with the greatest and least RFI and RME_m values.

The most inefficient hens (High RFI_{mat} x High RME_{mmat}) produced smaller eggs (61.9 g; P=0.08) and smaller chicks (39.4 g; P=0.005) than the other sub-groups (66.0 to 67.4 g and 42.8 to 45.7 g, respectively). Similarly, chicks from the most inefficient hens had lower yield (64% of egg weight) compared to the other chicks (65 to 67%). Inefficient hens may not only have had fewer nutrients available for egg formation, but their chicks may also have been less efficient using energy during incubation. Neither total nor relative muscle weights differed between RFI_{mat} or RME_{mmat} categories. No differences were evident for *biceps femoris* muscle section areas and myofibre density between RFI_{mat} or RME_{mmat} categories. The *biceps femoris* muscle of High RME_{mmat} chicks exhibited a 13% greater TFN (68,123 fibres) than that of Low RME_{mmat} chicks (60,359 fibres; P=0.10). These results suggest that broiler breeders with high maintenance requirements produced broilers with greater *biceps femoris* myofibre numbers. Myofibre characteristics may be a factor affecting the trade-off between broiler breeder energetic efficiency and broiler growth and yield.

7.1. Introduction

Selection for growth and meat yield has increased both the number and size of myofibres of broiler breast muscle (Remignon et al., 1995). Fast-growing chicken strains exhibit increased myofibre areas predominantly in fast contracting fibres, which has been associated with a greater incidence of degenerative changes in these muscles (Macrae et al., 2006). However, current market conditions support continued selection for broiler growth and breast yield (Pollock, 1999). Selection for breast muscle yield, although likely related to greater feed efficiency at the broiler level (Buyse et al., 1998), may also affect how broiler breeder hens partition nutrients to support reproduction (Robinson et al., 2007).

Exploration of the relationship between biological efficiency of broiler breeders and broiler meat production would benefit the process of evaluating the impact of selection programs on economic efficiency of the supply chain. Chapter 4 indicated that broiler breeders with high maintenance requirements, measured by calculation of residual maintenance ME requirement (RME_m), produced broilers with greater breast yield than hens with low maintenance requirements. These differences in breast yield may be caused by greater myofibre hyperplasia or hypertrophy of broilers from hens with high maintenance. Additionally, broiler breeders with high maintenance requirements and low residual feed intake (RFI; Bordas and Merat, 1981) produced broilers with greater growth rate (Chapter 5). Mechanisms leading to improved growth rate of broilers from High RME_m x Low RFI breeders may also include differences in muscle biology. This experiment was a preliminary study to evaluate the effect of maternal energetic efficiency (RME_m and RFI) on weight and total fibre numbers (TFN) of *biceps femoris* muscle of 1 d old chicks. Originally, TFN was going to be evaluated in *pectoralis major* as well, but technical problems with tissue processing and slide preparation did not allow consistent counts in these samples.

7.2. Materials and Methods

7.2.1. Stocks and Management

Seventy two Ross-708 broiler breeder pullets (Aviagen Inc., Huntsville, AL) were raised in floor pens to 16 wk as reported in Chapter 2. At this age, birds were placed in individual laying cages to 60 wk. Feed was allocated individually following the standard BW target for the strain. Starting at 30 wk, hens were inseminated weekly using 0.5 ml of pooled semen from 60 Ross roosters (Aviagen Inc., Huntsville, AL). At 59 wk, eggs were collected for 8 d, identified by hen and date, stored at 16 C and set into single stage incubators with a randomized location. At 19 d of incubation, eggs were transferred to individual hatching compartments with a newly randomized tray position in the hatcher. At hatch, chicks were feather-sexed and weighed. Thirty two chicks were euthanized by cervical dislocation and selected muscles dissected. The remaining broiler chicks were used for a different study.

This research project was carried out in compliance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984) and was approved by the University of Alberta Faculty Animal Policy and Welfare Committee.

7.2.2. Experimental Design

The experimental design was a 2 x 2 factorial with 2 levels of maternal RFI (RFI_{mat}; Low and High) and 2 levels of maternal RME_m (RME_{mmat}; Low and High). Egg weight and chick weight were investigated in 214 chicks hatched from 32 selected hens. *Pectoralis major* and *biceps femoris* muscle weights were assessed for 32 chicks, one from each hen. TFN was assessed for one *biceps femoris* muscle of 16 of these chicks, which were selected from hens with the greatest and least RFI and RME_m values. Muscle section was nested within chick for statistical testing of myofibre density.

7.2.3. Maternal Energetic Efficiency

The RFI was defined as the difference between observed and predicted ME intake; lower RFI values indicate a greater energetic efficiency. RME_m was defined as the difference between observed and predicted maintenance requirements based on the ME intake level; lower RME_m values indicate a greater energetic efficiency due to lower than expected ME requirement for maintenance.

Broiler breeder RFI was calculated from 20 to 56 wk of age as reported in Chapter 4. The 32 hens with the greatest RFI (High RFI; 16 hens) and lowest RFI (Low RFI; 16 hens) values were selected for egg collection. At the end of the broiler breeder trial, broiler breeder RME_m was calculated (20 to 60 wk; Chapter 4). The 32 selected hens were retrospectively assigned to a High or Low RME_m category with respect to the mean RME_m.

7.2.4. Myofibre Number Study

Immediately after being euthanized, the *biceps femoris* muscles were collected and placed in tin foiled containers with dry ice. Muscles were frozen in isopentane cooled in a liquid nitrogen bath, and stored at -80 C. Muscles were perpendicularly cut at the longitudinal half using a razor blade. Tissue sections of 12 μm were cut in a cryostat at -22 C and placed on poly-L-lysine coated slides. Sections were stained for laminin as reported by Putman et al. (2001) using goat serum (Vector, Burlington, ON) to prepare primary (MP Biomedicals, Solon, OH) and secondary (Vector, Burlington, ON) antibodies.

Myofibre numbers of *biceps femoris* muscles were counted in 5 random 25-fold magnification fields (0.113 mm^2 each; Figure 7-1) throughout the section, and section area was estimated using an optic microscope, image recording equipment and customized image analysis software (Skorjanc et al., 1997). Myofibre density was calculated for each filed as the number of myofibres divided by the field area. The TFN was estimated as the mean density times the total area of the muscle.

7.2.5. Statistical Analysis

Analyses of variance were performed using the Mixed procedure of SAS (SAS Institute, Cary, NC). Data are presented as LS-mean ± SEM. Significant differences between LS-means were determined using multiple t-tests. Unless specified otherwise, statements of significance are based on testing at $P \leq 0.05$.

7.3. Results and Discussion

7.3.1. Egg, Chick and Muscle Weights

No differences in egg and chick weight were found between RFI_{mat} categories (Table 7-1). Even though egg weight was not significantly different between RME_{mmat} categories (P=0.14), egg weights of 66.7 g for High RME_{mmat} and 64.2 g for Low RME_{mmat} were consistent with the results of Chapter 5, where greater egg weights were found in hens with lower maintenance requirements (RME_m). The fact that only part of the population reported in Chapter 5 was included in this study may have made this effect less evident. However, the most inefficient hens (High RFI_{mat} x High RME_{mmat}) did produce smaller eggs (61.9 g) than the other sub-groups. Similarly, chicks from these hens had lower hatch BW and chick yield. Not only inefficient hens may have had fewer nutrients available for egg formation, but also their chicks may have been less efficient using energy during incubation.

Neither total nor relative muscle weights differed between RFI_{mat} or RME_{mmat} categories (Table 7-1). Even though the *biceps femoris* muscle of High RFI_{mat} x High RME_{mmat} chicks weighed 119 mg compared to 129 to 149 mg in the other subgroups (P=0.08) , the relative weight of *biceps femoris* muscle of High RME_{mmat} was 0.32% of BW compared to 0.29% in the Low RME_{mmat} chicks (P=0.13). Nonetheless, the hypothesis that High RME_{mmat} chicks favoured pre-hatch development of muscles with high proportion of slow twitch fibres such as the *biceps femoris* may be tested in further studies. This hypothesis is also supported by TFN results of the current study.

7.3.2. Myofibre Density and Number

The *biceps femoris* muscle section area and myofibre density were similar among RFI_{mat} and RME_{mmat} categories (Table 7-2). Previous studies with serial muscle sample collection have found that differences in myofibre density in older birds are not evident at hatch (Remignon et al., 1995). The current study was designed specifically for analysis of TFN at hatch, and may therefore have been incapable of discovering myofibre density differences.

The *biceps femoris* muscle of High RME_{mmat} chicks exhibited a 13% greater TFN (68,123 fibres) than that of Low RME_{mmat} chicks (60,359 fibres; P=0.10). Scheuermann et al. (2004) assessed muscle characteristics of 7 d old chicks and reported a difference of 10% in TFN of *pectoralis major* muscle between a high breast yield and a classic strain. However, TFN of *pectoralis major* muscle was not assessed in the in the current study. The study reported in Chapter 5 identified differences in breast yield at slaughter between RME_{mmat} categories, but no differences in leg or thigh yield, which did not reflect the current difference in TFN of *biceps femoris*. It is hypothesized that differences in TFN may have a greater impact in the potential development of breast (including *pectoralis major*) than leg muscles (including *biceps femoris*), since fast twitch glycolytic fibres are more predominant in breast than leg muscles, and fast twitch fibres have a lower growth constraint due to their lower oxygen diffusion requirements (Macrae et al., 2006).

Among all subgroups, High RFI_{mat} x High RME_{mmat} chicks had the greatest TFN (70,899 fibres; P=0.26) in the *biceps femoris* muscle, although the interaction between RFI_{mat} and RME_{mmat} was not significant at a $P<0.05$ level. Greater chick size at hatch has been related to greater satellite cell activity and muscle growth post hatch (Sklan et al. 2003). Interestingly, the High RFI_{mat} x High RME_{mmat} chicks had the lowest hatch BW and chick yield, but the greatest TFN in the *biceps femoris*. It is possible that high maintenance requirements are related with a greater number of myofibres, which would increase energy expenditure reducing pre-hatch growth, although it would increase the muscle growth potential.

