12-2018

The Evaluation of Genetic and Phenotypic Differences Associated with Short Term Selection of Four Different Feed Efficiency Strategies in Japanese Quail

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The Evaluation of Genetic and Phenotypic Differences Associated with Short Term Selection of Four Different Feed Efficiency Strategies in Japanese Quail

A dissertation submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy in Poultry Sciences

by

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Literature Review

Per capita chicken consumption in the United States surpassed that of beef in 1992 (National Chicken Council, 2018). Since then chicken consumption has increased by 50% while beef consumption has steadily declined. By 2020, chicken is expected to become the world's most consumed meat (OECD/FAO, 2014). The ascent of chicken as a protein source is due to a variety of characteristics including religious neutralness, short generation intervals, reproductive efficiency, and dual-purpose capabilities. While it is hypothesized that chickens were domesticated as early as the Neolithic Period, the development of the modern broiler began less than 100 years ago (Siegel, 2014).

The modern broiler is a result of mass selection with emphasis placed on production traits such as body weight, yield, feed consumption, gain, and feed efficiency. The short generation interval and large number of progenies produced per mating pair, allows geneticists to fully utilize the techniques of quantitative genetics. Utilization of these techniques has led to rapid genetic improvement, demonstrated by Havenstien et al. (2003) and their calculation that 85-90 percent of progress in poultry production has been through genetics alone. Initially genetic selection focused on bodyweight and breast yield, as these traits have moderate heritabilities and are of high economic importance. Selection for increased bodyweight was also considered an indirect selection method to improve feed efficiency (FE). However, selecting for increased body weight increased fat deposition and maintenance costs (Leclerq et al., 1989; Pym, 1990). Increases in fat yield leads to several economic disadvantages such as decreased yield of premium products, negative consumer perception, and increased production costs. To address these issues poultry breeders began selecting for improved FE.

Feed efficiency is described as the ability of the bird to convert feed consumed into a desired output. For the purpose of this manuscript FE is the bird's ability to convert consumed feed into body mass. Accurately measuring FE requires considerable investment to be made in facilities and human capital. Individual caging or electronic id systems are required to determine individual feed consumption, along with human labor to weigh birds and feed at the beginning and end of test periods. The economic justification for these investments is a consequence of feed costs contributing between 50 to 70% of all costs associated with raising broilers. Minor improvements in FE is therefore capable of substantially reducing production costs. In 2012, the US produced approximately 34 billion lbs of broiler meat at an average FCR of 1.9. In 2017, average FCR for US poultry production was 1.85. For comparison purposes if we assume feed cost was $250 ton in 2012 and 2017 the five-point improvement in FCR between these periods would result in 1.7 billion lbs of less feed to produce the same quantity of broiler meat. The reduction in feed would result in a savings of over 212 million USD (National Chicken Council, 2018).

In addition to substantial money savings, improvements in FE impacts sustainability. By 2050 it is projected the world's population will reach 9.1 billion people. The 34% increase in population is projected to primarily occur in developing countries and result in increased urbanization (FAO, 2009). The increase in human population and decreasing farmland places a great burden on the agriculture sector to increase yield at an efficient rate. Poultry researchers will continue to find opportunities to improve nutrition and management practices; however, as Havenstein et al. (2003) showed, genetic selection offers the greatest means for improving poultry production efficiency. Selection for FE will need to continue to be a primary focus of poultry breeders and poultry researchers will need to continue to better understand the variety of factors impacting FE, along with developing new metrics to increase the accuracy of FE.

Environmental Factors Affecting Feed Efficiency

The phenotypic merit of an individual is determined by the individual's genotype and environment (Falconer, 1960). An individual's phenotype can be improved through genetic selection, environmental improvements, or a combination of both. The economic importance of FE has compelled poultry companies to improve FE through the enhancement of genetic and management conditions. Research on environmental factors involved in broiler production shows rearing temperatures, lighting programs, housing ventilation, feed form, feed particle size, and nutrient density to be environmental factors with the greatest influence on FE.

Rearing Temperature

Rearing temperatures play a critical role in feed consumption and growth rates of poultry, consequently affecting FE. In addition, carcass composition, an indicator of FE, is influenced by rearing temperatures (Leenstra, 1986). Birds grow and perform optimally in a distinct temperature range. Deviations from these thermoneutral temperatures adversely affect the bird's behavior and metabolic activity. Birds reared in high temperatures have low FE because of decreased feed intake with lower weight gain and higher fat deposition (Adams et al., 1962; Mickelberry et al., 1966; Howlider and Rose, 1989; Chwalibog and Eggun, 1989; Suk and Washburn, 1995). In contrast birds grown in low temperatures have increased feed intake and weight gain with higher levels of protein accretion. However, production gains in low temperatures come at high energy costs, thereby reducing FE (Scheele et al., 1987; Leenstra and Cahaner, 1991). The temperature range required for optimal growth and performance is dependent on age, poultry type, and strain. Proper management of a chicken's ambient temperature is critical for efficient poultry production.

Lighting

A bird's energy balance is dependent on feed intake (FI) and activity levels (Weaver and Siegel, 1968; Foshee et al., 1970; Hooopayw and Goodman, 1972). Exposure to light alters these parameters as birds go into a resting phase during dark periods and increase FI and activity levels during light periods. Lighting programs most commonly used and researched include intermittent (periodic light periods followed by dark periods) and continuous lighting. Studies comparing these lighting programs show intermittent lighting to cause improved FE (Quarles and Kling, 1974; Dorminey and Nakaue, 1977; Goodman, 1978). The improvement in FE may be attributed to slow early growth resulting in lower maintenance costs compared to birds grown on continuous light. The literature has consistently shown male broilers grown under intermittent lighting to have lower levels of carcass fat, indicating more efficient growth. Lastly, the recurring dark periods in intermittent lighting decrease physical activity and energy expenditure, leading to improved efficiency (Buyse et al., 1996).

Ventilation

Atmospheric ammonia is produced under normal brooding conditions when uric acid comes in contact with water promoting microbial activity (Weaver and Meijerhof, 1990). Ammonia levels exceeding 25 ppm decrease growth and efficiency levels in poultry and are known to damage tracheal mucous membranes (Nagaraja et al., 1983), increase air sac lesions, increase breast blisters (Quarles and Kling, 1974), and lead to immune deficiency (Quarles et al., 1975; Reece et al., 1980). To avoid these adverse effects, multiple management practices have been implemented to maintain ammonia levels less than 25 ppm. Management practices include applying additives to the litter, using nipple waterers opposed to plasson waterers, continuous litter removal, and mechanical ventilation. Within these methods mechanical ventilation has consistently been shown to be the most effective at maintaining low levels of ammonia through the reduction of litter moisture (Valentine, 1964; Carr and Nicholson, 1980).

Feed Characteristics

In addition to housing conditions, characteristics of the feed being consumed can alter FE. Pelleted diets increase weight gain, feed intake, and FE compared to mash diets (Nir et al., 1994; Engberg et al., 2002; Svihus et al., 2004). Improvements in FE and its component traits are hypothesized to be the result of improved starch digestibility, increased nutrient intake, reduced feed wastage, and decreased energy expenditure during feeding (Amerah et al., 2007). If circumstances do not allow pelleted diets to be fed, coarsely ground mash is advantageous to medium ground mash due to the bird's preference for larger sized particles and lower viscosity of digesta (Proudfoot and Hulan, 1989; Nir et al., 1994; Amerah et al., 2007). Feed intake (FI), a component of FE, is strongly influenced by the nutrient levels in feed. Chickens adjust their FI levels to satisfy energy requirements; therefore, birds fed high nutrient diets will have decreased FI. Decreasing FI reduces energy costs associated with feed consumption and digestion, ultimately leading to improved FE (Plavnik et al., 1997; Brickett et al., 2007).

Quantitative Methods for Measuring Feed Efficiency

While improvements in broiler management practices have undoubtedly contributed to the improvement of FE, genetic selection is thought to contribute to 85-90% of the change in broiler growth since the 1950's (Havenstein et al., 2003). Genetic evaluation of FE has been primarily researched in poultry, cattle, and swine as these species are most widely used for commercial protein production. Within each species a variety of component traits and quantitative methods are considered in the determination of FE. In meat-type poultry the component traits under consideration include body mass, yield, and FI. The primary metrics used to quantify FE are shown in Table 1 and include feed conversion ratio (FCR), residual feed intake (RFI), residual gain (RG), and residual intake and bodyweight gain (RIG).

Feed Conversion Ratio

Feed conversion ratio is the most widely used and researched FE method used in poultry production (Hess et al. 1941; Hess and Jull, 1948; Thomas et al. 1958; Wilson 1969). Being a composite trait FCR is made up of two components, weight gained, and feed consumed during a defined period. Feed conversion ratio is therefore defined as the amount of feed consumed per unit of weight gained, resulting in lower values being favorable (Skinner-Noble and Teeter, 2003). Research efforts have revealed heritabilities for FCR ranging between 0.2 and 0.8, indicating potential for genetic improvement through selection (Thomas et al. 1958; Wilson 1969; Guill and Washburn, 1974; Pym and Nicholls, 1979; Chambers et al., 1983; Leenstra and Pitt 1987; Pakdel *et* al., 2005; Aggrey et al. 2010.) Selecting for FCR has led to favorable responses in other economically important traits such as increased body weight, growth, and yield, while also lowering feed intake and fat deposition (Pym, 1990; Buyse et al., 1999; Varkoohi et al., 2010). However, because FCR is a ratio trait there are a variety of concerns related to the use of this method to quantitate and improve FE in poultry.

The use of ratios in biological sciences has been highly controversial as ratios are known to have certain statistical and genetic disadvantages. Ratios violate multiple statistical assumptions, such as having no real mean or variance along with not being normally distributed (Atchley and Anderson, 1978). Because of these statistical violations, selection pressure gets applied disproportionately to the numerator (Gunsett, 1984). The disproportion of selection pressure makes it difficult for breeders to predict the genetic improvement of FCR’s component traits in subsequent generations and reduces the rate of genetic progress for each component trait compared to index selection. (Campo and Rodriguez, 1990; Famula, 1990). Lastly, selection for ratio traits are most useful when the components of the ratio are lowly correlated. As components of the ratio become increasingly correlated selection for one trait can be used to indirectly select for the other trait. (Gunsett, 1984). Because feed intake and weight gain have moderate to moderately high genetic correlations, selection for FCR may only be marginally better than direct selection for one component trait and relying on indirect selection to improve the other component trait.

Residual Feed Intake

In attempt to avoid the statistical and genetic limitations of FCR, poultry breeders have used RFI as a method for improving FE. Residual feed intake was first introduced by Byerly (1941) and used by Koch *et al*. (1963) in beef cattle and in poultry by Wing and Nordskog (1982). Residual feed intake is defined as the difference between actual and predicted FI when taking into account regression requirements for body maintenance and growth (Van Der Werf, 2004). Individuals with an actual FI lower than their predicted FI will have a negative RFI value and will be considered to grow more efficiently. Residual feed intake is calculated as RFI = FI – $[\mu + (b_1 * X) + (b_2 * Y)]$, where FI represents feed intake over a defined period of time, μ represents the average feed intake of the tested population, and b_1 and b_2 represent the partial regression coefficients. X is used to define two traits, average daily gain (ADG) or weight gain during test period (Van Bebber and Mercer, 1994; Pakdel et al., 2005., Aggrey et al., 2010; Case et al., 2012). Y is used to define mid metabolic body weight (MMW) or initial body weight (Luiting et al., 1991; Van Bebber and Mercer, 1994; Aggrey et al., 2010; Case et al., 2012). Mid metabolic body weight is referred to as the organism's metabolic bodyweight midway through the test period. Metabolic bodyweight is defined as an organism's active tissue mass and can be determined by multiplying an organism's bodyweight to the exponent 0.75 (Kleiber, 1932; Kleiber, 1947). Therefore, MMW is calculated as ((ending body weight – initial body weight)/2) ^ 0.75. Similar to FCR, a considerable amount of genetic variation for RFI has been found in poultry, resulting in heritability estimates ranging from 0.2 – 0.6 (Van Bebber and Mercer, 1994; Aggrey et al., 2010; Case et al., 2012). In addition to having moderate heritabilities, RFI is known to have low phenotypic correlations with production traits. The independence of RFI from production traits gives breeders the confidence to incorporate RFI into a multiple-trait selection index with minimal effects on the production traits included in the index. Selection for reduced RFI improves FE through a reduction in FI with minimal changes in production. (Aggrey et al., 2010).

While selection for decreased RFI is a viable method for improving feed efficiency, RFI is thought to inherently penalize highly productive animals. Studies show high phenotypic and genetic correlations between feed intake and weight gain, meaning high producing animals consume larger amounts of feed (Van Bebber and Mercer, 1994; Aggrey et al., 2010; Case et al., 2012). A consequence of high FI is an increase in heat production known as diet-induced thermogenesis (Swennen et al., 2004). As FI increases, energy lost to heat increases contributing to an increase in RFI. Therefore, higher producing birds may have unfavorable RFI values compared to slower growing birds, eating smaller amounts of feed. These consequences of RFI were shown in turkeys, as turkeys with the most favorable RFI values were also shown to have the lowest bodyweights (Willems et al., 2013).

Residual Bodyweight Gain

The adverse relationship between RFI and high producing animals prompted the development of residual bodyweight gain (RG). Residual bodyweight gain is defined as the difference between actual and predicted gain using multiple regression including metabolic weight and FI as independent variables. Residual body weight gain can be calculated as follows $RG = Gain - [\mu + (b_1 * X) + (b_2 * Y)]$, where gain is equal to an individual's body weight gain during the testing period, μ is the population's average bodyweight gain during the testing period, b_1 and b_2 represent the partial regression coefficients. X is used to represent MMW and Y represents FI (Koch et al., 1963; Crowley et al., 2010). Conversely to RFI, positive or increasing RG values are favorable. Studies investigating the genetic parameters of RG in poultry are limited; however, Willems et al. (2013) found the heritability of RG in turkeys to be 0.19 with moderate genetic correlations between FI (-0.41) and body weight gain (0.43). These results are similar to a study in Irish beef cattle where researchers found the heritability of RG to be 0.29, along with genetic correlations between feed intake and average daily gain (ADG) to be 0.00 and 0.70, respectively (Crowley et al., 2010). Results from Crowley et al. (2010) and Willems et al. (2013) indicate that selection for RG should improve feed efficiency primarily through increased growth, while selection for RFI improves FE primarily through decreased FI.

Residual Intake and Bodyweight Gain

Selection for RFI and RG improve FE, while having differing effects on the components of feed efficiency. With the hypothesis that adjoining RFI and RG will allow breeders to take advantage of the benefits from each linear model, a linear combination of RFI and RG was developed. Residual intake and bodyweight gain (RIG) is calculated by first standardizing RFI and RG to a variance of 1 and subtracting RFI from RG (RG-RFI). Taking the negative of RFI puts RG and RFI on a positive scale (Willems et al., 2013). The above calculation results in RIG being a linear function of RFI and RG which are in them linear functions of their component traits feed intake, mid metabolic bodyweight, and gain. Similar to RG, heritability estimates for RIG are limited. Willems et al. (2013) found the heritability of RIG in turkeys to be 0.23. The genetic correlations of RIG between feed intake and gain were -0.57 and 0.29, respectively. These genetic correlations indicate that improvements in FE should be expected as selection for RIG will result in a moderate decrease in feed intake and a slight increase in bodyweight gain. When calculating RIG as previously explained the breeder should expect results intermediate to selection for RFI and RG; however, because RIG is a linear function of RFI and RG, RIG can be utilized as an index. Depending on the breeding objective, breeders could place different weighting on RFI and RG. Different weighting strategies for RIG are thoroughly discussed in Willems et al. (2013). However, a brief example may include a breeding strategy where the focus is to increase growth. In this example, the breeder may place 80% of the weight on RG and 20% on RFI. In this selection strategy the breeder would expect improvements in FE to be reached primarily through increased body weight gain with minor reductions in FI. After selection and data is collected on progeny the breeder could adjust the index if a different outcome is desired. If the 80/20 weighting resulted in favorable weight gains but inadequate decreases in FI the breeder could adjust the weighting to 70/30 in the following generation and continue to fine tune the weighting as need in subsequent generations.

<u>Genetic Components of Feed Efficiency</u>

As described above FE can be quantitated using various methods. Each method alters FE through distinct adjustments to feed intake, bodyweight, and growth. Adjustments made to these components must be considered by the breeder when determining which method to use as a selection criterion. **Table 1** is a composite of multiple studies looking at the genetic parameters of multiple FE strategies and their components in chickens and turkeys. In general, heritabilities for the different feed efficiency strategies tend to be moderately low, ranging between 0.14-0.23 (de Verdal et al., 2011; Case et al., 2012: Willems et al., 2013). However, one study in chickens found the heritability for RFI (0.46) to be moderate (de Verdal et al., 2011), while another study in turkeys found the heritability for FCR (0.05) to be abnormally low (Willems et al., 2013). Among the component traits metabolic bodyweight (MBW) or mid-metabolic bodyweight (MWW) was found to have the highest heritability followed by FI and then gain. Genetic correlations between FE strategies, while high in some cases, remained below 1, inferring that selection for each feed efficiency strategy will target individuals with different genetic characteristics. RIG had very high genetic correlations with FCR (-0.93), RFI (0.93), and RG (0.94). RIG's high genetic correlations between RFI and RG are likely a result of RIG being a linear combination of the two methods. The strong genetic correlation between RIG and FCR may be a result of RIG and FCR having similar objectives, as both strategies are hypothesized to improve feed efficiency by simultaneously decreasing feed intake and increasing growth. Residual feed intake tends to have the strongest genetic correlation with FI (0.33-0.67), while RG has the strongest correlation with gain (0.43). These strong genetic correlations are expected as selection for RFI primarily influences FI and selection for RG primarily influences growth.

Physiological Responses to Feed Efficiency Selection

Carcass Composition

Selection for increased bodyweight was initially used to indirectly select for improved FE. Long term selection for increased body weight with no constraint on feed efficiency led to excess levels of carcass fat. This response is likely attributed to the high correlation (0.70-0.85) between weight gain (WG) and feed consumption. The relationship between WG and feed consumption led to fast growing birds consuming nutrients in excess of levels required for lean growth. Choct et al. (2013) found modern broiler strains to contain 15-20% carcass fat and greater than 85% of this was not physiologically required. Fat levels beyond the physiological requirement are waste products with low economic value that reduce carcass yield and consumer acceptance. For this reason, excess levels of fat are considered a wasted dietary energy.

The relationship between carcass composition and FE has been researched within a variety of genetic lines selected for FE, FI, WG, and decreased abdominal fat (Washburn et al., 1975; Pym and Solvyns, 1979; Leenstra and Pit, 1987). Across all studies an improvement in FE was associated with a decrease in fat deposition but not necessarily an increase in carcass protein. For example, when selecting for improved FE and decreased carcass fat Leenstra and Pit (1987) found fat deposition to be lower in both lines, but also having significantly lower body weights compared to the line in which both originated. No differences were found in the proportional weight of breast and leg meat; however, absolute weights for leg and breast meat were higher in the control line (Leenstra and Pit, 1987). Other researchers have found decreases in carcass fat to correspond with improvements in FE along with elevated protein deposition, enhanced dietary protein utilization, and an increase in meat yield (Leclereq, 1983; Richard et al., 1983; Whitehead and Griffin, 1984; Cahaner et al., 1986). While the improvement in FE has consistently been shown to decrease carcass fat, the imperfect relationship between FE and protein deposition results in the need for careful evaluation of the cost and benefits of selection for feed efficiency as protein deposition and FE are both traits of high economic importance.

Gastrointestinal Organs

Feed efficiency is directly related to the bird's ability to digest and absorb consumed nutrients. The efficacy of digestion and absorption is dependent on the characteristics of organs located in the gastrointestinal tract (GIT). Therefore, as FE is altered through selection, alterations to GIT organs are probable. de Verdal et al. (2011) conducted a comprehensive study evaluating GIT organs (crop, proventriculous, gizzard, liver, duodenum, jejunum, and ileum) along with their genetic components in broilers divergently selected for apparent metabolisable energy corrected for zero nitrogen retention (AMEn). The heritability estimates of GIT organ weight tended to be moderate ranging between 0.21 and 0.53 with the exception of proventriculus and liver weights having low heritabilities, 0.09 and 0.05 respectively (de Verdal et al., 2011). Overall the moderate heritabilities of GIT organs indicate that direct or indirect selection will lead to modification in size and functionality of the organs.

Birds in the high AMEn line (D+) had enhanced digestibility while birds in the low AMEn line (D-) had worsened digestibility. Birds in the D+ line were found to have higher bodyweight at selection age (d23). Feed efficiency data was collected on both lines between d17 and d23. During this time the D+ line gained significantly more weight while consuming significantly less feed. This consequently led to the D+ line having significantly improved FCR and RFI values compared to the D- line. In addition to altering growth and FE, selection for AMEn altered the growth of GIT organs. Proventriculus and gizzard weights relative to bodyweight were significantly higher in the D+, while relative weights of the liver, duodenum, jejunum, and ileum were significantly lower. The high relative weights of the proventriculus and gizzard found in the D+ line is likely related to the physiological and complimentary roles these organs play in conditioning the feed for nutrient absorption in the small intestine. The increased size of the gizzard and proventriculus is likely advantageous for increasing nutrient availability and digestibility (de Verdal et al., 2011).

The weight, length, and density of each segment of the small intestine were significantly lower in the D+ line. The inverse relationship between the size of the gizzard and small intestine agrees with Nir et al. (1994) who found feeding coarser diets lead to heavier gizzards and lighter small intestines. The size of the small intestine is hypothesized to be dependent on the functionality of the gizzard. This hypothesis stems from previous findings, where histology confirmed the D- line to have thicker absorptive epithelium and muscle layer (de Verdal et al., 2010). The smaller gizzard in the D- line is hypothesized to have a lower level of functionality thereby requiring the small intestines to work more rigorously during nutrient absorption. This agrees with the moderately negative genetic correlations found between small intestine density and gizzard size (de Verdal et al., 2011). Similar to the small intestine, relative liver weight was smaller in the D+ line and had a negative genetic correlation (-0.51) with gizzard weight. While liver size was smaller in the D+ line, the functionality of the liver appeared unaffected as lipid digestibility was higher in the D+ line (Mignon-Grasteau et al., 2004).

Genetic correlation estimates for relative weight, length, and density between the three small intestine segments were high, ranging from 0.62 to 0.92 (de Verdal et al., 2011). This indicates that selection for AMEn modified all parts of the small intestine in a similar manner. While selection consistently affected each part of the small intestines, the highest genetic correlations were found between the jejunum and ileum. This may be a result of the jejunum and ileum having closer related functionalities compared to the duodenum. Nutrient absorption primarily takes place in the jejunum and ileum due to both segments having more favorable pH and enzyme levels along with higher activity levels of α-amylase and trypsin. In addition, there are differences in post hatch development between the segments. Duodenum growth is largely complete by 7 days post hatch while the jejunum and ileum continue growing past 2 weeks of age (Rance et al., 2002).

The genetic relationship between GIT organs and production traits varies. de Verdal et al. (2011) found 23d bodyweight to be correlated (0.42-0.96) with weight, length, and density of the small intestines and upper GIT organs excluding the crop. Among GIT organs, liver weight and small intestine length expressed the strongest negative genetic correlations (0.90-0.96) with 23d bodyweight. Similar to bodyweight, WG during test period had the strongest negative genetic correlations with liver weight and small intestine length (0.83-0.98). Conversely to bodyweight the genetic correlation between small intestine density and WG was much lower (0.25-0.37). Feed intake was found to have the highest negative genetic correlations with liver weight, small intestine length, and small intestine density (0.46-0.64), while having low negative genetic correlations with small intestine weight (0.03-0.08). Different FE strategies, FCR and RFI, expressed different genetic correlations between the upper and lower GIT organs. Overall, FCR was positively correlated with liver weight, small intestine weight, and small intestine density, while RFI was correlated with all parts of the GIT tract except small intestine weight. Results from de Verdal et al. (2011) indicate that GIT organs play an influential role in the growth and efficiency of broilers; however, the degree of influence the GIT organ has is dependent on the growth or efficiency trait.

Growth Curve

An overruling objective of genetic selection in the modern broiler is to increase growth rate (Clayton, 1980; Nestor et al., 1987; Anthony et al., 1991). Early selection practices primarily focused on selecting individuals with high body weights at specific ages and did not consider other production traits such as FE (Anthony, 2017). Poultry breeders quickly began to understand the economic importance of FE and the commercial goal became to reduce the feed amount required to grow birds to a constant weight. With this breeding goal, fast growing birds were favored since they reached market weight at an earlier age resulting in energy requirements for maintenance costs to make up a smaller percentage of total energy intake.

At its broadest level, feed utilization can be categorized into maintenance and growth. Maintenance is defined as the conservation status of an animal that is not performing work or producing product (Armsby and Moulton, 1925). Nutritionist and geneticists have worked to partition out the efficiencies of maintenance and growth through various FE measurements described by Willems et al. (2013). While each method has shown to improve FE, each metric partitions feed utilization differently influencing maintenance and growth efficiency to varying degrees. Arthur et al. (2001) found selection for FCR to result in greater average daily gain and larger mature size indicating selection for FCR to primarily improve feed utilization through enhanced growth. Selection for RFI is shown to keep mature size constant, lower heat production, and reduce the weight of visceral organs (Alende et al., 2016; Carstens and Tedeschi, 2006). The culmination of these findings along with improved FE suggest RFI reflects inherent variation in biologically relevant processes related to FE but not necessarily growth (Carstens and Tedeschi, 2006).

Differences in feed utilization between maintenance and growth costs of FE are likely to alter the individual's growth pattern or curve. The growth curve for poultry is characterized as having a sigmoid shape and has most commonly been described using logistic, Gompertz, or Von Bertalanffy equations (Ricklefs, 1967). Each equation utilizes three parameters to statistically model birds' growth pattern over time. The three parameters involved in each equation include weight at age zero, instantaneous relative growth rate, and the asymptotic value or mature bodyweight (Ricklefs, 1983). These parameters can then be used to graphically illustrate the growth curve along with determine age and weight of inflexion.