Differences in myofibre type may also be related to broiler breeder energetic efficiency and merit further studies investigating broiler chicks of at least 14 d, when a fair degree of differentiation of myosin heavy chain isoforms has been attained (Bandman and Rosser, 2000). Soike and Bergmann (1998) found a greater proportion of fast twitch oxidative and fast twitch glycolytic fibres in meat-type than layer-type chickens, both in the *supracoracoideus* and the *flexor cruxis medialis* muscles. Similarly, Remignon et al. (1996) reported that selection for high breast yield and low abdominal fat increased the proportion of glycolytic fibres in the *sartorius* muscle although no differences in *pectoralis major* fibre types were observed. Since anaerobic pathways are less energy efficient than aerobic pathways, a greater proportion of glycolytic fibres may additionally increase total energy demands of birds with increased muscularity.

Overall, hens with both high maintenance requirements (high RME_m) and high RFI produced chicks with reduced pre-hatch growth. These results suggest that broiler breeders with high maintenance requirements produced broiler chicks with greater TFN in the *biceps femoris* muscle. Myofibre characteristics may be a factor affecting the trade-off between broiler breeder energetic efficiency and broiler growth and yield.

7.4. References

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Table 7-1. Egg and chick weight, chick yield, and total and relative weight of the *pectoralis major* and *biceps femoris* muscles of 1 d old chicks classified in two RFI_{mat}[1] and two RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Egg weight	Chick weight	Chick yield[3]	Muscle weight *P. major*	Muscle weight *B. femoris*	Relative weight[4] *P. major*	Relative weight[4] *B. femoris*
		(g)	(g)	(% egg)	(mg)	(mg)	(% BW)	(% BW)
Low		66.3	43.7	66.0	191.9	136.9	0.438	0.313
High		64.6	42.5	65.6	194.5	124.1	0.450	0.292
SEM		2.4	1.3	0.8	16.8	9.8	0.032	0.016
	Low	66.7	44.2	66.2	205.4	126.9	0.456	0.287
	High	64.2	42.0	65.4	181.0	134.1	0.432	0.318
	SEM	2.5	1.4	0.9	17.9	10.2	0.034	0.017
Low	Low	66.0	42.8^{a}	65.0^{ab}	189.0	124.5	0.440	0.289
Low	High	66.6	44.6^{a}	67.0^{ab}	194.8	149.4	0.437	0.337
High	Low	67.4	45.7^{a}	67.4^{a}	221.7	129.3	0.472	0.285
High	High	61.9	39.4^{b}	63.8^{b}	167.2	118.9	0.428	0.299
SEM		3.0	1.9	1.4	29.2	14.2	0.055	0.027
Source of variation		------------	------------	------------	Probability	------------	------------	------------
RFI_{mat}		0.31	0.37	0.70	0.91	0.19	0.78	0.30
RME_{mmat}		0.14	0.09	0.49	0.28	0.46	0.58	0.13
RFI_{mat} x RME_{mmat}		0.08	0.005	0.019	0.18	0.08	0.62	0.42

[1] Maternal residual feed intake calculated from 35 to 56 wk of age.
[2] Maternal residual maintenance ME requirement calculated from 20 to 60 wk of age.
[3] Chick BW at hatch as a proportion of fresh egg weight.
[4] Mean chick muscle weight as a proportion of BW at hatch.
[a,b] LS-means within a column within effect with no common superscript differ (P<0.05).

Table 7-2. Total muscle area, total fibre number and fibre density of *biceps femoris* muscles of 1 d old chicks classified in two RFI_{mat}[1] and two RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Total muscle area[3] (mm²)	Fibre density[4] (#/mm²)	Total fibre number[5] (#)
Low		13.86	4,788	64,263
High		14.10	4,789	64,220
SEM		1.31	451	5,487
	Low	13.92	4,624	60,359
	High	14.04	4,954	68,123
	SEM	1.22	422	4,900
Low	Low	14.06	4,728	63,179
Low	High	13.66	4,849	65,346
High	Low	13.79	4,519	57,540
High	High	14.42	5,059	70,899
SEM		1.85	638	6,869
Source of variation		------------------	Probability	------------------
RFI_{mat}		0.89	0.99	0.99
RME_{mmat}		0.95	0.59	0.10
RFI_{mat} x RME_{mmat}		0.77	0.73	0.26

[1] Maternal residual feed intake calculated from 35 to 56 wk of age.
[2] Maternal residual maintenance ME requirement calculated from 20 to 60 wk of age.
[3] Measured at a perpendicular section on the middle of the muscle using image analysis software.
[4] Estimated myofibre density. Myofibres were counted at five random fields (25X) on a perpendicular section on the middle of the muscle. Sections of 12μm thickness were stained with lamimin.
[5] Estimated myofibre number. Total area times myofibre density.

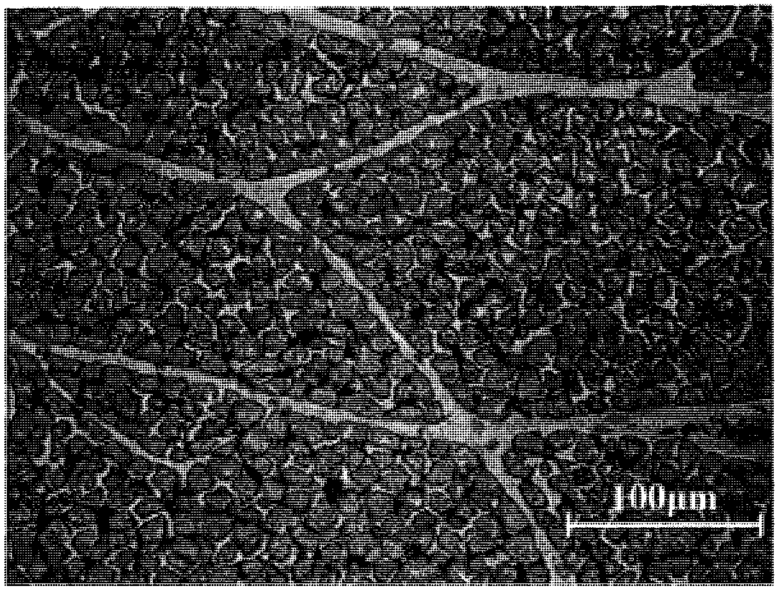

Figure 7-1. Microscopic field (25-fold magnification) of a *biceps femoris* muscle section (12μm thick) stained with laminin. Myofibre numbers were counted in five random fields throughout the section area of each *biceps femoris* muscle.

Chapter 8. A Data Envelope Analysis to Assess Factors Affecting Technical and Economic Efficiency of Individual Broiler Breeder Females

Abstract. This study evaluated the effect of feed allocation and energetic efficiency on technical and economic efficiency of broiler breeder females using the data envelope analysis (DEA) methodology, and quantified the effect of variables affecting technical efficiency. A total of 288 Ross-708 pullets were placed in individual cages at 16 wk and assigned to one of four feed allocation groups. Three of them had feed allocated on a group basis with divergent BW targets: Standard, High (Standard x 1.1) and Low (Standard x 0.9). The fourth group had feed allocated on an Individual bird basis following the Standard BW target. Birds were classified in three energetic efficiency (EnE) categories: Low, Average and High based on estimated maintenance requirements. Technical efficiency considered saleable chicks as output and cumulative ME intake and time as inputs. Economic efficiency of feed allocation treatments was analyzed under different price scenarios.

The Low feed allocation exhibited a lower technical efficiency (69.4%) than Standard (72.1%) as Low hens had a reduced egg production rate. In the High treatment, feed allocation could have been reduced by 10% with the same chick production as the Standard treatment. The Low treatment had increasingly negative economic efficiency at greater capital costs whereas High had increasingly negative economic efficiency at greater feed costs. The Average EnE hens had a reduced technical efficiency in the Low compared to the Standard feed allocation. A 1% change in the maintenance requirement affected technical efficiency by -0.23% while a 1% change in the ME intake had a -0.47% effect. The negative relationship between technical efficiency and ME intake was counter balanced by a positive correlation of ME intake and egg production. The negative relation of technical efficiency and maintenance requirements was synergized by a negative correlation of hen maintenance and egg production. Economic efficiency methodologies are effective tools to assess the economic impact of selection and flock management programs since both biological and allocative factors can be analyzed independently.

8.1. Introduction

Economic efficiency has been divided into technical and allocative efficiency by production economists, based on theoretical developments in efficiency analysis since the middle of the 20th

century (Farrell, 1957; Coelli et al., 2005). Technical efficiency measures the level at which a firm approaches a technology production frontier (the most efficient way to produce) and allocative efficiency measures the adequacy of input utilization in response to price signals (Coelli et al., 2005). Modern empirical studies of economic efficiency use either stochastic estimations of production function frontiers (Aigner et al., 1977) or Data Envelope Analysis (DEA; Charnes et al., 1978) to measure efficiency. DEA is a deterministic method that uses linear programming to calculate efficiency, and has the advantage that assumptions regarding functional forms are not required. Recent studies have used DEA to assess the impact of managerial practices on technical efficiency at the farm (pork production; Galanopoulos et al., 2006) and individual production unit level (pear trees; Wang et al., 2006).

Economic analyses of breeding, nutrition and management programs in animal science have traditionally used deterministic financial equations that relate individual performance to profitability (Harris, 1970; Harris and Newman, 1994; Groen et al., 1998). These methodologies are sensitive to price assumptions and fail to separate technical from market (i.e. price) effects. Production economics methodologies can be used to address these issues. In cattle and pig nutrition, methodologies to minimize feed costs based on deterministic isoquant estimations (input combinations to produce an output amount) have been developed (Heady et al., 1956; Sonka et al., 1976; Brokken and Bywater, 1982). However, these applications have been limited to input utilization decisions. The concepts of technical, allocative and economic efficiency may allow a better understanding of bio-economic relationships in animal production by separating biological and allocative factors. In the individual animal, input-output relationships are constrained by biological processes; in the industry, the addition of biological and other technologic constraints determine the production frontier; and producers make input utilization decisions that affect economic efficiency.