The genetic correlations between growth curve parameters and FE strategies, such as FCR and RFI, were evaluated by N'Dri et al. (2006). In this study the initial specific growth rate of the bird was moderately correlated with FCR (0.42) and RFI (0.51), indicating birds with a slower initial growth rate are more efficient. In addition, abdominal fat yield, which is negatively correlated with FE, was found to be increased in birds with high initial specific growth rates and decreased age of inflexion. These findings were supported by Pym and Nicholls (1979) who found birds with greater bodyweights at younger ages to be less efficient from increased maintenance costs. N'Dri et al. (2006) also found age of inflection to be negatively correlated with FCR while maturation and FCR were positively correlated. The negative correlation between FCR and age of inflection indicates birds achieving rapid growth rate at a later age have improved FCR and reiterates the positive correlation between FCR, initial specific growth rate, and maturation rate (N'Dri et al., 2006).

General Purpose of Dissertation

The concept of feed efficiency (FE), one unit of feed required to improve one unit of desired output, is relatively simple. However multiple outputs are desired in a commercial poultry breeding program, resulting in the need for nutrients to be partitioned in a particular manner. At the broadest level, nutrients are partitioned between production and maintenance requirements. The requirements for production and maintenance varies between birds. It is the poultry breeder's responsibility to select individuals most aligned with the breeding objective. Irrespective of the breeding objective, various related and non-related traits influence a bird's FE. To effectively improve FE, the breeder must be aware of the relationship between FE and the other traits in the breeding program to understand the advantages and consequences that will result from FE selection.

Over several decades, poultry researchers and breeders have developed different FE strategies to consolidate and simplify the relationship between feed intake and biological functions necessary for life and growth. However, current FE strategies are still unable to account for large portions of the variation in feed intake and do not give the poultry breeder the ability to select for production and maintenance components separately. The objective of this set of experiments was to first develop four independent sublines of Japanese coturnix quail through the selection of 4 different FE strategies. Prior to this study, the Japanese quail underwent long term selection for high 4-week body weight making them an appropriate model for the commercial broiler. Two of the FE strategies, feed conversion ratio (FCR) and residual feed intake (RFI), are widely used in commercial farming. The remaining two FE strategies have been tested in simulations and provide an alternative to traditional RFI. These alternative RFI models were developed to allow the breeder to identify bird specific growth and maintenance efficiencies through random regression in concert with population parameters to explain variation in feed intake. After four generations of selection, genetic and phenotypic parameters for each FE strategy and their component traits were evaluated and compared between lines. We hypothesize different genetic and phenotypic relationships will be present between FE strategies and their FE components such as bodyweight, weight gain, and feed intake. These differences should indicate if certain FE strategies are more suitable for improving production efficiency over maintenance efficiency or vice versa.

In trials 2 and 3 we included the random bred control line (RBC) that each of the four sub-lines originated, allowing for comparisons to be made between FE selected lines and a non-selected FE line. The objective of these two trials were to evaluate growth and development characteristics between lines. Trial 2 involved evaluating the development of supply and demand organs in each line to determine how each FE strategy influenced the way nutrients were partitioned between the different types of organs. Feed efficiency strategies superior at promoting growth efficiency, are likely to have higher weights for demand organs such as breast and leg meat. Whereas, feed efficiency strategies promoting maintenance efficiency will likely result in smaller relative weights of visceral organs known to account for large maintenance costs in proportion to their size. In addition to evaluating the development of supply and demand organs, the second trial focused on phenotypic differences in the component traits of FE during FE testing between 14 and 28 days of age. This two-week period served as the testing period during the development and selection of the four lines. This information will help to confirm the genetic and phenotypic relationships found in trial 1.

In the third trial, growth curves were developed for all FE lines and the RBC. Selection for FE affects a variety of growth traits. Researchers and poultry breeders are most commonly interested in feed efficiency's association with weight gain and ending body weight. However, additional insight can be gained by evaluating the growth curve. Measuring growth curve parameters identifies the weight and age a bird is expressing its most rapid weight gain along with the weight of maturity. Identifying these parameters in each line shows how selection for different FE strategies shifts the growth due to changes in inflection point and asymptote values.

The purpose of this set of experiments was to test the practicality of newly proposed FE strategies and investigate how these along with traditional FE strategies influence production related traits during the grow out period. Providing this knowledge to poultry breeders will allow them to choose the FE strategy most appropriate for their breeding objective.

Table 1. Literature based heritabilities for feed efficiency measurements and the genetic correlations between feed efficiency measurements and their component traits.

Trait	Species	Test Period	MMW	WG	FI	FCR	RFI	RG	RIG	Sources
WG	Chicken	17-23d	-	**0.3**	0.6	-0.35	0.54	-	-	de Verdal et al., 2011
FI			-	-	**0.47**	0.64	0.99	-	-	
FCR			-	-	-	**0.21**	0.57	-	-	
RFI			-	-	-	-	**0.46**	-	-	
FCR	Chicken	28-34d	0.62	-0.13	0.45	**-**	-	-	-	Aggrey et al., 2010
RFI			0.29	0.54	0.56	0.31	-	-	-	
FCR	Chicken	35-42d	0.57	-0.14	0.54	-	-	-	-	Aggrey et al., 2010
RFI			0.45	0.34	0.33	0.84	-	-	-	
MBW	Chicken	35-42d	**0.44**	0.18	0.48	0.35	-	-	-	Aggrey and Rekaya, 2013
WG			-	**0.09**	0.4	-0.08	-	-	-	
FI			-	-	**0.22**	0.63	-	-	-	
FCR			-	-	-	**0.14**	-	-	-	
FI	Turkey	15-19wks	-	-	**0.25**	0.06	0.62	-	-	Case et al., 2012
FCR			-	-	-	**0.16**	0.65	-	-	
RFI			-	-	-	-	**0.21**	-	-	
MMW	Turkey	16-20wks	**0.3**	0.62	0.67	-0.04	0.09	-0.28	-0.22	Willems et al., 2013
WG			-	**0.13**	0.63	-0.64	-0.07	0.43	0.29	
FI			-	-	**0.2**	0.21	0.67	-0.41	-0.57	
FCR			-	-	-	**0.05**	0.36	-0.66	-0.93	
RFI			-	-	-	-	**0.23**	-0.76	0.93	
RG			-	-	-	-	-	**0.19**	0.94	
RIG			-	-	-	-	-	-	**0.23**	

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Chapter 2

Selection Response to Different Feed Efficiency Strategies

Introduction

Feed efficiency (FE) is a complex trait driven by a variety of component traits with positive and negative interactions. At the broadest level, traits influencing FE can be categorized as either growth or maintenance related. Historically commercial animal breeding has seen significant improvements in FE through selection for feed conversion ratio (FCR). Improvements in FCR have primarily occurred due to genetic improvements in growth potential and body composition. Feed conversion ratio is primarily expressed as the amount of feed intake (FI) per weight gained (WG) but does not take into account one third of the FI variation related to body maintenance processes such as basal metabolism, protein turnover, thermoregulation, physical activity, immune function, nutrient digestion, and nutrient absorption (Knap and Wang, 2012). In addition to its biological limitations, FCR has statistical limitations. FCR is a ratio trait, meaning it is not normally distributed and without a true mean or variance (Atchley et al., 1976). The non-normality of ratios is worsened when the numerator and denominator are strongly correlated as is found with FI and WG. Direct selection for a ratio trait, such as FCR, is difficult due to the disproportionate way selection pressure is placed on the component traits of the ratio (Aggrey et al., 2010).

Another widely used selection criteria for FE is Residual Feed Intake (RFI). RFI was developed to account for FI requirements for growth and maintenance. Residual feed intake is the difference between actual and expected feed intake, with lower values implying the individual ate less feed than expected for its growth and body weight. (Koch et al., 1963). Dissimilar to FCR, the distribution properties of the regression procedure, results in RFI being phenotypically independent from production traits such as body weight and WG. (Aggrey et al., 2010). The measurement of RFI is a combination of two efficiencies: 1) efficiency of maintenance (RFI_M) and 2) efficiency of growth (RFI_G), where the individuals mid metabolic body weight (MBW) is used to determine RFI_M and WG during the testing period is used to determine RFI_G. Residual Feed Intake defined by Koch et al. (1963) is a fixed model, meaning regression coefficients for MBW and WG are determined from the average of the population. Using regression coefficients based off the population average assumes that MBW and WG contribute to the FI of all tested individuals to the same degree. Based on the genetic variation in feed efficiency we know this assumption to be wrong. Therefore, individual differences in RFI_M and RFI_G are grouped into the error term and RFI becomes biased to the magnitude of the variance in the error term (Aggrey and Rekaya, 2013).

To reduce the intrinsic bias of traditional RFI, Aggrey and Rekaya (2013) proposed a new RFI model. The proposed RFI model utilizes random regression to determine bird specific regression coefficients in addition to the population-based parameters. The bird specific regression coefficients in the proposed model could be used as selection criterion by geneticists to identify how FI was being influenced by MBW and WG in individual birds. It is also hypothesized that this proposed model reduces the variation in the error term resulting in a less biased RFI model. A second RFI model proposed by Aggrey and Rekaya (unpublished) included the same mixed model approach but in this model average values for MBW and WG within a contemporary group are used rather than bird specific values for MBW and WG. The premise of this model is that if you already have MBW and WG data collected from a contemporary group you could use the average MBW and WG values of the group to determine RFI on individuals in the contemporary group where this information is not known.

Prior to this study the proposed RFI strategies were evaluated through simulations but have not been tested in a selection trial. The objective of this experiment was to evaluate these proposed models in a selection trial in addition to the selection for traditional RFI and FCR. After four generations of selection, comparisons in the response of each FE strategy were made along with their phenotypic and genetic relationships with their component traits.

Feed Efficiency Metrics

Four FE metrics were exposed to independent short-term selection study for 4 generations. Metrics studied included feed conversion ratio (FCR) and three variations of RFI.

The standard FCR model used in the study is shown in equation 1.

$$\text{Feed Intake / Weight Gain} \qquad [1]$$

The traditional RFI model (equation 2) proposed by Koch et. al. (1963) is shown below:

$$y_i = a_0 + a_1 MBW_i + a_2 BWG_i + \varrho_i \qquad [2]$$

where y_i is FI for bird i, a_j is a fixed regression ($j = 0, 1, 2$), and ϱ_i is the error term assumed to be normally distributed with zero mean and variance equal to $\sigma^2\varrho$. The proposed mixed model is an extension of the classical Koch model and assigns bird specific regression coefficients in addition to population level parameters for MBW and WG. Residual and random regression variance components are necessary for this model and therefore pedigree information must be known (Aggrey and Rekaya, 2013). It is hypothesized that considering bird specific regression coefficients will reduce the magnitude of bias in the error term of RFI.

This model (equation 3) is written below and will be referred to as RFI2:

$$y_i = a_0 + a_1 MBW_i + a_2 BWG_i + u_1 MBW_i + u_2 BWG_i + \varrho_i \qquad [3]$$

In this model y_i is the FI for bird i, a_j is a fixed regression ($j = 0, 1, 2$) as in equation [1], and u_{ji} ($j = 1,2$) is the random regression specific to bird i and ϱ_i is the error term assumed to be normally distributed with zero mean and variance equal to $\sigma^2\varrho$. Similar to RFI2, the second proposed model is dependent on pedigree information being known. In this model, $\overline{MBW}$ and $\overline{WG}$ values are the average of the MBW and WG found in the contemporary group. Random regression coefficients are determined within the contemporary group, it is hypothesized that this model may be useful in determining RFI on individuals with incomplete FE records (Aggrey and Rekaya, unpublished).

This model (equation 4) is written below and will be referred to as RFI3:

$$y_i = a_0 + a_1MBW_i + a_2BWG_i + u_1\,\overline{MBW} + u_2\,\overline{WG} + \varrho_i \qquad [4]$$

where aj is a fixed regression (j = 0, 1, 2) as in model [1], and uji (j = 1, 2) is the random regression specific to the bird's contemporary group and ϱ_i is the error term assumed to be normally distributed with zero mean and variance equal to σε.

Sub Line Formation

The base population, AR Heavy, used in this study formed when two heavy Japanese quail lines with over 120 generations of combined selection for high four-week bodyweight were crossed (Marks, 1978 and Nestor et. al., 1990). The perpetual selection for high body weight in this line results in these quail serving as a strong model for the commercial broiler After the AR Heavy line was formed, the population was maintained in a 90 pair random bred population for 6 generations before being used in this study. Two hatches (n=425) of AR Heavy were hatched and tested in FE trials between 14 and 28 days of age. Data from these trials were used to calculate

FE metrics for each of the FE models mentioned in equations 1-4. Five sublines (the fifth subline not included in the document) were derived from the 90 pair population by randomly assigning 18 families to each line. In the F0 generation and subsequent generations ten males and thirty females were kept as breeders for each subline and 1 male was mated to 3 females. Natural mating was used but hens were kept in individual cages, so eggs could be identified with its respective hen. Males were rotated every other day between hen pens to maintain fertility.

After the four sublines were developed, each subline was tested and selected three generations for their respective FE metric. In the following three generations, FE data was collected on a minimum of 300 birds per subline. A minimum of 8 and a maximum of 12 progeny per hen were tested each generation to reduce family bias. On average two hatches, with a two-week egg collection period, was necessary to attain FE records on 300 birds per subline. Direct selection based on breeding values were used to select the top 10 males and top 30 females in each line for their respective FE metric. In selecting the top males and top females, constraints were put in place to help minimize inbreeding. In the selection of males, constraints included a maximum of 1 male per dam family and 2 males per sire family. Female selection constraints included a maximum of 3 females per dam family and 6 females per sire family.

Feed Efficiency Testing

Feed efficiency testing procedures were consistently followed for each line and each generation. The four sublines were hatched and placed in FE testing together. At hatch birds were individually wing banded and placed straight run, with lines intermixed in a large litter flooring pen. Birds were reared intermixed up to d13. On d14 birds were individually weighed and randomly distributed across individual cages to minimize environmental effect. Birds remained in individual cages until d28 when individual body weight measurements were taken. During the two-week period feed and water were provided *ad libitium.* Data collected during the FE testing period included body weight at d14 (d14BW), body weight at day 28 (d28BW), and feed intake between day 14 and day 28 (FI). Additional measurements derived from the collected data included weight gained between d14 and d28 (WG), and midpoint metabolic body weight ((d14BW + d28BW)/2) ^ 0.75

Statistical Analysis

Four generations of FE data were collected on 1178, 1198, 1194, and 1178 individuals in FCR, RFI, RFI2, and RFI3 lines respectively. Heritability, genetic correlations, and breeding value estimates for d14BW, d28BW, WG, FI, MBW, FCR, and RFI were conducted according to DMU procedures outlined by Madsen and Jensen (2000). An animal model was used in each line for each trait. Single trait runs were conducted for each trait to determine the significance of the tested fixed effects as well as to determine if heritability was different from zero. For all traits, fixed effect of sex, generation, and hatch were found to be significant. Phenotypic correlations between FE components and FE strategies were derived using the Pearson correlation procedure in SAS software (SAS Institute Inc., 2013). Breeding values for each line and trait were regressed against generation to determine the slope or generational change of the respective trait. Slope comparisons between lines were conducted using ANCOVA in JMP (JMP, 2009).

Results and Discussion

Number of individuals tested per line along with average phenotypes for the component traits of FE are shown in **Table 1**. Selection of the different FE strategies altered the component traits of FE between lines and therefore impacted the feed conversion ratio within each line over the generations of selection shown in Figure 1. Phenotypic differences for FCR and component traits of FE are a consequence of genetic parameters differing between the FE strategies. Heritability estimates for FCR and RFI found in **Table 2** are similar to those found in turkeys and quail but not as high as estimates found in chickens (Aggrey, et al., 2010; Case, et. al., 2012; Varkoohi, et. al., 2012). The moderately low estimates for FCR and RFI heritability indicate selection for either trait will result in genetic improvement at similar rates. Moderately positive genetic and phenotypic correlations were present between FCR and RFI. These correlations are intermediate to the high correlations found in turkeys and low correlations found in quail (Case et. al., 2012; Varkoohi et. al., 2011). The positive correlations indicate selection for either strategy will have a favorable impact on the other; however, the moderate level of the correlation indicates different genes, or a portion of the same genes are being impacted differently through selection for each strategy. Selection for the 4 FE strategies did not impact heritability estimates of FE component traits. Heritability estimates found in **Table 3** show moderate heritabilities for d14BW and moderately high heritabilities for d28BW across the four lines. These estimates were higher than the moderately low estimates for d14BW and d28BW found in previous quail studies (Varkoohi et. al., 2011; Foomani et. al., 2014). The moderate estimates of heritability for WG, FI, and MBW found in this study agree with those found in chickens (Aggrey, et. al., 2010) but are higher than the moderately low estimates for WG and FI found in turkeys and quail (Case, et. al., 2012; Varkoohi, et. al., 2011).

Phenotypic correlations (Rph) between FE components in **Table 4** show the components to have various positive relationships with each other. The highest Rph were present between d14BW: MBW and d28BW: MBW. The high correlation between these traits is expected since MBW is a function of d14BW and d28BW. The remaining Rph were moderate to moderately high excluding the Rph between d14BW and WG. The weak relationship between d14BW and WG shows initial body weight to be a poor indicator of growth rate during the FE testing period. This weak relationship could be an artifact of a variety of growth patterns being present in quail evaluated in this study. Overall d28BW was closer associated with other component traits compared to d14BW. This indicates significant biological changes occur during the testing period differentiating birds from one another at 28 days of age and ultimately leading to differences in FE.

The genetic and phenotypic correlations shown in **Table 5** provide insight in how FCR and RFI accomplish improved FE in their respective ways. A moderately strong negative genetic and phenotypic correlation present between FCR and WG, indicate WG during the testing period to be a strong determinant of FCR. The low positive correlation between FCR and FI indicate a slight reduction in FI occurs through FCR selection but is not the primary cause of improved FE. The low genetic and phenotypic correlations between FCR and MBW (-0.09) can be deceiving if the correlations between FCR and components of MBW (d14BW and d28BW) are not considered. The low correlation between MBW and FCR indicates little change occurred to average metabolic body weight during the testing period. However, FCR selection is associated with notable genetic and phenotypic changes in initial and ending body weight. **Table 5** shows moderate to moderately low positive phenotypic and genetic correlations present between FCR and d14BW while moderately low negative correlations are present between FCR and d28BW. The relationship between FCR and these traits indicate that birds favored in FCR selection enter the testing period at a lower metabolic weight, undergo significant weight gain and therefore have a slightly increased ending metabolic body weight. While FCR selected birds do exhibit increased d28BW the net effect of increased d28BW and reduced d14BW results in a slight reduction of MBW during the testing period.

Dissimilar to FCR, RFI is phenotypically independent from d14BW, d28BW, WG, and MBW due to the distributing properties of the regression procedure (Netter et al., 2004). While RFI is phenotypically independent from these traits, Kennedy et. al (1993) found RFI was not genetically independent from body weight and weight gain. The genetic correlations between RFI and the production traits in **Table 5** are low but higher than the phenotypic correlations present between these traits and RFI. These low genetic correlations indicate that RFI may have slight impacts on production traits but will not impact production traits to the same degree as selection for FCR.

Changes in the genetic merit of FE components through selection of different FE strategies is illustrated by graphing the changes in estimated breeding values for the respective traits over the 4 generations of selection. In Figure 2, BVs for d14BW trended in a moderately upward direction for all FE lines excluding FCR. Similar to the moderate positive Rph between FCR and d14BW the downward slope of d14BW BVs in FCR are an indication of maintenance costs and growth patterns being altered through FCR selection. N'Dri et al. (2006) found the initial specific growth rate in a slow growing chicken line to have a moderate positive genetic correlation with FCR. This relationship indicates birds with quicker growth rate in the beginning are less efficient due to increased maintenance costs. FCR is a measure of feed intake required for both maintenance and growth components. Energy costs increase with bodyweight (Lasiewski and Dawson, 1967; MacLeod and Jewitt, 1988) leading to the adverse relationship between FCR and body weight. In addition to lower maintenance costs, the downward slope of d14BW BVs indicates the growth curve for FCR selected birds is being altered by delaying rapid growth until the start of FE testing. Delaying rapid growth rate in this way results in FCR selected birds reaching the point of inflection during the test period rather than before. The decrease in d14BW BVs found in this study contradict the increase in BW found at all ages in an FCR selected line compared to a random bred control by Varkoohi et al. 2010. However, it should be noted the base population for these lines preceding the study were selected for 4-week body weight over 120 generations. Chronic selection of 4-week BW likely lead to a growth curve with a point of inflection prior to d14. Therefore, selection for FCR would favor birds with growth curves delayed in comparison to the original population.

While Rph between RFI and production traits are not present it is well noted in the literature that genetic correlations between RFI and these traits are present (Kennedy et. al., 1993) Changes in RFI, RFI2, and RFI3 BVs for each component trait support this to be true. Moderate positive slopes for d14BW BVs in RFI, RFI2, and RFI3 were present showing slight increases in maintenance costs at the start of the testing period. This also suggests that FE improvement in these strategies are not as strongly driven by WG and are therefore not as dependent on rapid growth rate during testing. The low genetic correlations between RFI and WG (0.03-0.24) shown in the literature indicate this to be true (Hoque and Suzuki, 2009; Johnson et. al., 1999; Von Felde et. al., 1996; Mrode and Kennedy, 1993).

In Figure 3, BVs for d28BW increased across all lines indicating FE selection did not penalize larger animals supporting the findings in turkeys (Case et. al., 2012). Increases in d28BW and WG BVs, shown in Figures 3 and 4, were significantly greater in FCR and RFI3 compared to RFI and RFI2. Strong increases in d28BW BVs for FCR and RFI3 are a result of the improvement in WG. This indicates selection for FCR and RFI3 improve the growth component of FE more so than RFI and RFI2. Similar to the genetic and phenotypic correlations presented in Table 5 the increase in FCR's d28BW BVs were offset by the reduction in d14BW BVs resulting in only a slight increase for MBW BVs. Moderate increases in d14BW and d28BW BVs resulted in RFI3 having the significantly greatest change in MBW BVs, while the change in MBW BVs for RFI and RFI2 were intermediate to RFI3 and FCR. Changes in FI BVs in Figure 5 clearly depict that selection for the three RFI strategies significantly decreased FI compared to FCR.

Conclusion

Heritability's of FCR and RFI indicate selection for each strategy will result in improved FE. Choosing the FE metric most appropriate for a breeding program is dependent on the breeding objective. Selection for FCR focuses on improving growth efficiency and will result in greater WG, heavier ending BW, and minor reductions in FI. While selection for RFI will more effectively improve maintenance efficiency through significant reductions in FI and moderate increases in WG and ending BW. In addition to choosing the appropriate FE metric, the age for when the testing period should occur is critical. Selection for all FE strategies in this study resulted in increased WG. Increased growth rate will occur through FE selection and therefore the testing period should occur at an age when rapid growth rate is desired.

Changes in FE component traits through selection for RFI2 and RFI3 indicate that these FE strategies closely mimic RFI in a practical selection study. While, significant differences were not present between the response of traditional RFI and the responses of the proposed RFI strategies, the proposed strategies do provide RFI_M and RFI_G efficiency information on individual birds. Further research is needed to determine if utilization of the random regression coefficients as a selection criterion may be useful in targeting birds with higher or lower efficiencies for RFI_M and RFI_G. For example, a selection study involving two sub-lines of RFI2 could be carried out where individuals with the highest regression coefficients for RFI_M were selected for sub line 1 and individuals with the highest regression coefficients for RFI_G were selected for sub line 2. The hypothesis for this study would be that individuals selected in the RFI_M subline would accomplish feed efficiency through reduction in associated maintenance costs while individuals in the RFI_G subline would accomplish feed efficiency through improvement in costs associated with growth. A selection study of this type would involve further disaggregation of FE and provide additional insight into the biological factors differing between individuals accomplishing improved FE through different biological efficiencies.

Table 1. Average phenotype weights (g) for the component traits of feed efficiency for the four selected lines over four generations of selection.

	n[1]	d14BW[2]	d28BW[3]	MBW[4]	FI[5]	WG[6]
FCR	1178	93 $\pm$ 0.39	213 $\pm$ 0.58	43 $\pm$ 0.09	303 $\pm$ 0.85	119 $\pm$ 0.46
RFI	1198	92 $\pm$ 0.39	210 $\pm$ 0.57	43 $\pm$ 0.09	292 $\pm$ 0.83	119 $\pm$ 0.45
RFI2	1194	89 $\pm$ 0.36	204 $\pm$ 0.56	42 $\pm$ 0.09	288 $\pm$ 0.82	116 $\pm$ 0.44
RFI3	1178	88 $\pm$ 0.34	207 $\pm$ 0.53	42 $\pm$ 0.09	290 $\pm$ 0.77	120 $\pm$ 0.42

[1]Number of individuals tested over 4 generations
[2]Body weight at 14 days of age
[3]Body weight at 28 days of age
[4]Mid metabolic body weight between 14 and 28 days of age
[5]Feed intake between 14 and 28 days of age
[6]Body weight gained between 14 and 28 days of age

Table 2. Heritabilities (on diagonal), genetic correlations (below diagonal), phenotypic correlations (above diagonal) between FCR and RFI

Traits[1]	FCR	RFI
FCR	0.22 + 0.06	0.43
RFI	0.50	0.12 + 0.05

[1]Feed conversion ratio (FCR) and Residual Feed Intake (RFI)
[2]Heritabilities, genetic correlation, and phenotypic correlations were calculated in each line and the average was taken.

Table 3. Heritability's for component traits of feed efficiency in lines selected for FCR, RFI, RFI2, and RFI3 in Japanese quail measured between 14 and 28 days of age after 4 generations of selection.