Broiler breeder feed intake is a variable controlled by managers. Feed allocation decisions affect the bird reproductive performance (Hocking, 2004) and energy expenditure (Spratt et al., 1990). If production rate decreases, the capital cost per chick increases. If feed allocation exceeds the requirements for optimal reproduction, the feed cost per chick increases. This trade-off between feed and capital costs supports the utilization of feed intake and time as inputs subject to economic decisions. Similarly, individual technical efficiency may be determined by variables affecting reproduction and nutrient utilization. Measuring the effect of such variables on technical efficiency will allow calculating the economic implications of different genetic or management programs. This study used DEA to make economic inferences of technical and allocative nature, considering each hen an experimental unit. The objectives of the study were 1) to compare the technical efficiency of different feed allocation strategies and energetic efficiency categories in broiler breeder females; 2) to analyze the impact of variables contributing to hen technical inefficiency; and 3) to study the potential effect of feed allocation decisions on economic efficiency broiler breeder flocks.

8.2. Materials and Methods

8.2.1. Stocks and Management

Broiler breeders were managed as reported in Chapter 3. Briefly, a total of 600 Ross-708 (Aviagen Inc., Huntsville, AL) 1 d old pullets were reared in floor pens until 16 wk when 288 birds were placed in individual laying cages. Photostimulation occurred at 23 wk. Beginning at 30 wk, hens were inseminated each wk using 0.5 ml of undiluted semen from 60 roosters. Wheat and soy based diets (Appendix A) in mash form were supplied as follows: starter (2,900 kcal ME, 19% CP, 1.18% lys), from 0 to 3 wk; grower (2,900 kcal ME, 16.7% CP, 1% lys), from 3 to 25 wk; breeder 1 (2,870 kcal ME, 16% CP, 0.72% lys), from 25 to 49 wk; and breeder 2 (2,870 kcal ME, 15.5% CP, 0.70% lys), from 49 to 60 wk.

This research project was carried out in compliance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1984) and was approved by the University of Alberta Faculty Animal Policy and Welfare Committee.

8.2.2. Experimental Design

The design was a 4 x 3 factorial with four feed allocation treatments and three energetic efficiency categories. Feed allocation treatments were assigned randomly at 16 wk. Three groups of birds had feed allocated on a group basis with divergent BW targets achieved by 20 wk of age: Standard, High (Standard x 1.1) and Low (Standard x 0.9). The fourth group had feed allocated on an Individual bird basis following the Standard BW target. Based on residual maintenance ME requirement (RME_m, Chapter 4), birds were classified in three energetic efficiency categories: Low, Average and High, taking the mean ± 0.5 SD as threshold. A higher energetic efficiency meant a lower estimated maintenance requirement. Technical efficiency scores, input radial movements and input slacks (Appendix C) were compared.

Economic efficiency scenarios were analyzed using a one way ANOVA with four feed allocation treatments. The effect of different variables on hen technical inefficiency was estimated.

8.2.3. Data Collection

Individual body weight, sexual maturity age, egg and chick production data were recorded as reported in Chapters 2 and 3. Settable eggs were defined as total minus eggs with defective shells, double yolks, as well as deformed and small (<52 g) eggs. Hatchability was calculated weekly for every hen. Total chick production was calculated as the number of settable eggs multiplied by hatchability. Cumulative ME intake was calculated from 1 d to the end of each wk. Since birds were individually placed at 16 wk, the average ME intake was considered before that age.

8.2.4. Technical. Allocative and Economic Efficiency

Technical efficiency refers to the ability of a firm (in this case a biologic unit) to produce as large as possible an output from a given set of inputs (Farrell, 1957). DEA is a non-parametric method to calculate efficiency based on a linear convex hull approach to frontier estimation (Farrell, 1957; Charnes et al., 1978). DEA involves the use of linear programming to construct a non-parametric piece-wise surface over the data (Coelli et al., 2005), which represents a production function frontier. Technical efficiency of each unit is evaluated relative to this surface (Appendix C). Thereby, efficient and inefficient units can be identified. The most efficient units are given a rating of one, whereas the degree of technical inefficiency of the rest is calculated based on the Euclidian distance of the input-output ratio to the frontier (Galanopoulos et al., 2006).

Assuming data on N inputs (X) and M outputs (Q) for each of I firms, the linear programming problem is described as (Coelli et al., 2005):

$$\begin{aligned} &\text{Min}_{\theta\lambda}\ \theta, \\ &\text{st} \quad -q_i + Q\lambda \geq 0, \\ &\qquad \theta x_i - X\lambda \geq 0, \\ &\qquad \lambda \geq 0, \end{aligned}$$

Where θ is a scalar and λ is a Ix1 vector of constants. The obtained value of θ is the efficiency score of the ith firm. This DEA model assumes constant returns to scale (CRS), which means that for this segment of the production function frontier, a change on the scale of production is equi-proportionally related to input utilization.

A variation from the original DEA model (Banker et al., 1984) relaxes the assumption of CRS, allowing variable returns to scale (VRS). This specification ensures that inefficient firms are only benchmarked against firms of similar size; in this case, against production units at a similar level of production. By using this configuration, scale efficiency can be measured (Appendix D). Scale efficiency is defined as the level at which the production unit approaches the optimal scale, where productivity is maximized. If the technology (in this case, the biologic process) exhibits CRS at the observed input-output combination, the scale efficiency measure equals one (Weersink et al., 1990).

Besides the assumption of CRS, the original DEA model assumes strong disposability. This means that the production unit can costlessly dispose of unwanted inputs (Coelli et al., 2005). However, a production function may exhibit negative marginal product when inputs are used in excess, which is referred to as input congestion. Byrnes at al. (1984) relaxed the assumption of strong disposability of inputs to obtain a measure of congestion efficiency (Appendix D). Congestion efficiency measures the level at which inefficiency is being caused by an excess of input utilization. Therefore, by using DEA, technical efficiency can be decomposed in three different components: 1) scale efficiency, 2) congestion efficiency, and 3) pure technical efficiency (Byrnes et al., 1984).

Measures of technical efficiency under CRS and VRS, as well as scale efficiency were presented in this study. Congestion efficiency was not presented because there was not evidence of input congestion in the data. Additionally, two measures of input reduction were presented: slacks and radial movements (Appendix C). A slack was defined as a non-axial reduction of input utilization that is possible without affecting output production. A radial movement was defined as a feasible axial reduction of input utilization, which means possible reductions in each input to reach the frontier surface.

Considering market constraints such as the input prices, two additional measurements of efficiency can be obtained: allocative and economic efficiency (Appendix C). Allocative efficiency measures to what extent the response of the firm to market signals is appropriate, by choosing a combination of inputs (or producing an adequate combination of outputs) that minimizes cost (or maximizes profit). Allocative efficiency is calculated in reference to the isocost line/surface tangent to the frontier surface. This isocost line/surface is function of the relationship among input prices. Therefore, an increased cost of one input would favour reduction of utilization of that input with respect to other inputs, and vice versa. Economic efficiency considers both technical and allocative efficiency; therefore, it measures the overall efficiency of the firm with respect to the economic objective of cost minimization (Farrell, 1957).

In the current study, each hen was defined as the experimental unit, which used a certain ME intake and took a period of time (wk) to produce a certain output of saleable chicks. For calculation of efficiency scores, the Data Envelope Analysis Program (DEAP, CEPA, Armidale, Australia) was used. The data set consisted of cumulative numbers of chicks, cumulative ME intakes and ages per hen from 31 to 60 wk. Efficiency scores at 60 wk were reported. For the economic efficiency analysis, the cost of capital ($/hen/wk) was expressed as a proportion of the feed cost ($/Mcal ME).

8.2.5. Inefficiency Model

An inefficiency model was designed to measure the contribution of different variables on the technical efficiency of individual hens. The inefficiency model included the estimated hen maintenance requirement from 20 wk (Mcal/d), the cumulative energy intake per unit of average metabolic BW (Mcal/$BW^{0.54}$; Chapter 3) from 20 wk, total BW gain from 16 wk, sexual maturity age, egg production percentage from sexual maturity, average egg weight, non-settable egg percentage and hatch rate per hen. Hen ME_m requirements were estimated as reported in Chapter 4, and were adjusted by feed intake level (RME_m; Chapter 4). Technical efficiency under CRS was the dependent variable. Based on the parameters calculated in the inefficiency model, elasticities were calculated at the mean values as:

$$e = \frac{\partial y}{\partial x} \cdot \frac{\bar{x}}{\bar{y}}$$

Where y was a technical efficiency score and x was an independent variable. Elasticities indicated the percentage change in efficiency per 1% change in the independent variable.

8.2.6. Statistical Analysis

Analyses of variance were performed using the Mixed Procedure of SAS (SAS Institute, Cary, NC) with a critical probability of $P<0.05$. When effects were significant, means were separated using pair wise t tests. A Tobit model (Tobin, 1958) was used (Qlim Procedure; SAS Institute, Cary, NC) to calculate linear coefficients of the inefficiency model. Pearson's correlation coefficients were calculated using the Corr Procedure of SAS (SAS Institute, Cary, NC).

8.3. Results and Discussion

8.3.1. Technical Efficiency

Hens in the Low feed allocation treatment exhibited a lower technical efficiency than hens in the other treatments under both CRS and VRS (Table 8-1). Low hens took from 1.3 to 1.8 wk more time than hens in the other treatments to produce the same number of chicks. That indicates that reproduction (chicks/wk) was negatively affected by a lower feed intake. Fattori et al. (1991), based on a deterministic economic analysis, reported that a severe feed restriction was economically advantageous compared to the standard feeding program of that time. Results of the current study suggest that current BW standards are minimizing feed consumption and maximizing reproduction. Since no significant differences were found in scale efficiency, it may be inferred that all feed allocation treatments were operating on scales where the most efficient hens showed constant returns.