Trait[1]	FCR	RFI	RFI2	RFI3
d14BW	0.50 ± .07	0.52 ± .08	0.39 ± .07	0.3 ± .07
d28BW	0.70 ± .08	0.56 ± .07	0.53 ± .07	0.64 ± .07
WG	0.44 ± .07	0.34 ± .07	0.38 ± .07	0.57 ± .08
FI	0.48 ± .07	0.40 ± .07	0.31 ± .07	0.45 ± .07
MBW	0.62 ± .07	0.64 ± .08	0.50 ± .07	0.58 ± .07

[1]Body weight at d14 (d14BW), Body weight at d28 (d28BW), Weight gained between d14 and d28 (WG), Feed intake between d14 and d28, FE strategy in its respective column, mid metabolic body weight between d14 and d28 (MBW)

Table 4. Phenotypic correlations measured between feed efficiency component traits and feed efficiency strategies in four Japanese quail lines selected for FCR, RFI, RFI2, and RFI3 feed efficiency strategies over 4 generations

Trait[1]	Phenotypic Correlations[2]
d14BW : d28BW	0.65 - 0.75
d14BW : gain	0.03 - 0.15
d14BW : FI	0.53 - 0.56
d14BW : MBW	0.86 - 0.89
d28BW : WG	0.74 - 0.78
d28BW : FI	0.73 - 0.77
d28BW : MBW	0.91 - 0.94
WG : FI	0.53 - 0.60
WG : MBW	0.50 - 0.56
FI : MBW	0.75 - 0.78

[1]Body weight at d14 (d14BW), Body weight at d28 (d28BW), Weight gained between d14 and d28 (WG), Feed intake between d14 and d28, Average metabolic body weight between d14 and d28 (MBW) Feed Conversion Ratio (FCR), and Residual Feed Intake (RFI)
[2]Range of phenotypic correlations between feed efficiency component traits in selected lines (FCR, RFI, RFI2, and RFI3)

Table 5. Genetic and phenotypic correlations between feed conversion ratio and residual feed intake component traits in Japanese quail lines selected for feed conversion ratio and residual feed intake over 4 generations

	Genetic Correlations		Phenotypic Correlations	
Trait[1]	**FCR[2]**	**RFI[3]**	**FCR[2]**	**RFI[3]**
d14	0.24	-0.05	0.46	-0.03
d28	-0.25	-0.10	-0.18	0.01
gain	-0.63	-0.09	-0.67	0.04
FI	-0.09	0.53	0.21	0.64
MBW	-0.09	-0.08	-0.09	-0.02

[1]Body weight at d14 (d14BW), Body weight at d28 (d28BW), Weight gained between d14 and d28 (WG), Feed intake between d14 and d28, Average metabolic body weight between d14 and d28 (MBW)
[2]Feed Conversion Ratio (FCR)
[3]Residual Feed Intake (RFI)

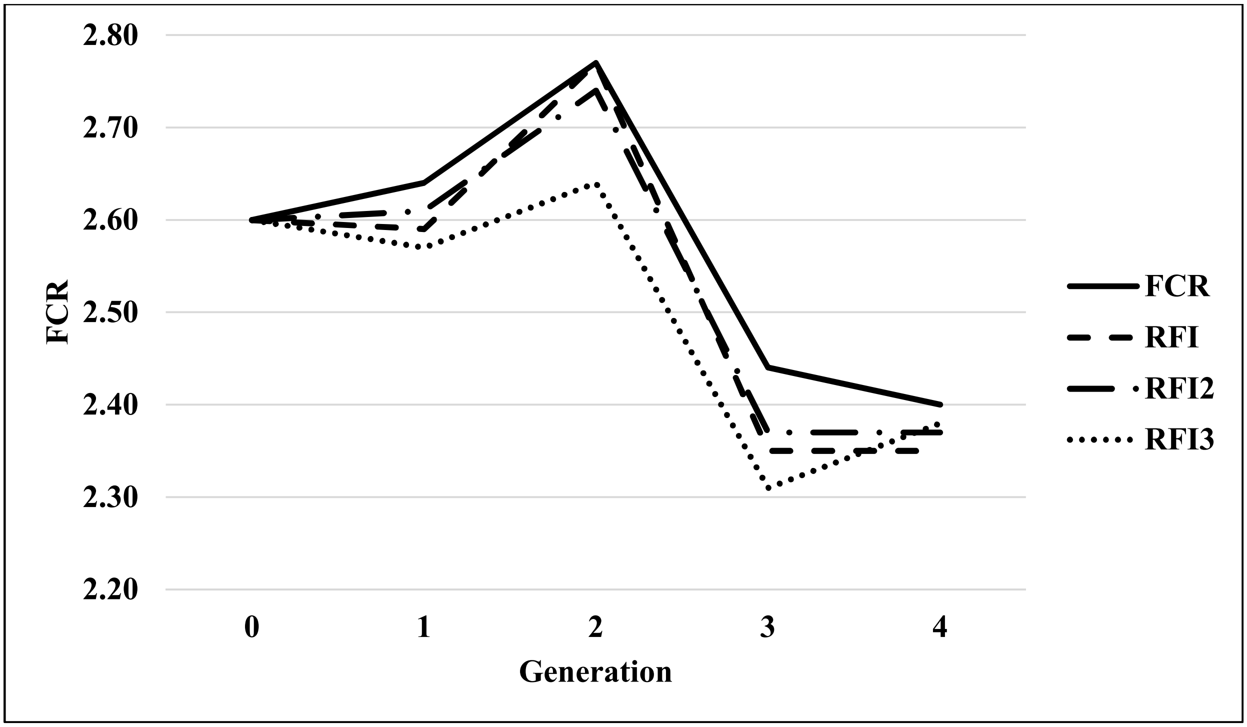

Figure 1. FCR phenotypes of the four selected lines over the four generations of selection.

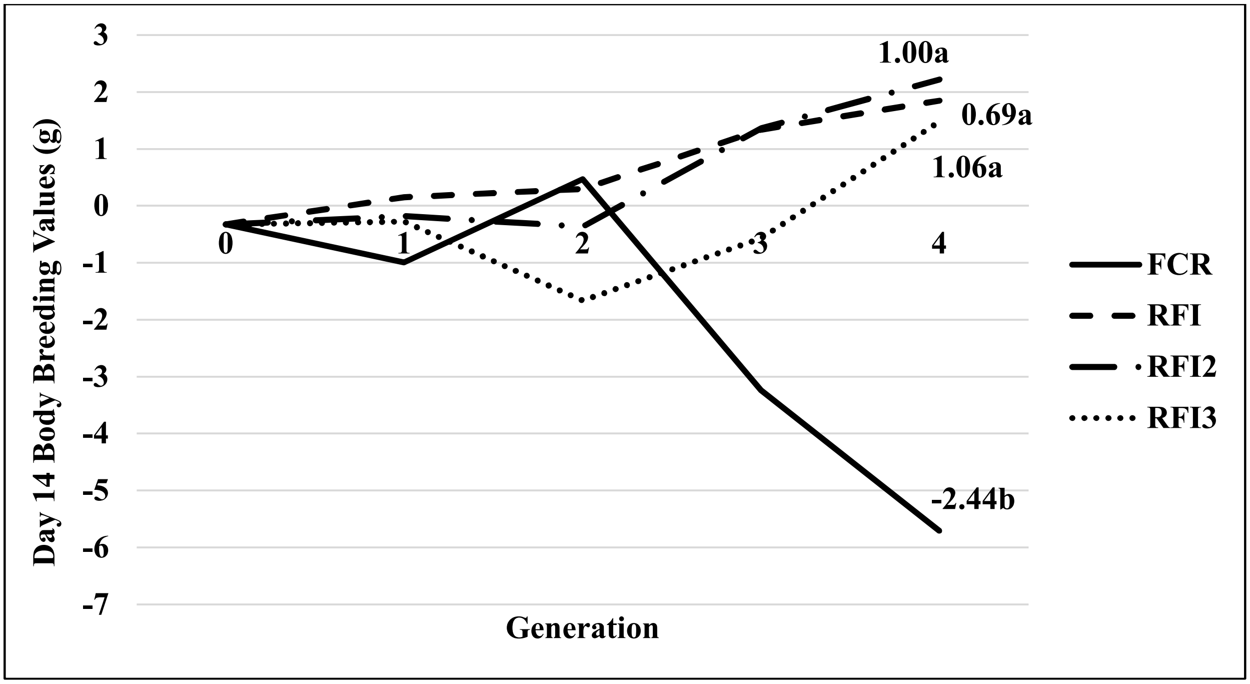

Figure 2. Day 14 body weight breeding values in Japanese quail selected for four feed efficiency strategies for 4 generations

[1]Change in breeding values by generation for each line indicated on graph

[2]Values with differing letters indicate significant difference at alpha level < 0.05

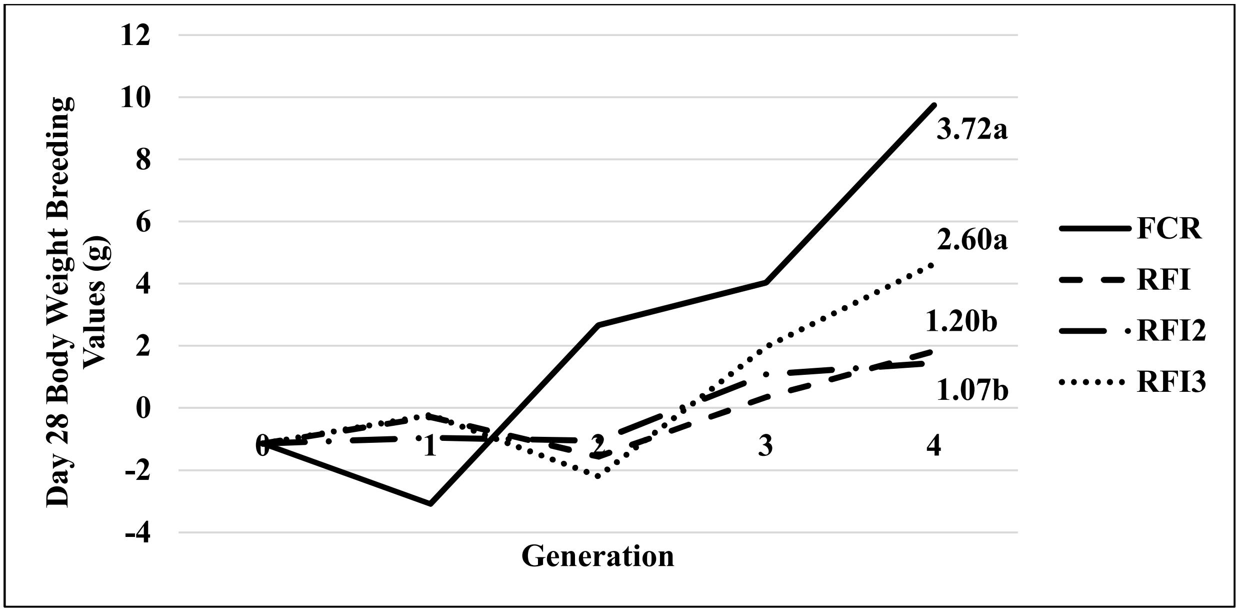

Figure 3. Day 28 body weight breeding values in Japanese quail selected for four feed efficiency strategies for 4 generations

[1]Change in breeding values by generation for each line indicated on graph

[2]Values with differing letters indicate significant difference at alpha level < 0.05

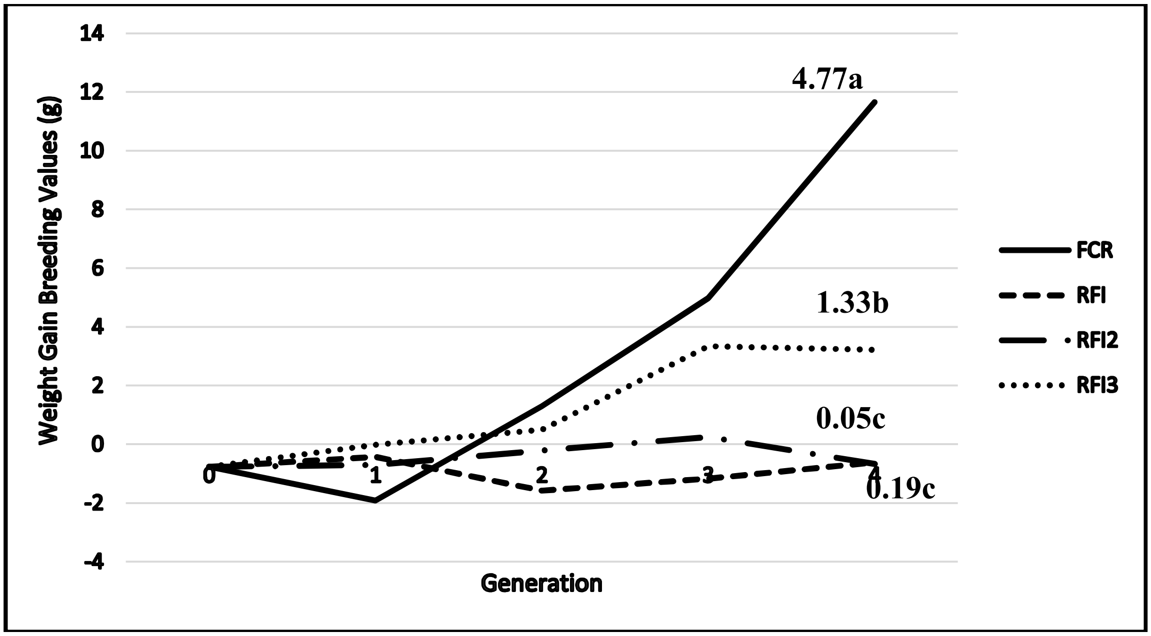

Figure 4. Weight gain breeding values in Japanese quail selected for four feed efficiency strategies for 4 generations

[1]Change in breeding values by generation for each line indicated on graph

[2]Values with differing letters indicate significant difference at alpha level < 0.05

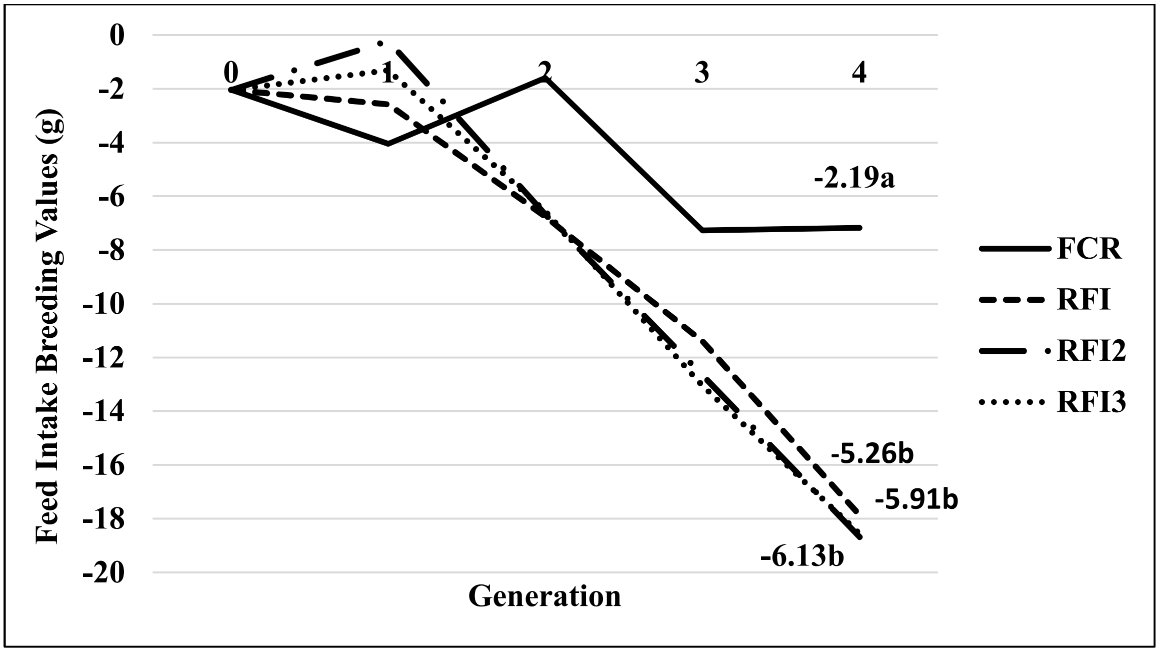

Figure 5. Feed Intake breeding values in Japanese quail selected for four feed efficiency strategies for 4 generations

[1]Change in breeding values by generation for each line indicated on graph

[2]Values with differing letters indicate significant difference at alpha level < 0.05

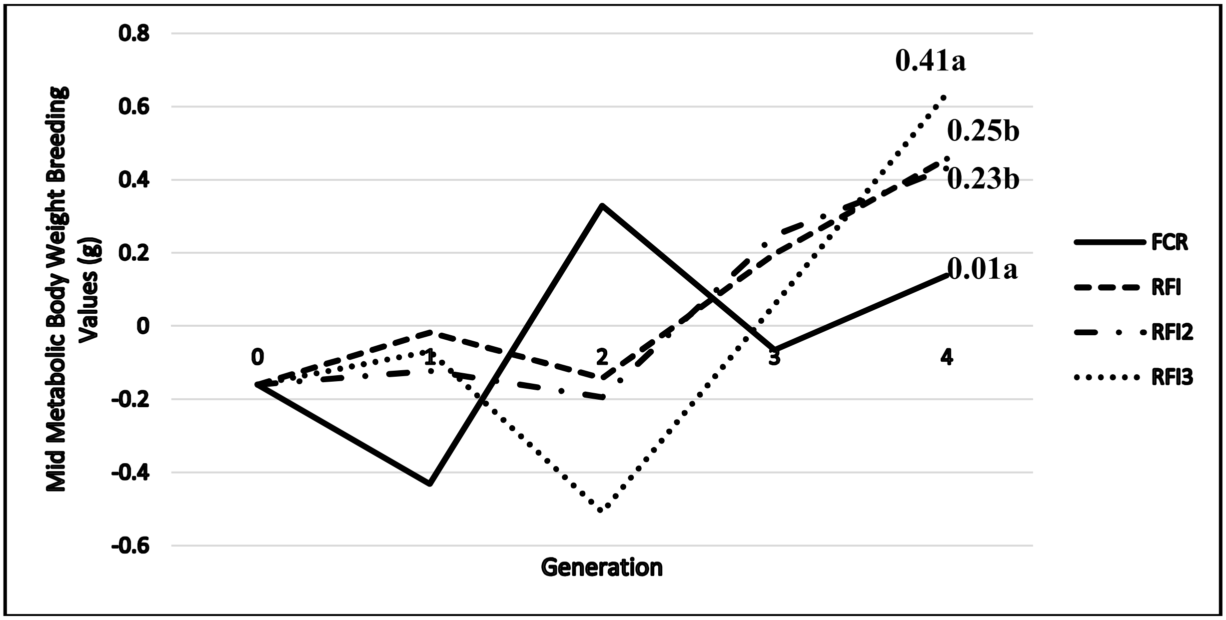

Figure 6. Mid Metabolic body weight breeding values in Japanese quail selected for four feed efficiency strategies for 4 generations

[1]Change in breeding values by generation for each line indicated on graph

[2]Values with differing letters indicate significant difference at alpha level < 0.05

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Chapter 3

The Effect of Feed Efficiency Selection on Feed Efficiency Component Traits and Organ Development

Introduction

Feed efficiency (FE) is commonly referred to in scientific literature as body weight gain per unit of feed consumed. While the concept of FE is simple, the trait itself is complex. Feed efficiency is a highly aggregate trait determined by the interaction of many component traits, including behavior, carcass composition, digestibility, appetite, growth rate, and basal metabolism (Emmerson, 1997). Component traits affecting FE do so through growth efficiency (GE) or maintenance efficiency (ME). GE involves weight gain (WG), while ME includes behavior, carcass composition, appetite, and basal metabolism. Unfortunately, most GE and ME traits are inversely related and therefore improvements in one efficiency comes at the cost of another. The inherent give and take relationship between the component traits of FE have resulted in a plethora of equations designed to improve traits deemed economically important by the breeder. Currently the two most widely used measurements of FE include feed conversion ratio and residual feed intake, commonly referred to as FCR and RFI respectively (Koch et al., 1963; Skinner-Noble and Teeter, 2003).

In poultry, researchers have found positive genetic correlations between FCR and RFI. In broilers, the genetic correlations between RFI and FCR range from 0.31 to 0.84 (Aggrey et al. 2010). Aggrey found the degree of genetic similarity in these measurements to be dependent on the age of the bird at which the measurement was taken. Between the ages of 28-35 days the genetic correlation was 0.31 but significantly increased to 0.84 a week later (Aggrey et al., 2010). In turkeys the genetic correlations were high (0.80) but found to be low in quail (0.26) Case et al., 2010; Varkoohi et al., 2011).

To truly evaluate the similarity in these feed efficiency measures, the breeder must evaluate how selection affects components traits such as feed intake, growth, body composition, and behavior. A holistic understanding of how improved efficiency is being reached is necessary to determine what economic losses and gains the breeder should expect with each FE measure. For example, selection for one measure may result in strong increases in growth and moderate increases in feed intake while selection for another measure may result in a reduction in feed intake with subdued growth rate. While efficiency could be improved to the same degree, one bird is now larger with increased feed intake and maintenance costs while the other eats less with lower growth potential and less maintenance costs.

While it's obvious that FE is controlled by two biological factors, GE and ME, traditional FE measurements are unable to ascertain the two components in a single metric. Strategies such as RFI2 and RFI3 have the potential to separate out these two efficiencies. However, before these strategies are exploited and used to select for the different efficiencies the objective of this study was to evaluate how selection for the baseline RFI2 and RFI3 models impacted the development of supply and demand organs along with the component traits of FE during the testing period compared to the selection of traditional FE strategies and the random bred control (RBC) that the lines originated.

Materials and Methods

The five quail lines evaluated in this study were reared and selected at the University of Arkansas Research Farm. Four of the five lines were selected for different feed efficiency strategies, while the fifth was the original line (RBC) each of the feed efficiency lines originated. The different lines of quail in this study will be referred to as FCR, RFI, RFI2, RFI3, and RBC. Mating structure of the evaluated lines along with a detailed explanation of each strategy is described on pages 33-35.

Quail evaluated in this study came from 2 hatches, each having a two-week egg collection period. From each hatch, 120 birds were wing banded for their respective line. To avoid bias from a breeding pair within a line we sampled a minimum of 2 and a maximum of 6 chicks per breeding pair. If a breeding pair was unable to produce 2 viable chicks the breeding pair was not represented. If a breeding pair produced more than 6 chicks, 6 chicks were chosen randomly while the remaining chicks were euthanized. Chicks were reared straight run with lines intermixed up to 14 days of age. On day 14, twelve birds from each line were randomly selected and euthanized. Euthanized birds were weighed and necropsied, at this time weight (hundredth of a gram) and length measurements (tenth of a centimeter) were collected on the bird's digestive organs along with yield data. Measurements taken include weight for drum and thigh bone-in, pectoralis major and minor, heart, crop, proventriculous, gizzard, liver, and pancreas. Intestinal measurements included weight, length, and density (weight/length) of the duodenum (pancreatic loop), jejunum (pancreatic loop to Meckel's diverticulum), ileum (Meckel's diverticulum to ileocecal junction), and large intestine (ileocecal junction to anus). Remaining birds were weighed and placed in individual cages for the measurement of FE data. Placement of birds in feed efficiency cages included birds from each line being randomly distributed across individual cages to minimize environmental effect. Feed efficiency data was collected between 14 and 28 days of age. At d28 twelve birds per line were randomly chosen and euthanized for the measurement of meat yield, along with the weight and length of digestive organs.

Organ Measurements

Once euthanized, 4 quail from each line were placed on one of three trays. Trays were then wrapped in plastic and placed in a refrigerator set at 4.5° C. Each tray remained in the refrigerator until cut-up. Cut-up was administered by the same team on each organ sampling day.

Disaggregation of the carcass and digestive tract occurred using an assembly line approach to ensure that each cut would be made by the same individual to minimize operator effect.

Statistical Analysis

Line differences for FE and its component traits including: d14 live weight, d28 live weight, and live WG were evaluated using ANOVA. LS means was used with the covariate live weight to evaluate FI along with weight and length of supply and demand organs. Significant differences were determined through post hoc Tukey HSD means separation at alpha level 0.05. Hatches 1 and 2 along with males and females were pooled by line in all test as no line by hatch or line by sex interactions were present. All statistical analysis was done using JMP Pro 12 (SAS, 2013).

Results

Feed Efficiency and Component Traits

In **Table 1** live weight differences were present on d14 and d28. On d14, RBC weighed heavier than all lines except RFI which was intermediate to RBC and remaining lines. Weight gain between d14 and d28 was highest in FCR and lowest in RBC and RFI2. RFI and RFI3 both expressed intermediate gains however RFI3 had higher gains compared to RBC and RFI2. At d28, FCR was found to have the heaviest live weight and RFI2 had the lowest. D28 live weight was heavier in RFI compared to RFI2 but not lower than FCR. The RBC weighed less compared to FCR but not more than RFI2, while RFI3 was intermediate to all lines. Feed intake between d14 and d28 was highest in the RBC line. Feed intake in FCR was higher than RFI and RFI2 but not lower compared to RBC. Feed intake for RFI3 was intermediate to FCR and RFI, but higher than RFI2. Feed efficiency differences were present with FCR expressing highest FE and RBC expressing lowest FE. Feed efficiency in RFI was intermediate to FCR and RBC. Feed efficiency in RFI2 and RFI3 was intermediate to FCR and RFI.

Gastrointestinal Organs

Upper Digestive Tract

In **Tables 2 and 3** differences for upper digestive organ weights adjusted to live weight were present on d14 and d28. Line differences in adjusted crop weight were only present at d28 with FCR, RBC, and RFI2 being the heaviest, RFI was intermediate, and RFI3 the lowest. At d14 adjusted proventriculus weight was greatest in FCR, RFI, and RFI2. D14 adjusted proventriculus weight for RBC was intermediate while RFI3 was lowest. D28 adjusted proventriculus weight was highest in FCR, RBC, and RFI2. D28 adjust proventriculus weight was intermediate in RFI3 and lowest in RFI. D14 adjusted liver weight was highest in RFI2 and lowest in RFI and RFI3. RBC was heavier than RFI and RFI3 but not different from RFI2, while FCR was lighter than RFI2 but not heavier than RFI3. On d28, adjusted liver weight was heaviest in RBC and FCR, intermediate in RFI2, and lightest in RFI and RFI3. No line differences were present for adjusted gizzard weight at d14 or d28.

Small Intestines

In **Table 4** differences in small intestine weights adjusted for live weight were present at d14 and d28. At d14 adjusted weights for duodenum, jejunum, and ileum were greatest in FCR, intermediate in RFI2, RFI3, RBC, and lowest in RFI. At d28, differences were only present in adjusted duodenum weight with RFI2 being the heaviest, RFI3, RBC, and FCR intermediate, and RFI lowest. Line differences in adjusted lengths or densities of the small intestine were not present at d14 or d28.