Ad libitum feeding reduces settable egg production and hatchability in modern broiler breeders (Yu et al. 1992). However, under the High feed allocation treatment, no evidence of congestion efficiency (decreased output caused by excessive input use; Byrnes et al. 1984) was found. High technical efficiency was not different than the Standard treatment. However, it was evident the presence of slacks in ME intake for Individual (-4.3 Mcal), Standard (-4.1 Mcal), and High (-12.8 Mcal) hens, which means that feed intake could have been further reduced relative to the proportions of inputs used by the most efficient hens. The presence of non-radial slacks has implications for allocative efficiency and may reflect an inappropriate input mixture (Ferrier and Lovell, 1990), which is addressed in the economic efficiency analysis.

As expected, differences in technical efficiency were proportionally related to energetic efficiency category under CRS ($P<0.0001$). Low EnE hens had lower technical efficiency than Average EnE and High EnE hens under VRS, which implies that Low EnE hens used more inputs than efficient hens at the same scale (comparable chick production levels). Additionally, High EnE hens had greater scale efficiency than Low EnE and Average EnE hens. Thus, part of their better CRS technical efficiency was explained solely by the fact that they were at a higher scale of production. In agreement with a greater ME requirement for maintenance, Low EnE hens had a greater non-radial ME intake slack than Average EnE and High EnE hens.

The interaction between feed allocation and energetic efficiency indicated that technical efficiency of Average EnE hens was negatively affected in the Low feed allocation treatment, possibly because of a reduction in egg production. Interestingly, as feed allocation was bird specific in the Individual treatment, scale efficiency did not differ among energetic efficiency categories, but it did in the other treatments where either Low EnE or Average EnE hens had lower scale efficiency. That suggests that managing individual BW allowed using the inputs according to the scale, which was determined by the reproductive potential. That was particularly relevant for Low EnE birds, as they had lower scale efficiency than Average EnE and High EnE birds in the Standard treatment. In both Individual and Standard treatments, absolute ME intake slacks were greater in Low EnE than Average EnE and High EnE birds.

These results underline the negative relationship between individual maintenance ME requirements and technical efficiency in broiler breeder hens. Greater maintenance requirements were related with a reduced technical efficiency due to higher ME utilization, lower reproductive rates and scale factors. Thus, selecting for low RME_m (Chapter 4) may be an alternative to select technically efficient hens. Nonetheless, technical efficiency of the entire broiler breeder-broiler system must be modeled before using this approach in selection programs, since mechanisms determining growth and feed efficiency in broiler chickens are different than those determining reproduction and feed efficiency in broiler breeder hens (Chapters 4, 5 and 6).

8.3.2. Economic Efficiency

The fact that capital costs ($/hen/wk) were expressed as proportion of feed costs ($/Mcal ME) allowed changes in the slope of the isocost line without assuming monetary values (Table 8-2). Consistent with the hypothesized trade-off between feed intake and time to reach a level of chick production, the analyzed scenarios suggested that the Low feed allocation treatment would be cost inefficient if the capital cost ($/hen/wk) was greater than or equal to 125% of the cost of feed ($/Mcal ME). In contrast, if the capital cost was lower than or equal to 125% of the cost of feed, the High feed allocation treatment would be cost inefficient. For instance, with a feed cost of $0.50/kg ($0.17/Mcal ME in a feed of 2,870 kcal/kg), a capital cost of $0.22/hen/wk would be the point (125%; Table 8-2) at which both Low (Std-10%) and High (Std+10%) feed allocation treatments are economically inefficient. The fact that the economic efficiency of the Standard treatment did not change in the different scenarios whereas Low and High changed in the opposite direction, suggests that the linear isoquant approached a constant proportions isoquant (Chambers, 1988). Therefore, the tangency point of the isocost line was always at the Standard combination whereas High used proportionally more feed and Low used more time than Standard for a given chick production.

For economic inference at commercial level, the question comes to what factors affect the average capital cost per hen. Besides the financial calculation of assets value and long term working capital, there are other eminently technical factors affecting the utilization of capital. For instance, stocking density (Mtileni et al., 2007) and mortality rate (Jiang et al., 1998) are important technical factors that should be taken in account for inferences at an aggregated level. Additionally, it may be argued that fixed costs of maintaining a flock, such as labour and energy costs, could be added to the capital costs in order to asses the total cost per unit of time. Newman et al. (1985), using mice as a model of bio-economic objectives for animal breeding programs, grouped labour and facilities costs as inputs because both are related to units of time.

8.3.3. Technical Inefficiency Model

The inefficiency model aimed to quantify the contribution of biological factors affecting technical efficiency in broiler breeders. Coefficients reflected the response on technical efficiency per unit of change in the independent variables while elasticities evidenced the proportional response (Table 8-3). Other authors have used partial budgeting techniques and sensitivity analysis to determine economic values for broiler breeding (Jiang et al., 1998; Groen, 1998). The advantage of using a technical inefficiency model is that it does not require assumptions regarding financial relationships and input prices, so conclusions are more general.

As expected, the biggest factors influencing technical efficiency were hatching rate (e=0.998) and egg production rate (e=0.962). Improvements in any of these variables would affect technical efficiency approximately in a 1:1 relationship. Although an increase in 1% of non-settable egg production reduced technical efficiency by 0.53%, the proportional effect was not as important (e=-0.02). Sexual maturity age (e=-0.38) showed a greater effect than non-settable egg production. One week delay in sexual maturity would decrease technical efficiency by 1.42%. Fattori et al. (1991) found a 1% increase in pullet cost per each wk of delayed maturity, although did not calculate effects on chick costs.

Hocking (2004) reported that sexual maturity age was accelerated by a higher plane of nutrition, which was consistent with the correlation between sexual maturity age and ME intake (r=-0.39; Table 8-4). Although a greater ME intake may accelerate sexual maturity, the combined effect of greater maintenance requirements and heat increment of feed may annul benefits on technical efficiency. Robinson et al. (2007) demonstrated a reduction in small eggs by delaying photostimulation to allow a greater carcass development before egg production, even though sexual maturity may be delayed. Results of the current study suggest that the effect of a change in photostimulation age on technical efficiency depends on the extent of the non-settable egg reduction: the decrease should be greater than 20% for a 1% delay in sexual maturity to improve technical efficiency.

A 1% change in the estimated maintenance requirements caused a -0.23% change on technical efficiency. This measure of maintenance took in account both the estimated hen variability in the requirements and the actual metabolic BW during production. Nonetheless, an additional part of the effect of maintenance on technical efficiency was the increased egg production of hens with lower estimated requirements as reported in Chapter 4. This coincided with the correlation between maintenance requirements and egg production (r=-0.31; Table 8-4). Another important factor to consider in commercial production is environmental temperature; increasing changes in technical efficiency are expected as temperatures get further from the thermoneutral zone, since the relationship of temperature and maintenance requirements is quadratic in broiler breeders (Sakomura et al., 2004). Surprisingly, ME intake had a greater effect (e=-0.47) on technical efficiency than maintenance requirements did. However, a positive correlation of ME intake and egg production (r=0.55) suggests the presence of a limit where reductions in feed intake would affect negatively reproduction and efficiency.

These results demonstrate that the current BW standard optimizes the trade-off between feed consumption and reproduction. The broiler breeder industry requires the development of relevant live performance indicators impacting economic efficiency, which will allow setting objectives for strategic management, and priorities for research. Economic efficiency methodologies present strengths to evaluate the economic impact of selection and flock management programs since analyses of both biological and allocative factors are possible.

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Table 8-1. Technical efficiency scores under constant returns to scale (CRS) and variable returns to scale (VRS), scale efficiency scores, radial movements and slacks for feed allocation treatments[2] and energetic efficiency categories[3]

Feed allocation	Energetic efficiency	Technical efficiency CRS[4]	VRS[5]	Scale[6] efficiency	Radial movement[7] MEI	Age	Slacks[8] MEI	Age[9]
Individual		0.725^{a}	0.821^{a}	0.879	-20.73	-10.88^{a}	-4.33^{b}	-0.02
Low		0.694^{b}	0.790^{b}	0.865	-22.25	-12.54^{b}	-0.36^{a}	-0.10
Standard		0.721^{a}	0.817^{a}	0.869	-20.78	-10.72^{a}	-4.12^{b}	0.00
High		0.705^{ab}	0.815^{a}	0.863	-23.77	-11.25^{ab}	-12.82^{c}	0.00
SEM		*0.009*	*0.005*	*0.006*	*0.97*	*0.51*	*0.25*	*0.03*
	Low	0.639^{c}	0.796^{b}	0.854^{b}	-27.12^{c}	-14.04^{c}	-6.28^{b}	0.00
	Average	0.712^{b}	0.816^{a}	0.868^{b}	-21.79^{b}	-11.34^{b}	-5.10^{a}	-0.03
	High	0.783^{a}	0.821^{a}	0.884^{a}	-16.74^{a}	-8.65^{a}	-4.85^{a}	-0.06
	SEM	*0.008*	*0.005*	*0.005*	*0.84*	*0.45*	*0.22*	*0.02*
Individual	Low	0.641^{e}	0.835	0.879^{a}	-26.41	-13.90	-5.96^{c}	0.00
Individual	Average	0.733^{cd}	0.815	0.873^{a}	-20.35	-10.75	-2.99^{b}	-0.05
Individual	High	0.801^{a}	0.813	0.884^{a}	-15.43	-7.98	-4.02^{b}	-0.02
Low	Low	0.657^{e}	0.778	0.867^{ab}	-25.10	-14.14	-0.28^{a}	0.00
Low	Average	0.665^{e}	0.787	0.839^{bc}	-23.81	-13.42	-0.70^{a}	-0.08
Low	High	0.759^{bc}	0.807	0.889^{a}	-17.84	-10.05	-0.09^{a}	-0.23
Standard	Low	0.627^{e}	0.782	0.831^{c}	-27.40	-14.13	-5.43^{c}	0.00
Standard	Average	0.737^{bcd}	0.825	0.880^{a}	-19.75	-10.18	-3.93^{b}	0.00
Standard	High	0.799^{a}	0.843	0.895^{a}	-15.20	-7.84	-3.01^{b}	0.00
High	Low	0.628^{e}	0.790	0.840^{bc}	-29.57	-14.00	-13.43^{d}	0.00
High	Average	0.712^{d}	0.836	0.882^{a}	-23.26	-11.01	-12.77^{d}	0.00
High	High	0.774^{ab}	0.821	0.867^{ab}	-18.47	-8.74	-12.27^{d}	0.00
	SEM	*0.017*	*0.010*	*0.012*	*1.70*	*0.90*	*0.44*	*0.05*
Source of variation		----------	----------	----------	Probability	----------	----------	----------
Feeding allocation		0.023	0.0002	0.068	0.079	0.05	<0.0001	---
Energetic efficiency		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	---
Feed allocation x Energetic efficiency		0.028	0.11	0.002	0.58	0.67	0.003	---