Supply *vs* Demand Organs

In **Table 5** supply and demand organ weight comparisons between lines were made through aggregation of supply organs (i.e. crop, proventriculus, gizzard, liver, duodenum, jejunum, and ileum) and demand organs (i.e. pectoralis major, pectoralis minor, and bone in thigh and drum). No line differences in adjusted supply or demand organ weight was present at d14. At d28, RBC and FCR expressed highest adjusted supply organ weight, RFI2 was intermediate, and RFI and RFI3 were lowest. For adjusted demand organ weight RFI and RFI2 expressed the heaviest weight, RFI2 was intermediate, and RBC and FCR were lowest.

Discussion

Four generations of FE selection improved FE in the four test lines between 11 and 17% compared to the RBC. At selection age (d28), the FCR line expressed the most notable improvement while FE improvements in RFI, RFI2, and RFI3 were intermediate. These results are in line with other selection studies in chickens and quail where genetic correlations between FCR and RFI were positive but moderately low, ranging between 0.26 and 0.31 (Varkoohi et al., 2010; Varkoohi et al., 2011; Aggrey et al., 2010). The positive genetic correlations between FCR and RFI indicate selection for one trait inherently improves the other; however, the moderate values indicate FCR and RFI are controlled by different genes. This statement is supported by the work of Varkoohi and Aggrey along with results of the present study, where selection for FCR improved FE to a greater degree compared to FE expressed by RFI and alternative forms of RFI.

Further support that FCR and RFI are controlled by different genes is shown through changes in correlated traits including d14 live weight, WG, FI, and d28 live weight. Selection for FE reduced d14 live weight in all lines compared to the unselected RBC line. Interestingly this observation has warranted little discussion in FE literature. With d14 being the start of the test period, it appears birds are penalized for high growth rates prior to selection. Suppressed growth prior to selection signifies an alteration to the bird's growth curve indicating how age at which FE selection occurs can impact a bird's growth pattern. While selection for FE lowered d14 live weights in all lines, d28 weights were increased in comparison to RBC excluding RFI2. In FE selected lines percent gain during the testing period ranged between 156% to 137% in comparison to the 128% gain found in the RBC. Percent gains found in the testing period for FE lines demonstrate how FE selection targets individuals expressing raid growth during the testing period. While RFI2 had lower d14 and d28 live weights in comparison to the control line, selection for FE still resulted in RFI2 having a higher percent gain compared to the control line. Compared to RBC, selection for FCR decreased FI at d28 by -1%, and increased WG by 15%. The disproportionate increase in gain compared to the decrease in FI indicates how FCR improves FE through enhanced growth. In contrast, FE improvements in RFI, RFI2, and RFI3 were primarily achieved through a reduction in FI ranging between -9.1% and -4.1%, whereas WG in these lines expressed slight improvements between 1 and 7.6% when compared to the RBC.

The ability of FCR and RFI to improve FE differently is supported throughout the literature. Varkoohi et al. (2011) showed genetic correlations between FI and RFI to be 0.74 and FI and FCR to be 0.26. Conversely, they found genetic correlations between WG and RFI to be 0.08 and WG and FCR to be -0.45. Improvements in FE for FCR and RFI occur differently due to biological efficiency being influenced by both ME and GE. Maintenance efficiency, the collection of all processes needed to stay alive excluding production costs, are estimated to account for one third of the variation in feed efficiency (Patience et al., 2015). Traits affecting

ME include activity levels, immune function, bodyweight, feed intake, and visceral organ size. In contrast GE is primarily involved with growth. Evaluation of these lines reveals how selection for different FE metrics places different emphasis on GE and ME.

Between d14 and d28 FCR expressed the highest level of gain. The high rate of gain during the selection period indicates selection for FCR successfully improves GE efficiency. However, improvements in GE efficiency through selection of FCR counter ME efficiency due to the increase in live weight. As bodyweight increases more feed per unit of gain is needed to maintain the higher live weight. It is this dynamic that is responsible for the great improvement in FE with a small decrease in FI compared to the other selected lines. In addition, large visceral organs were found in FCR birds indicating how selection for FCR hinders ME. Visceral organs play essential roles in the digestion and absorption of nutrients and for this reason have high energy requirements. In cattle, Smith (1970) found the liver to weigh 2% of the animal's body weight but it received 27% of the animal's cardiac output showing the disproportionately high energy requirements of visceral organs.

In comparison to RBC and FCR, selection for RFI resulted in intermediate levels of WG, indicating selection for RFI does in fact improve GE efficiency but not at the same level as selection for FCR. Greater gains in ME efficiency were achieved selecting for RFI through reduction in FI and visceral organ size. Adjusted visceral organ size was smaller in RFI birds while FI levels were intermediate to FCR and RFI2. Intermediate improvements in WG and FI coupled with a large reduction in visceral organ size illustrates how selecting for RFI improves FE by placing a more balanced emphasis on GE and ME compared to FCR. Of the four selected lines, RFI improved FE with the most balanced improvements in GE and ME. Similar to RFI, intermediate improvements were made to GE and ME by selecting for RFI2 and RFI3. RFI3 had higher FI and live weight compared to RFI while expressing similar weights for visceral organs. Selection for RFI2 was more successful at reducing ME by lowering FI and WG. Interestingly the reduction in FI and live weight gain did not result in RFI2 birds having smaller visceral organs compared to RFI and RFI3 birds. The intermediate visceral organ size in RFI2 birds indicate FI levels are not perfectly correlated to visceral organ size or maintenance requirements.

Conclusion

Irrespective of the feed efficiency selection criteria, improvements in FE were made in all lines compared to the RBC. However, manipulation of the component traits for FE varied considerably between selected lines. Selection for FCR resulted in the greatest increase in WG while RFI2 resulted in the greatest reduction in FI. Selection for RFI improved FE through balanced improvements in GE and ME along with the greatest reduction in visceral organ size. The results of this study show the complexity of FE and the inversely related relationship between ME and GE highlighting the need for FE metrics capable of ascertaining these two types of biological efficiencies. Further selection studies, exploiting the random regression components for mid metabolic body weight and weight gain found using RFI2 and RFI3 models may provide geneticists the ability to effectively target these specific biological efficiencies.

Table 1. Feed efficiency and component trait measurements taken between 14 and 28 days of age in Japanese quail after 4 generations of selection for different feed efficiency strategies.

Line	FE[1]	d14 Live weight (g)	d28 Live weight (g)	Live weight gain[2] (g)	FI[3] (g)
RBC	0.362 ± 0.004c	87.3 ± 1.3a	198.6 ± 2.3bc	111.6 ± 1.6c	308.7 ± 2.7a
FCR	0.424 ± 0.004a	82.2 ± 1.3b	210.2 ± 2.3a	128.4 ± 1.7a	304.6 ± 2.8ab
RFI	0.401 ± 0.004b	86.4 ± 1.3ab	204.6 ± 2.3ab	118.7 ± 1.7bc	292.4 ± 2.8c
RFI2	0.413 ± 0.004ab	81.7 ± 1.4b	193.5 ± 2.7c	112.2 ± 1.9c	280.8 ± 3.2d
RFI3	0.416 ± 0.004ab	82.3 ± 1.3b	201.7 ± 2.4abc	119.5 ± 1.7b	294.2 ± 2.8bc

[a,b,c] Means within the same column with different superscripts differ significantly ($P<0.05$)

[1]Average Feed Efficiency value (feed:gain) at 28 days of age.

[2]Difference between d28 live weight and d14 live weight

[3]Feed intake (FI), feed consumed between d14 and d28.

Table 2. Upper digestive organ weights (g) measured at 14 days of age and adjusted for live weight in 5 Japanese quail lines after 4 generations of selection for different feed efficiency strategies

Line	Crop	Proventriculus	Gizzard	Liver
RBC	0.39 ± 0.02a	0.57 ± 0.01ab	2.95 ± 0.11a	2.72 ± 0.05ab
FCR	0.38 ± 0.02a	0.59 ± 0.01a	3.37 ± 0.10a	2.56 ± 0.05bc
RFI	0.39 ± 0.02a	0.54 ± 0.01ab	2.98 ± 0.11a	2.48 ± 0.05c
RFI2	0.42 ± 0.02a	0.55 ± 0.01ab	2.97 ± 0.10a	2.76 ± 0.04a
RFI3	0.39 ± 0.02a	0.52 ± 0.01b	3.21 ± 0.10a	2.49 ± 0.04c

[a,b,c]Means within the same column with different superscripts differ significantly (P<0.05).

Table 3. Upper digestive organ weights (g) measured at 28 days of age and adjusted for live weight in 5 Japanese quail lines after 4 generations of selection for different feed efficiency strategies

Line	Crop	Proventriculus	Gizzard	Liver
RBC	0.77 ± 0.03a	0.95 ± 0.03a	4.66 ± 0.11a	5.95 ± 0.12a
FCR	0.77 ± 0.03a	0.97 ± 0.03a	4.79 ± 0.12a	6.04 ± 0.12a
RFI	0.72 ± 0.03ab	0.83 ± 0.03b	4.52 ± 0.11a	5.36 ± 0.12b
RFI2	0.74 ± 0.03a	0.95 ± 0.03a	4.62 ± 0.11a	5.59 ± 0.12ab
RFI3	0.58 ± 0.03b	0.91 ± 0.03ab	4.58 ± 0.11a	5.45 ± 0.12b

[a,b,c]Means within the same column with different superscripts differ significantly (P<0.05).

Table 4. Small intestine weights (g) measured at 14 and 28 days of age and adjusted for live weight in 5 Japanese quail lines after 4 generations of selection for different feed efficiency strategies

	Duodenum[1]		Jejunum[2]		Ileum[3]	
Line	**d14**	**d28**	**d14**	**d28**	**d14**	**d28**
RBC	6.66 ± 0.13ab	0.54 + .02ab	6.66 ± 0.13ab	0.74 + .02a	6.66 ± 0.13ab	0.62 +.02a
FCR	6.96 ± 0.13a	0.50 + .02ab	6.96 ± 0.13a	0.73 + .02a	6.96 ± 0.13a	0.58 + .02a
RFI	6.41 ± 0.13b	0.48 + .02b	6.41 ± 0.13b	0.73 + .02a	6.41 ± 0.13b	0.58 + .02a
RFI2	6.73 ± 0.13ab	0.55 + .023a	6.73 ± 0.13ab	0.68 + .02a	6.73 ± 0.13ab	0.55 + .02a
RFI3	6.63 ± 0.13ab	0.49 + .02ab	6.63 ± 0.13ab	0.68 + .02a	6.63 ± 0.13ab	0.59 + .02a

[a,b] Means within the same column with different superscripts differ significantly ($P<0.05$).

[1] Pancreatic loop.

[2] End of pancreatic loop to Meckel's diverticulum.

[3] Meckel's diverticulum to ileocecal junction.

Table. 5 Aggregated supply and demand organ weights (g) measured at 14 and 28 days of age and adjusted for live weight in 5 Japanese quail lines after 4 generations of selection for different feed efficiency strategies

	Supply[1]		Demand[2]	
Line	**d14**	**d28**	**d14**	**d28**
RBC	7.73 ± 0.16a	14.91 ± 0.21a	26.73 ± 0.25a	79.21 ± 0.59b
FCR	8.11 ± 0.15a	15.07 ± 0.2a	26.21 ± 0.24a	80.56 ± 0.6b
RFI	7.60 ± 0.16a	13.92 ± 0.21b	26.84 ± 0.25a	82.74 ± 0.59a
RFI2	7.91 ± 0.15a	14.42 ± 0.21ab	26.40 ± 0.24a	81.46 ± 0.59ab
RFI3	7.73 ± 0.15a	14.02 ± 0.21b	26.80 ± 0.24a	82.70 ± 0.59a

[a,b] Means within the same column with different superscripts differ significantly (P<0.05).
[1]Cummulative weight of supply organs including: crop, proventriculus, gizzard, liver, and small intestines.
[2]Cummulative weight of bone in breast and bone in drum and thigh.

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Chapter 4

Effect of Feed Efficiency Selection on Growth Curve Parameters

Introduction

The growth pattern an individual follows on its path to maturity is the growth curve. As described by Ricklefs, (1968, 1973, 1979) growth curve variations are present in bird species. The most extreme differences exist between precocial and altricial species, resulting from post hatch differences in vison, mobility, and feeding habits (Ricklefs, 1973). The enhanced post hatch characteristics found in precocial species such as chickens, turkeys, and quail result in them being advantageous for commercial farming. Despite vast differences in size and physiological growth, the growth patterns of all precocial species follow the sigmoid curve (Brody, 1945; Anthony et al., 1991a). The sigmoid shape is mathematically described using logistic, Gompertz, or Von Bertalanffy equations (Ricklefs, 1967). Each equation utilizes three parameters to statistically model birds' growth pattern over time. The three parameters used in each equation include weight at age zero, instantaneous relative growth rate, and the asymptotic value or mature bodyweight (Ricklefs, 1983). These parameters can then be used to graphically illustrate the growth curve, determine age and weight of inflection, along with the weight and age at maturity.