[1] The Data Envelope Analysis Program (CEPA, Armidale, Australia) was used.
[2] Three feed allocations were group-based with respect to a BW target. Standard; Low=Standard x 0.9; and High=Standard x 1.1. One feed allocation was Individual bird-based following the Standard BW target.
[3] Based on estimation of residual maintenance ME requirements (Chapter 4). Higher efficiency is related with lower maintenance requirements. Birds were classified into three energetic efficiency categories: Low, Average, and High.
[4] Constant returns to scale. Calculation assumes that input proportions are not affected by scale.
[5] Variable returns to scale. Calculation assumes that input proportions are affected by scale of production. Individuals are benchmarked against individuals at similar chick production.
[6] Measure differences between CRS and VRS technical efficiency.
[7] Movement in ME intake and age to reach the production frontier.
[8] Possible additional reductions in inputs given the linear approximation of the isoquant.
[9] No probability values were reported because distribution was not normal.

Table 8-2. Price sensitivity analysis on economic efficiency[1] comparing feed allocation treatments[2]

Capital/feed cost[3]	Individual	Low	Standard	High	F Probability
	----------------------Economic efficiency----------------------				
25%	0.715[a]	0.685[ab]	0.715[a]	0.655[b]	0.017
50%	0.714[a]	0.680[ab]	0.715[a]	0.660[b]	0.027
75%	0.714[a]	0.675[ab]	0.715[a]	0.664[b]	0.035
100%	0.714[ab]	0.671[bc]	0.715[a]	0.668[c]	0.038
125%	0.714[a]	0.668[b]	0.715[a]	0.671[b]	0.039
150%	0.713[a]	0.666[b]	0.715[a]	0.673[ab]	0.037
175%	0.713[a]	0.663[b]	0.715[a]	0.675[ab]	0.034
200%	0.713[a]	0.661[b]	0.715[a]	0.677[ab]	0.032

[1] The Data Envelope Analysis Program (CEPA, Armidale, Australia) was used.
[2] Three feed allocations were group-based with respect to a BW target. Standard; Low=Standard x 0.9; and High=Standard x 1.1. One feed allocation was Individual bird-based following the Standard BW target.
[3] Capital cost is expressed as $/hen/wk and feed cost as $/Mcal ME. The ratio was used to avoid using monetary values.

Table 8-3. Parameter estimates of technical inefficiency model[1]. R^2=88.6

Parameter	Unit	Estimate (t probability)	Elasticity[(2)]
Intercept	----	-0.518 (0.0002)	----
Maintenance[3]	Mcal/d	-0.603 (0.018)	-0.225
ME intake[4]	$Mcal/kg^{0.54}$	-0.005 (0.0001)	-0.467
Total gain[5]	kg	-0.031 (0.014)	-0.078
Egg production[6]	%	0.963 (<0.0001)	0.962
Egg weight[7]	g	0.011 (<0.0001)	0.939
Sexual maturity[8]	d	-0.001 (0.0003)	-0.382
Non-settable eggs[7]	%	-0.539 (<0.0001)	-0.018
Hatch rate[7]	%	0.828 (<0.0001)	0.998
Sigma[(9)]	----	0.044 (<0.0001)	----

[1] A Tobit model for limited variables was used.
[2] Change in technical efficiency for 1% change in the independent variable. Calculated at the mean values.
[3] Average daily maintenance requirement from 20 to 60 wk of age. Included the effect of metabolic BW and variability in individual requirements.
[4] Cumulative intake per unit of average metabolic BW. $BW^{0.54}$ was calculated in a previous study (Chapter 3).
[5] Total BW gain from 20 to 60 wk of age.
[6] Individual egg production rate from first egg to 60 wk.
[7] Individual average until 60 wk of age.
[8] Age at first egg.
[9] Standard deviation of the error term.

Table 8-4. Pearson's correlation coefficients of variables included in the technical inefficiency model

Variable	ME intake	Total gain	Egg production	Egg weight	Sexual maturity	Non-set. eggs	Hatching rate[5]
Maintenance[1]	0.12	0.59	-0.31	0.00	-0.09	0.05	-0.03
	(0.06)	(<0.001)	(<0.001)	(0.94)	(0.16)	(0.41)	(0.65)
ME intake[2]		-0.09	0.55	-0.07	-0.39	0.03	-0.01
		(0.13)	(<0.001)	(0.26)	(<0.001)	(0.58)	(0.93)
Total gain[3]			-0.33	0.02	0.09	0.09	0.01
			(<0.001)	(0.76)	(0.15)	(0.15)	(0.86)
Egg production[4]				-0.30	-0.25	0.01	0.07
				(<0.001)	(<0.001)	(0.85)	(0.24)
Egg weight[5]					0.21	0.11	-0.12
					(0.001)	(0.08)	(0.06)
Sexual maturity[6]						-0.02	-0.04
						(0.69)	(0.51)
Non-set. eggs[5,7]							-0.49
							(<0.001)
Units	Mcal/kg$^{0.54}$	kg	%	g	D	%	%
Mean	61.9	1.77	0.71	61.4	186.8	0.02	0.86
SD	2.6	0.27	0.09	3.6	7.4	0.04	0.09

[1] Average daily maintenance requirement from 20 to 60 wk of age. Included the effect of metabolic BW and variability in individual requirements.
[2] Cumulative intake per unit of average metabolic BW. BW$^{0.54}$ was calculated in a previous study (Chapter 3).
[3] BW gain from 20 to 60 wk of age.
[4] Individual egg production rate from first egg to 60 wk.
[5] Individual average until 60 wk of age.
[6] Age at first egg.
[7] Non-settable eggs. Include eggs with abnormal shape, shell defects and double yolk.

Chapter 9. Optimizing the Broiler Breeder – Broiler Production System

9.1. Conclusions and Applications

The main technical variables controlled by broiler breeder managers are feed allocation and BW profiles. These results demonstrated that altering the BW profile of underweight pullets to reach the BW target before 20 wk of age increased egg production, although more small eggs were produced. This increased egg production was mainly due to an earlier onset of production. Individual-based feed allocation did not decrease variability on ovarian morphology at sexual maturity, but it increased variability at the end of the production cycle. Individual-based feed allocation, although may help to select birds with superior rates of lay by annulling limiting effects of low BW, may also decrease the dietary nutrient availability for egg production of efficient hens. Assessment of energetic efficiency for maintenance appears to be a stronger method to select broiler breeders with superior rates of lay and productivity as compared to individually-based feed allocation.

In order to assess animal energetic efficiency and nutrient partitioning consistently, better prediction equations of ME intake were developed. The most important contribution of this thesis to current models of energy balance was the utilization of mixed models to estimate individual maintenance requirements, which were assumed to be a function of the absolute or relative energy intakes. This assumption allowed separating energetic efficiency in two components: 1) energetic efficiency of maintenance requirements, and 2) residual energetic efficiency. The former, which was called residual maintenance ME requirement (RME_m), estimated systematic variation in maintenance requirements, and the second, residual feed intake (RFI), included all other sources of variation. The RME_m proved to be consistently related to egg production, chick production, and feed conversion rates of broiler breeders regardless of the feed allocation strategy. This measurement presents a high potential for genetic selection towards greater feed efficiency in chickens, and other species. In broilers, estimation of RME_m together with RFI presents practical advantages as compared to current methodologies for assessment of feed efficiency because the effect of feed intake and body size can be more accurately accounted for. Therefore, standardization is possible.

This thesis demonstrated that maternal energetic efficiency is deeply related to broiler performance. Figure 9-1 illustrates productive profiles of broiler breeder hens classified by RME_m and RFI. Results of this thesis suggest that high maintenance requirements in broiler breeder hens may be related with increased muscularity and may be advantageous for broiler growth when other efficiency traits are present (low RFI). Even though minimizing maintenance requirements may increase broiler breeder productivity, it may not be compatible with maximizing broiler growth and meat yield. However, maximizing broiler and breeder feed efficiency may be achieved simultaneously. The trade-off between maintenance requirements and muscle yield may shape strategies of broiler genetic selection in the future.

Utilization of production economics techniques such as data envelope analysis to assess technical efficiency of individual animals provided a valuable tool to relate biological and economic factors. By using these techniques, technical-biological and allocative factors can be separated. Therefore, specific strategies to improve economic efficiency may be developed. A basic analysis of two inputs (feed and time) and one output (chicks) was used to study technical and economic efficiency in broiler breeders. Technical efficiency was positively related to hen energetic efficiency. However, low feed intakes may decrease technical efficiency. An inefficiency model quantified factors affecting technical efficiency in broiler breeders. The most important factors were hatching rate, total egg production, dietary thermogenesis, sexual maturity age and individual maintenance requirements. The current standard BW profile proved to optimize economic efficiency of Ross-708 flocks. Changes in BW profile to optimize economic efficiency in response of capital or feed price changes may be limited to small deviations from the current standard profile.

Overall, this thesis provided new tools for designing strategies to:

- Modify the broiler breeder - broiler production frontier. Breeder companies can optimize the relationship between energetic efficiency and broiler performance. Additionally, they can quantify more accurately economic effects of modifications in breeding programs and respond more effectively to changes in market conditions.
- Achieve the broiler breeder production frontier in the field. Producers can optimize flock technical efficiency by managing BW profiles for segments of the population.
- Make right input utilization decisions in broiler breeder production. Producers can maximize economic efficiency by controlling more effectively BW profiles.

9.2. Future Considerations

- The egg production benefits of correcting the BW profile of underweight broiler breeder pullets deserves further research to avoid reductions in egg weight. Earlier BW adjustments during rearing and nutritional means to improve egg weight during early production may be considered.

- The effect of increasing egg production of light broiler breeder females on mean broiler performance should be economically modeled before recommending these strategies at the commercial level.
- Utilization of prediction equations of ME intake in broiler breeders might improve consistency in BW control in the field. However, the equations developed in this thesis require to be adjusted by temperature and activity effects of floor housing systems.
- The model of energy partitioning of this thesis requires validation with calorimetric and/or comparative slaughter studies. Conversely, analysis of existent data of energy utilization would greatly benefit by using the mathematical approach of this thesis, which is consistent with the assumptions of accepted theories of energy partitioning.
- Calculation of individual maintenance requirement and its relationship with energy intake levels may be used to evaluate breeds and management practices by energetic efficiency, and to estimate heat increment of feedstuffs and diets. New methodologies for feedstuff quality evaluation may be developed.
- Empirical estimation of energy requirements by considering an energy-mass balance may be a powerful tool to analyze field data and develop strategies to improve economic efficiency.
- The RME_m improved the information supplied by RFI without requiring additional parameters. Current work in RFI in different species could be improved by analyzing RME_m as well.
- For future utilization of RME_m in broilers, the experimental design should have different feed restriction levels to increase variability on the intake-gain response. Additionally, an accurate measure of environmental temperature is essential.
- In order to use the RME_m as a selection criterion in meat-type chickens, further studies on genetic variation are required. That would also allow developing simulation models of energy partitioning for the supply chain because heritability of energy utilization traits from broiler breeders to broilers could be modeled.
- Molecular genetics techniques may be used to find genetic markers correlated to RME_m and/or RFI. The current methodology requires a fairly big set of phenotypic information

and may be costly. Finding correlated genetic markers would facilitate implementation of these measurements as selection criteria.

- Results of this thesis suggest that differences in muscle fibre numbers may be related to differences in maintenance requirements. Breast muscle myofibre numbers should also be analyzed. The technique used to dissect and preserve the anatomical position of *pectoralis* muscles must be carefully considered in future studies. Utilization of older chicks (10 to 15 d) may also facilitate this task.
- Studying the relation of myofibre types with energetic efficiency measures may give additional information about the mechanisms leading to energetic efficiency in chickens.
- A great variety of mechanisms of energetic efficiency from intracellular pathways to mechanical temperature isolation barriers may also be studied by using the approach of this thesis.
- The broiler breeder industry would benefit by using the economic efficiency model of this thesis to assess flock performance because feed and capital utilization can be included in a single measurement (Appendix E).
- Stochastic estimations of production frontiers using field data may be the next step for application of production economics techniques in the poultry meat industry. This would allow the improvement of feed back systems for the industry that could identify priorities for selection programs and scientific research.
- Data envelope analysis and stochastic production frontiers have a great potential to link biological-technical and economic issues in animal science. More complex multi-input and multi-output problems can be analyzed with these standardized methods that allow technical and economic optimization.

Maternal RME_m	Maternal RFI −	Maternal RFI +
+	Breeder production + Broiler growth +++ Broiler breast yield +++ Broiler efficiency ++	Breeder production + Broiler growth ++ Broiler breast yield +++ Broiler efficiency ++
−	Breeder production +++ Broiler growth ++ Broiler breast yield + Broiler efficiency +++	Breeder production +++ Broiler growth + Broiler breast yield + Broiler efficiency +

Figure 9-1. Productive profile of birds classified by residual feed intake (RFI) and residual maintenance ME requirement (RME_m). Different production variables were quantified among hen efficiency categories (RFI x RME_m) by a relative scale from + (lowest) to +++ (highest).

Appendix A. Composition and Analysis of Broiler Breeder Diets

Ingredient and analysis	Starter (0 to 3 wk)	Grower (3 to 25 wk)	Breeder 1 (25 to 49 wk)	Breeder 2 (49 to 60 wk)
	(g/kg)			
Wheat	394.1	479.9	546.2	562.4
Soybean meal (44% CP)	175.9	100.5	104.8	90.7
Ground corn	150.0	150.0	64.8	58.5
Oats	150.0	150.0	100.0	100.0
Canola meal	50.0	50.0	50.0	50.0
Canola oil	23.8	14.5	32.5	33.0
Dicalcium phosphate	19.8	18.5	16.6	13.5
Calcium carbonate	15.8	14.1	70.4	77.7
Choline chloride premix	5.0	5.0	5.0	5.0
Broiler premix[1]	5.0	5.0	0.0	0.0
Layer premix[2]	0.0	0.0	5.0	5.0
Salt	4.5	4.5	3.2	2.7
D, L-methionine	2.1	3.8	0.9	0.7
L-lysine	3.6	3.7	0.2	0.4
Avizyme	0.5	0.5	0.5	0.5
Total	1,000.0	1,000.0	1,000.0	1,000.0
Calculated nutrient composition				
CP (%)	19.0	16.7	16.0	15.5
ME (kcal/kg)	2,900	2,900	2,870	2,870
Calcium (%)	1.10	1.00	3.10	3.31
Available phosphorus (%)	0.50	0.47	0.43	0.37
Lysine (%)	1.18	1.00	0.72	0.70
Methionine (%)	0.52	0.65	0.37	0.34

[1]Broiler premix provided per kilogram of diet: vitamin A (retinyl acetate), 10,000 IU; cholecalciferol, 2,500 IU; vitamin E (DL-α-tocopheryl acetate), 35 IU; vitamin K, 2.0 mg; pantothenic acid, 14 mg; riboflavin, 5.0 mg; folacin, 0.8 mg; niacin, 65 mg; thiamine, 2.0 mg; pyridoxine, 4.0 mg; vitamin B12, 0.015 mg; biotin, 0.18 mg; iodine, 0.5 mg; Mn, 70 mg; Cu, 8.5 mg; Zn, 80 mg, Se, 0.1 mg; Fe, 100 mg.

[2]Layer premix provided per kilogram of diet: vitamin A (retinyl acetate), 12,000 IU; cholecalciferol, 3,000 IU; vitamin E (DL-α-tocopheryl acetate), 40 IU; vitamin K, 2.0 mg; pantothenic acid, 14 mg; riboflavin, 6.5 mg; folacin, 1.0 mg; niacin, 40 mg; thiamine, 3.3 mg; pyridoxine, 6.0 mg; vitamin B12, 0.02 mg; biotin, 0.2 mg; iodine, 0.5 mg; Mn, 75 mg; Cu, 15 mg; Zn, 80 mg, Se, 0.1 mg; Fe, 100 mg.

Appendix B. Composition and Analysis of Broiler Diets

Ingredient and analysis	Starter	Grower	Finisher
		(g/kg)	
Corn	180.0	180.0	150.0
Vegetable fat	37.7	33.6	41.3
Fish meal - menhaden	30.0	50.0	35.1
Soybean meal	268.7	162.1	151.0
Wheat	429.3	532.4	580.4
Calcium carbonate	15.0	10.5	10.7
Dicalcium phosphate	15.5	10.0	10.8
Salt	4.3	3.4	3.6
L-lysine	2.3	1.5	1.5
D,L-methionine	2.3	1.0	0.9
L-threonine	0.5	1.0	0.3
Broiler Premix[1]	14.5	14.5	14.5
Total	1,000.0	1,000.0	1,000.0
Calculated nutrient composition			
CP (%)	23.0	20.2	19.0
ME (kcal/kg)	3,068	3,152	3,196
Calcium (%)	1.10	0.90	0.85
Available phosphorus (%)	0.50	0.45	0.42
Lysine (%)	1.35	1.10	1.01
Methionine (%)	0.60	0.46	0.42
Methionine + cysteine (%)	0.97	0.79	0.75

[1] Broiler premix provided per kilogram of diet: choline chloride premix, 3000 mg; generic enzyme, 500 mg; coccidiostat, 500 mg; antibiotic growth promoter, 500 mg; vitamin A (retinyl acetate), 10,000 IU; cholecalciferol, 2,500 IU; vitamin E (DL-α-tocopheryl acetate), 50 IU; vitamin K, 2.0 mg; pantothenic acid, 14 mg; riboflavin, 5.0 mg; folacin, 0.8 mg; niacin, 65 mg; thiamine, 2.0 mg; pyridoxine, 4.0 mg; vitamin B12, 0.015 mg; biotin, 0.18 mg; iodine, 0.5 mg; Mn, 70 mg; Cu, 8.5 mg; Zn, 80 mg; Se, 0.1 mg; Fe, 100

Appendix C. Linear Approximation of Frontier Isoquant

Frontier Isoquant

An isoquant is defined as a function that describes input combinations necessary to produce a determined output quantity. Technology determines the frontier production function, which refers to the input-output relationships under ideal conditions of production. The data envelope analysis method performs a linear approximation of the frontier isoquant. Figure C-1 represents this linear approximation in reference to firms C, D and E (y=Q). Combinations of inputs x_1 and x_2 are used to produce Q units of output y.

Technical Efficiency

The approximation of the frontier isoquant is based on firms C, D and E (Figure C-1) because these points had the lowest input utilization to produce Q units of output y. Point A represents an inefficient firm using x_1 and x_2 at the same ratio as D, but at greater quantities. The ratio $\overline{OD}/\overline{OA}$ is defined as the technical efficiency of A. Technical efficiency of firms C, D, and E equals one (Farrell, 1957; Coelli et al., 2005).

Slacks

Since sections of the frontier run parallel to the axes, it is argued that technical efficiency of point B' (Figure C-1) is questionable. Firm B could further reduce utilization of input x_2 without an output reduction. The segment $\overline{B'C}$ is known as input slack of the firm B.

Radial Movements

Radial movements are possible reductions of input utilization to reach the frontier isoquant with respect to the origin. Therefore, radial movement of firm B (Figure C-1) is the movement along axis x_1 and x_2 to reach the point B' on the frontier isoquant.

Isocost Line

An isocost line ($\overline{x_1^{'}x_2^{'}}$; Figure C-2) represents input combinations with equal cost. The slope of the isocost line is determined by the ratio of input prices ($-w_1/w_2$). The tangency point of the isoquant y=Q and the isocost line $\overline{x_1^{'}x_2^{'}}$, determines the cost minimizing proportion of inputs (that used by firm D).

Allocative Efficiency

Firm A (Figure C-2) is technically inefficient but allocatively efficient because it is using the same input ratio as firm D, but at greater quantities. Instead, firm B is technically and allocatively inefficient. Allocative efficiency of firm B is defined as the ratio $\overline{OB''}/\overline{OB'}$ (Farrell, 1957; Coelli et al., 2005).

Economic Efficiency

Economic efficiency takes into account both technical and allocative efficiency. Economic efficiency of firm B is defined as the ratio $\overline{OB'}/\overline{OB}$, and it is equal to the multiplication of technical and allocative efficiency of this firm ($\overline{OB'}/\overline{OB}$ x $\overline{OB''}/\overline{OB'}$; Farrell, 1957; Coelli et al., 2005).

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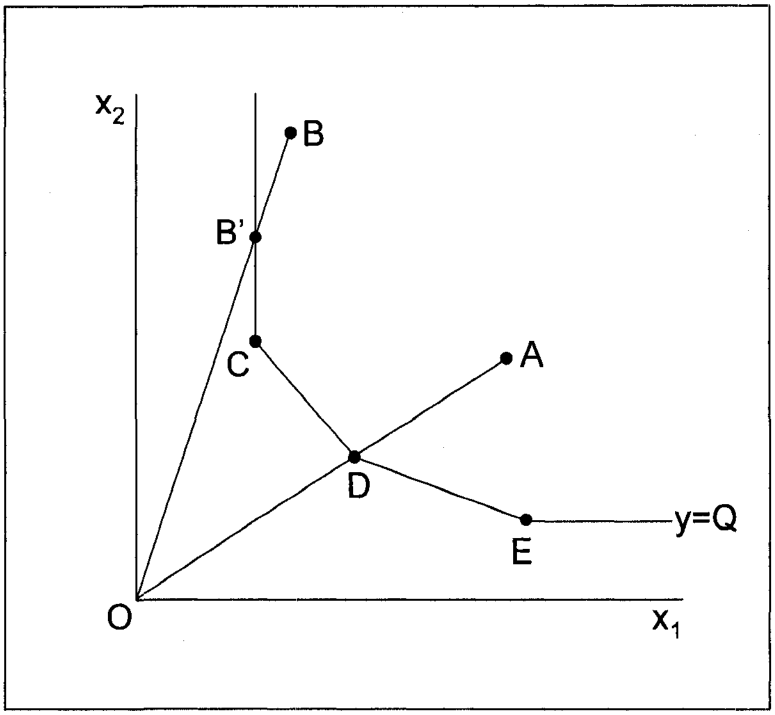

Figure C-1. Linear approximation of frontier isoquant. Combinations of inputs x_1 and x_2 are used to produce Q units of output y. The frontier isoquant is linearly approximated in reference to the most efficient units of production: C, D and E.

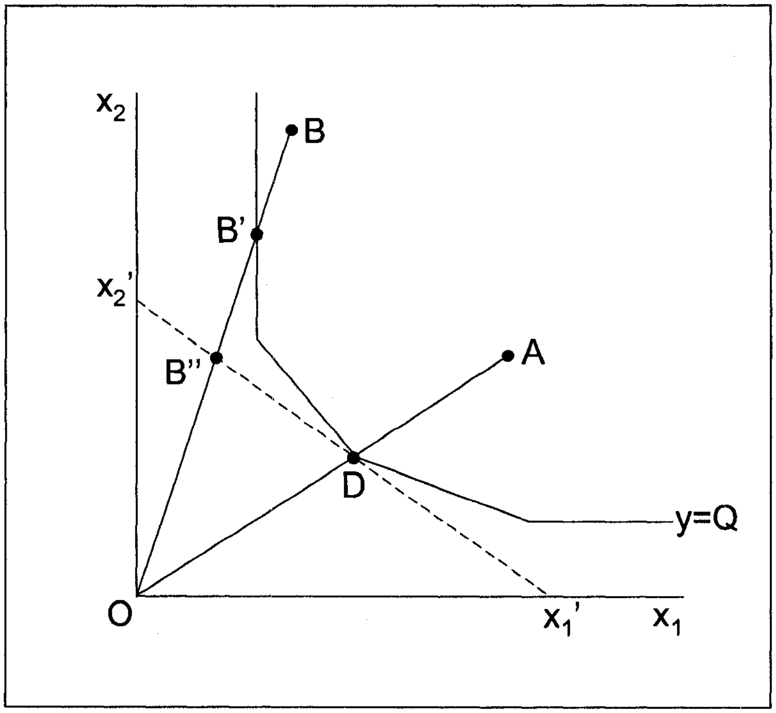

Figure C-2. Linear approximation of frontier isoquant and isocost line. Combinations of inputs x_1 and x_2 are used to produce Q units of output y. The isocost line $\overline{x_1^{'}x_2^{'}}$ determines input combinations with the minimum cost.

Appendix D. Scale and Congestion Variations in the Data Envelope Analysis Methodology

Variable Returns to Scale

Relaxing the assumption of constant returns to scale (CRS) to allow variable returns to scale (VRS), the DEA model can be solved by adding a convexity constraint: $I1'\lambda=1$. For a matrix of N inputs (X), M outputs (Q) and I firms, the linear specification is described as (Banker et al., 1984; Coelli et al., 2005):

$$
\begin{aligned}
\text{Min} \quad & _{\theta\lambda}\ \theta, \\
\text{St} \quad & -q_i + Q\lambda \geq 0, \\
& \theta x_i - X\lambda \geq 0, \\
& I1'\lambda = 1, \\
& \lambda \geq 0.
\end{aligned}
$$

Where I1 is an Ix1 vector of ones. This modification forms a convex hull of intersecting planes that envelope the data points more tightly than the CRS conical hull. Scale efficiency is calculated as technical efficiency under CRS divided by technical efficiency under VRS. Therefore, if the production function exhibits CRS at the analyzed scale of production, scale efficiency equals one.

Weak Input Disposability

Additionally to the assumption of VRS, the assumption of strong disposability of inputs can be relaxed to allow weak input disposability. This DEA model changes the inequalities in the input restrictions to equalities and introduces a δ parameter in the input restrictions. The problem becomes (Byrnes et al., 1984; Coelli et al., 2005):

$$
\begin{aligned}
\text{Min} \quad & _{\theta\lambda}\ \theta, \\
\text{St} \quad & -q_i + Q\lambda \geq 0, \\
& \delta\theta x_i - X\lambda = 0, \\
& I1'\lambda = 1, \\
& \lambda \geq 0, \\
& 0 < \delta \leq 1.
\end{aligned}
$$

Congestion efficiency is calculated as technical efficiency under VRS divided by technical efficiency under weak input disposability. Therefore, if the production function does not exhibit input congestion at the analyzed scale of production, congestion efficiency equals one.

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Appendix E. An Application of Economic Efficiency for Assessment of Broiler Breeder Flocks[1]

A very common problem for animal production managers is finding adequate methods to measure the efficiency of the production process and the farm as an economic entity in a meaningful and consistent fashion. It's important to find out whether the technical and managerial decisions are being effective. In the case of broiler breeder production, there are different levels of sophistication in the evaluation of flocks and farms. They go from the simple percentage of production, right up to the measurement of unitary costs in real time. In this article, we present an alternative approach to measure flock and farm success based on existing methodologies of production economics.

The most straight forward evaluation method used to measure flock performance is total egg production. Using percent production as a measure of success is very tempting. Having a flock peaking at 90 per cent definitely feels good, whether you are selling eggs or chicks. But mortality and settable egg rates need to be accounted for; therefore, many companies and farmers prefer to measure settable eggs per housed hen. This is a fairly good indicator of the efficacy of the production process because at least we know if we are setting (or selling) the number of eggs we could if everything went well and if we are meeting our production budget.

However, for a company that sells one-day-old chicks or is paid based on potential chick production, eggs per housed hen only tells part of the story of what is happening on the farm. Here, different methods to assess saleable chick production are used. Some companies can only generate an estimated hatchability rate for each flock whereas other companies are capable of having very accurate counts of chick production per flock.

In any case, managers can calculate chick production per housed hen, which is an even better indicator of the efficacy of the process. But does this really measure economic success? Not necessarily. Some companies use feed conversion ratios to try to overcome the limitations of simple production parameters. However, even a low feed-to-chick ratio may not translate into improved economic results if feed intake was limiting and production rates were compromised.

From the production perspective, what really determines the competitiveness of broiler breeder companies is the cost of chicks. In turn, there are two main questions that determine the cost: 1) Is

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[1] A version of this paper has been submitted for publication in the Canadian Poultry Magazine.

the flock in the most biologically appropriate conditions to have ideal performance?; and 2) Is the manager making right input utilization decisions?

Companies may be capable of answering these two questions as a whole on a day to day basis if they have a real time production/accounting system, but we would venture to say that there are still many companies that only have an estimate of unitary costs at the end of the production cycle, when it is too late to make any decision. Even assuming that the company knows what the unitary cost of today's chicks is, it is not easy to measure the causes of a higher than normal cost. At the very least, it is time consuming and may not account for the nature of the biologic process, particularly if the analysis is only done from an accounting perspective.

A New Measure of Performance

These complexities of commercial production brought us to develop a new approach to measure flock and farm performance, which is both simple and effective. This approach is based on the measure of economic efficiency, which is an area of production economics that has been used to evaluate national industries and firms, especially in the manufacturing sector. For the purpose of this article, all concepts are focused on one-day-old chick production, and each broiler breeder flock is considered to be the unit of production.

Economic efficiency measures the extent to which the flock has the lowest unitary chick cost possible. A flock with 100 per cent economic efficiency has the lowest chick cost. As previously discussed, this measure is made up of a biologic/technical and input utilization factors, which are measured by what is called technical and allocative efficiency, respectively.

Broiler breeder production involves a great variety of inputs. Consequently, some simplifications are necessary to develop applicable methods. For this particular example, we are accounting only for two types of inputs: time related inputs and feed. The rationale of using time related inputs is that capital and fixed costs have an important share on the unitary costs of one-day-old chicks. On the other hand, feed is usually the single most important cost of animal production.

Under optimal conditions, broiler breeder flocks will require a minimum combination of feed and time to produce a number of chicks (e.g. 130 chicks). This optimal input-output relationship is called the "frontier of production." This frontier is determined by the genetics of the strain and is represented by the line in Figure E-1. Flocks A, B, and C are all technically efficient because birds could not do any better in optimal conditions. In contrast, flock D is utilizing more feed and time than should be necessary with that input combination, probably because of management or health problems; this flock is therefore technically inefficient.

However, flock B is using more feed, and flock C is using more time than flock A to produce 130 chicks. This situation usually occurs because a manager decides (or allows) to use a higher (flock B) or lower (flock C) body weight profile than what it is recommended for this strain of broiler breeders despite birds being managed in optimal environmental conditions. These decisions are responsible for a cost increment.

Both flocks B and C are allocativelly inefficient because the input combination is not optimal. The more the cost of feed increases, the more allocativelly inefficient flock B becomes due to unnecessary expensive feed being used. The more the fixed and capital costs increase, the more allocativelly inefficient flock C is because birds are taking too long to produce these chicks. The combination of both technical and allocative efficiency determines the economic efficiency of the flock, i.e. how far is the flock from the minimum cost?

Since production frontier calculation requires complex statistical methods, we have made some assumptions to develop a simple method for flock assessment. We can compare economic efficiency of flocks with the production targets based on the input cost conditions of a farm or company. Let's assume that point A is the target feed-time combination to produce 130 chicks. We can draw a line (line 1, Figure E-2) of input combinations that have the same cost as target A, although some of these combinations may not be technically possible.

The slope of this line depends on the relative cost of a kilogram of feed versus the average weekly cost of having a bird in the barn. If line 1 defines the minimum cost combinations, flock B is more efficient than flock C because it is closer to the line. If the cost of feed increases relative to the capital and fixed costs per hen, the position of the line changes (line 2) and we would prefer to use less feed; so, flock C would be more efficient than flock B.

Figure E-2 is just a geometrical representation of what being economically inefficient means. Of course, what we want is to be able to assess economic efficiency at every level of production. In our experience, the performance objectives provided by the primary breeder companies constitute a fairly good indicator of the input combination that determines the production frontier. Then, having a table of input combinations to produce each level of output (saleable chicks or settable egg numbers) allows calculating economic efficiency with relatively simple equations.

For example, we can calculate economic efficiency (EE) of flock B (Figure E-2) relative to the target A (Eq. 1). The variables that we need are the feed and time used by flock B, the target feed and time to produce this number of chicks ($feed_A$, $time_A$), the cost of feed ($cost_{feed}$; \$/kg), and the average weekly capital and fixed costs per housed hen ($cost_{time}$; \$/hen/wk). Some instrumental variables (a, b, c) are also used just to make equations simpler in the calculation of optimum feed ($feed_{opt}$) and time ($time_{opt}$).

$$a = \frac{feed_B}{time_B}$$

$$b = \frac{(feed_A . cost_{feed}) + (time_A . cost_{time})}{cost_{feed}}$$

$$c = \frac{cost_{time}}{cost_{feed}}$$

$$time_{opt} = \frac{b}{a + c}$$

$$feed_{opt} = a.time_{opt}$$

$$EE_B = \frac{\sqrt{feed_{opt}^2 + time_{opt}^2}}{\sqrt{feed_B^2 + time_B^2}} \qquad \text{Eq.1}$$

The EE of flock B should correspond to a value from 0 to 1. However, it is possible that good flocks will exhibit values greater than 1 because we are using the target values to define the frontier. In general, a better economic performance is expected from flocks with greater EE. These EE values can be used independently to compare flocks and farms, or to perform additional analyses.

For instance, the effect of mortality as a source of inefficiency can be evaluated by comparing EE at zero mortality, normal mortality and actual mortality scenarios. Two flocks from the same farm were compared at 50 wk of age; both had similar peak of production, but one of them (flock 1) had greater mortality than the other (flock 2). The EE scores were 0.87 and 0.94 for flock 1 and 2, respectively. When analyzed on a zero mortality scenario, EE scores were 0.93 and 0.96. Therefore, chicks from flock 1 were expected to have 13% over cost compared to the target unitary costs. From that 13%, 6% was caused by mortality and 7% was caused by management or health issues. For flock 2, 2% over cost was caused by mortality and 4% by management or health. Evidently, there was still potential in this farm to reduce unitary costs besides the effect of any eventual sanitary complication. A 4% reduction in cost can make a big difference in the economic results of the farm. Other factors such as settable egg and hatchability rates can also be assessed using this type of analysis.

Overall, the utilization of economic efficiency as a criterion to evaluate flocks has the advantage of a more consistent relationship with the actual cost of the chicks and the economic results of the company. A more objective system will often mean better decisions and better results. Instead of focusing on increasing production, managers can focus on optimization of economic results, which is what the company expects from them. Ultimately, financial success is not always associated with the highest number of chicks.

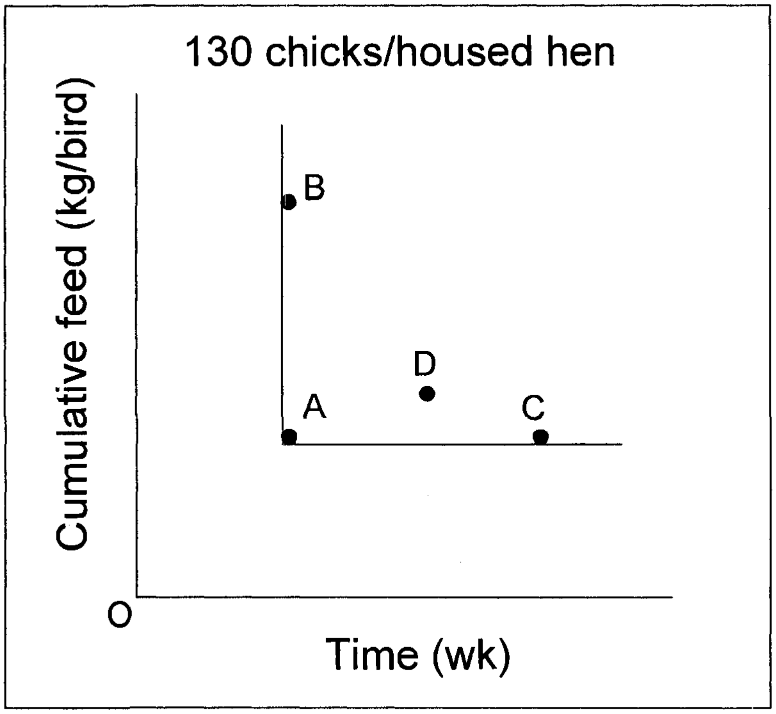

Figure E-1. Possible combinations of cumulative feed intake and time to produce a certain number of chicks are represented by the production frontier line. Flocks A, B, and C are technically efficient, but flock D is not.

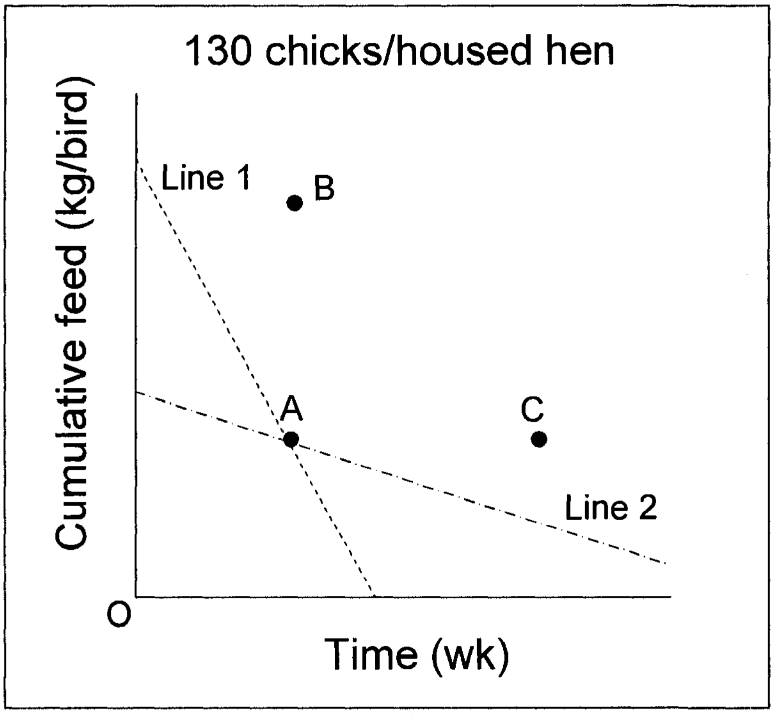

Figure E-2. Minimum cost combinations of cumulative feed intake and time to produce a certain number of chicks are represented by the broken lines. Flock A is economically efficient and flocks B and C are not.