While the overall shape of the growth curve is sigmoidal, growth curve analysis has revealed selection for body weight to alter the pattern of growth (Anthony et al., 1995). Vast growth curve differences were found in Japanese quail divergently selected for 4-week body weight. Quail selected for high 4-week body weight reached point of inflection 11 days prior to their counterparts and reached a 52% heavier asymptote weight in half the time (Anthony et al., 1986). Similarly, selection in turkeys for increased body weight at 16 weeks, resulted in the selected population reaching point of inflection and asymptotic age earlier and at higher weights (Anthony et al., 1991b). In addition to selection for bodyweight at a point in time, other selection trials targeting exponential growth rate (Barbato et al., 1992), weight gain on split and complete diets (Marks, 1995), and weight gain between different ages have shown to alter the growth curve in poultry (Anthony, 1995).

Research involving the relationship between feed efficiency and growth parameters is less documented. The genetic correlations between growth curve parameters and FE strategies, such as FCR and RFI, were evaluated by N'Dri et al. (2006). In this study the initial specific growth rate of the bird was moderately correlated with FCR (0.42) and RFI (0.51). The objective of this study was to identify how selection for FCR, RFI, RFI2, and RFI3 altered the three components of the growth curve in comparison to the Random Bred Control (RBC).

Materials and Methods

The five lines evaluated in this study will be referred to as RBC, FCR, RFI, RFI2, and RFI3. Mating strategy and selection criterion used to develop these lines is as described on pages 33-35. Two one-week hatches for each line were used to evaluate growth curve differences between lines. At hatch individual birds from each of the 5 lines were wing banded and a maximum of 2 chicks per breeding pair were used to avoid family bias within a line. Two hundred chicks per hatch were reared straight run and intermixed in a large pen on wood shavings under thermoneutral conditions with feed and water *ad libitium*. Body weight measurements were taken at hatch and weekly up to 56 days of age. Only individuals with body weight records at every age were included in the analysis. Gompertz-Laird model was used to define growth curve parameters (Laird et al., 1965). The form of the equation is as described below:

$$\mathbf{W_t = W_o \exp[(L/K)(1\text{-}expKt)]}$$

W_t = Weight of bird at time t
W_0 = Initial bodyweight (weight at hatch)

L = instantaneous growth rate (per week)
K = rate of exponential decay (measure the rate of decline in growth rate)

Individual growth curves were fitted for each bird. Parameters of the Gompertz-Laird model were used to derive inflection point (ti), weight of inflection (Wi), and weight at asymptote (W_A).

$Ti = (1/K) \log(L/K)$
$Wi = (W_o \exp((L/K)^{-1})$
$W_A = W_o \exp(L/K)$

ANOVA was used to test for hatch by sex and line by sex interactions for W_0, Ti, Wi, and W_A. Interactions were not present and therefore birds were pooled by line. Gompertz-Laird growth curve model and ANOVA was ran in JMP Pro 12 (SAS, 2013).

Results

Alterations to the bird's growth pattern were evident and dependent on the FE metric used for a selection criterion. In **Table 1**, W_0 was highest in FCR, intermediate in RFI, and lowest in RFI2, RFI3, and RBC. Age of inflection was increased in all selected lines compared to the RBC, and Ti for FCR and RFI3 lines were greater compared to RFI and RFI2. Similarly, FCR and RFI3 had the greatest Wi, while Wi for the RBC was not significantly different from the RFI and RFI2 lines. The W_A was unchanged in RFI and RFI2 compared to the RBC but was increased in birds selected for FCR and RFI3. The average growth curves for each of the 5 lines are plotted in figure 1. From this figure it is evident that birds selected for FCR and RFI3 have a different growth curve compared to birds in the RFI, RFI2, and RBC lines. Therefore, growth curves in FCR and RFI3 lines were pooled together and growth curves in RFI, RFI2, and RBC were pooled together. These two growth curves are shown in **Figures 2 and 3.** In **Figure 2** the growth curves are plotted between 0 and 21 days of age. In this figure it is evident that the RFI3-FCR growth curve begins to separate from the RFI-RFI2-RBC growth curve shortly after the beginning of the FE testing period between 14 and 21 days. In **Figure 3,** the two growth curves are plotted between 0 and 56 days of age showing the continuation of the increased body weights in the RFI3-FCR growth curve compared to the RFI-RFI2-RBC growth curve.

Discussion

Selection for the 4 FE metrics evaluated in this study altered the growth pattern of each line compared to the RBC. Overall FE selection decreased early rapid growth and extended the period of rapid growth closer to the point of FE testing. RBC chicks were lightest at hatch but outgained their counterparts during the first week and were found to have the heaviest 4 and 7-day BW's. Relative growth rate between d0 – d4 was 110% for the RBC and on average 25% higher than the 4 FE lines. Relative growth rate at d7 for the RBC had decreased and was only superior to FCR, by d14 the relative growth rate for RBC was on average 12% lower compared to the 4 FE lines. Similar results were found by Marks (1979) between broilers selected for bodyweight and unselected broilers. Marks found relative growth rate to be the highest in the selected line during the first week before sharply diminishing in the following weeks. It should be noted that the RBC line was derived from two quail lines with long term selection for 4-week bodyweight. Similar selection objectives for the RBC in the current study and the selected broiler line in Marks (1979) study indicate how selecting for increased bodyweight causes early rapid growth but gains in relative growth rate diminish quickly after the first week.

Shifts in early rapid growth resulting from selection for FE appears to be related to Ti. Ti was on average delayed 0.81 days compared to the RBC. The delay in Ti is likely a result of the sigmoidal shape of the growth curve found in all precocial poultry species (Brody, 1945). The sigmoidal shape of the growth curve in poultry species is a function of initial slow growth increasing to a maximum rate (Ti), after maximum growth rate is reached the rate of growth decreases until reaching the asymptote level (Brody, 1945). The phenomena of the sigmoid shape along with moderately high genetic correlations (0.60) between FE and gain (Fox and Bohren, 1954) indicate how superior FE values should be expected in individuals with accelerated growth during FE testing rather than individuals expressing decelerated growth during FE testing. In the current study FE testing began at d14 causing the shift from 14.69 in the RBC to an average of 15.50 for FE lines. The shift in Ti for FE lines indicates that birds in FE lines experienced accelerated growth rates for the first 1.5 days of the test while RBC birds experienced accelerated growth rate for 0.69 days of the test. Therefore, during the 14-day FE testing period RBC birds experienced decelerated growth for 95% of the testing period while FE lines experienced decelerated growth for 89% of the testing period. Similar findings were present in N'Dri et al (2006) where Ti was found to have a positive genetic correlation with FE. In addition to superior growth rate during the testing period, positive correlations between FE and Ti can be attributed to individuals being smaller at the beginning of the testing period leading to lower maintenance cost and improved efficiency (Pym and Nicholls, 1979).

Similar to Ti, FE was also found to alter asymptote levels. Asymptote levels were significantly higher in FCR and RFI3 lines while selection for RFI and RFI2 were unchanged compared to RBC. Different asymptote levels for FCR and RFI support the inherent differences between these two FE metrics. RFI adjusts expected FI for BW and gain in attempt to be phenotypically independent of production traits (Koch et al., 1963; Kennedy et al., 1993) while FCR is a ratio trait having a positively correlated numerator and denominator resulting in increased FI, gain, and mature size (Gunsett, 1984). The positive correlation between maintenance requirements and bodyweight support how selection for RFI improves FE by penalizing individuals with high maintenance costs, while selection for FCR improves FE by favoring high gaining individuals with greater mature weights and therefore increased maintenance costs. Similarly, to RFI, selection for RFI2 had no effect on mature size. Maintaining mature weight in the RFI2 line is likely a result of the phenotypic independence between RFI2 and production traits. While the statistical properties of RFI3 are similar to RFI and RFI2, it appears selection for RFI3 had a larger impact on growth and body weight traits. Using average MBW and WG values may have resulted in the values for these traits being skewed towards higher values compared to if actual values for each bird were used.

Conclusion

In conclusion a bird's growth pattern can be highly influenced by the FE metric. In general, bird's maintenance costs will be reduced early in life through a reduction in early rapid growth rate and point of inflection will be delayed (Ti) in relation to the time of testing. The strong relationship between FE and gain causes Ti to be influenced by the age of FE testing. Testing at an early age will cause Ti to occur earlier than FE testing at an older age, since FE will be more favorable in individuals experiencing the greatest accelerated growth during the testing period. The impact the FE metric will have on Ti is dependent of the correlation between the FE metric and gain. Selecting for FE metrics highly correlated with gain will lead to stronger impacts on Ti compared to selecting for FE metrics with weaker correlations to gain. The FE metric used to measure and select for FE also has an impact on the asymptote of the growth curve. Asymptote levels will increase if FE is improved primarily through growth. Increases in growth will be accompanied by increases in FI, mature weight, and maintenance costs. Mature weight is more likely to stay constant in lines where FE improvements are highly influenced by a reduction in maintenance costs. It is important to understand the effect FE metrics have on growth patterns and how those affects will align with the breeding goal. Mainstream poultry has had great success improving FE through selection for FCR. These improvements have primarily occurred through early rapid growth rate and reaching market weight at younger ages. As new markets develop, and consumer demand increases for slower growing bird's new methods for accomplishing improved FE will be necessary. These newer methods will likely include moving away from FCR and relying more on index related metrics placing a more balanced emphasis on growth and maintenance efficiencies.

Table 1. Growth curve parameters in 5 Japanese quail lines after 4 generation of selection for different feed efficiency strategies

	[1]W_0	[2]Ti	[3]Wi	[4]W_A
RBC	9.50 ± 0.08b	14.69 ± 0.16b	100 ± 1.27b	276 ± 3.41b
FCR	10.19 ± 0.09a	15.52 ± 0.18a	109 ± 1.39a	296 ± 3.74a
RFI	9.83 ± 0.10ab	15.31 ± 0.20ab	102 ± 1.59b	278 ± 4.27b
RFI2	9.73 ± 0.11b	15.33 ± 0.22ab	99 ± 1.69b	273 ± 4.54b
RFI3	9.60 ± 0.09b	15.82 ± 0.18a	109 ± 1.42a	295 ± 3.82a

[1] W_o = weight at day zero (hatch weight)
[2] Ti = Age of inflection
[3] Wi = Weight of inflection
[4] W_A = Asymptote weight

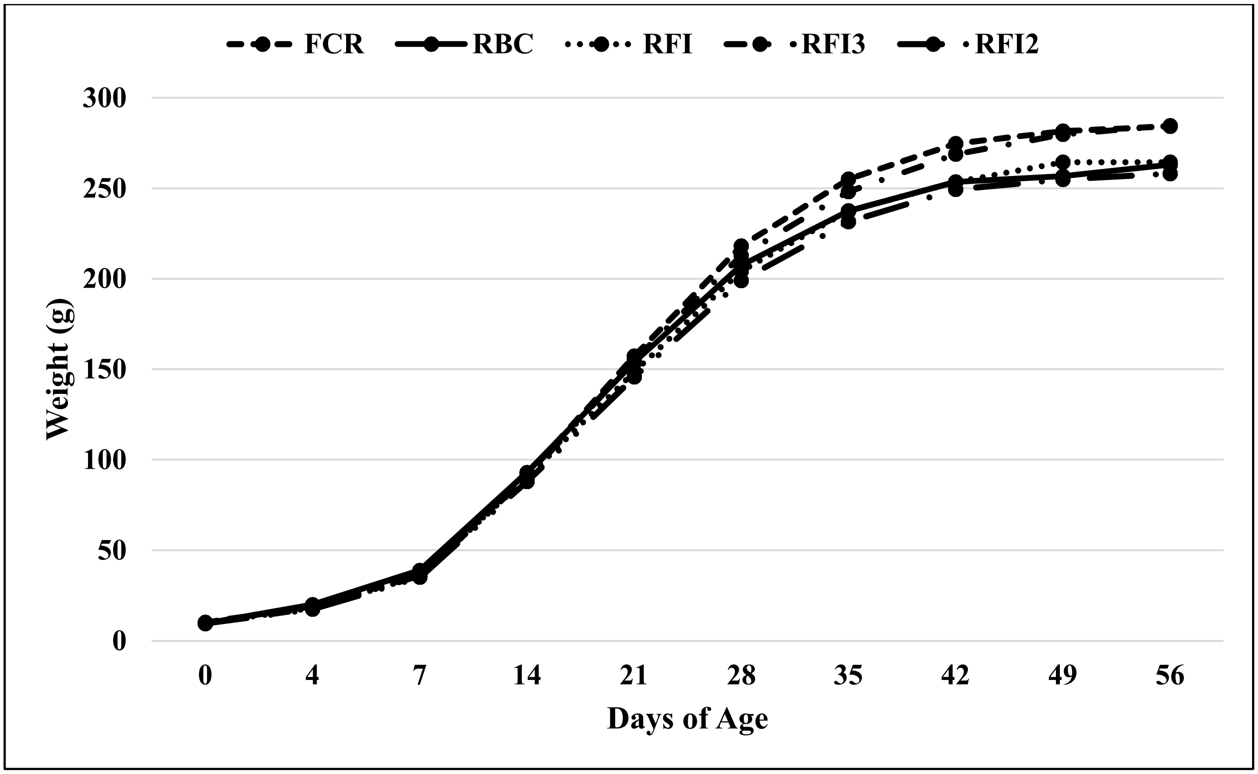

Figure 1. Growth curves of 5 Japanese quail lines selected over 4 generations for different feed efficiency strategies

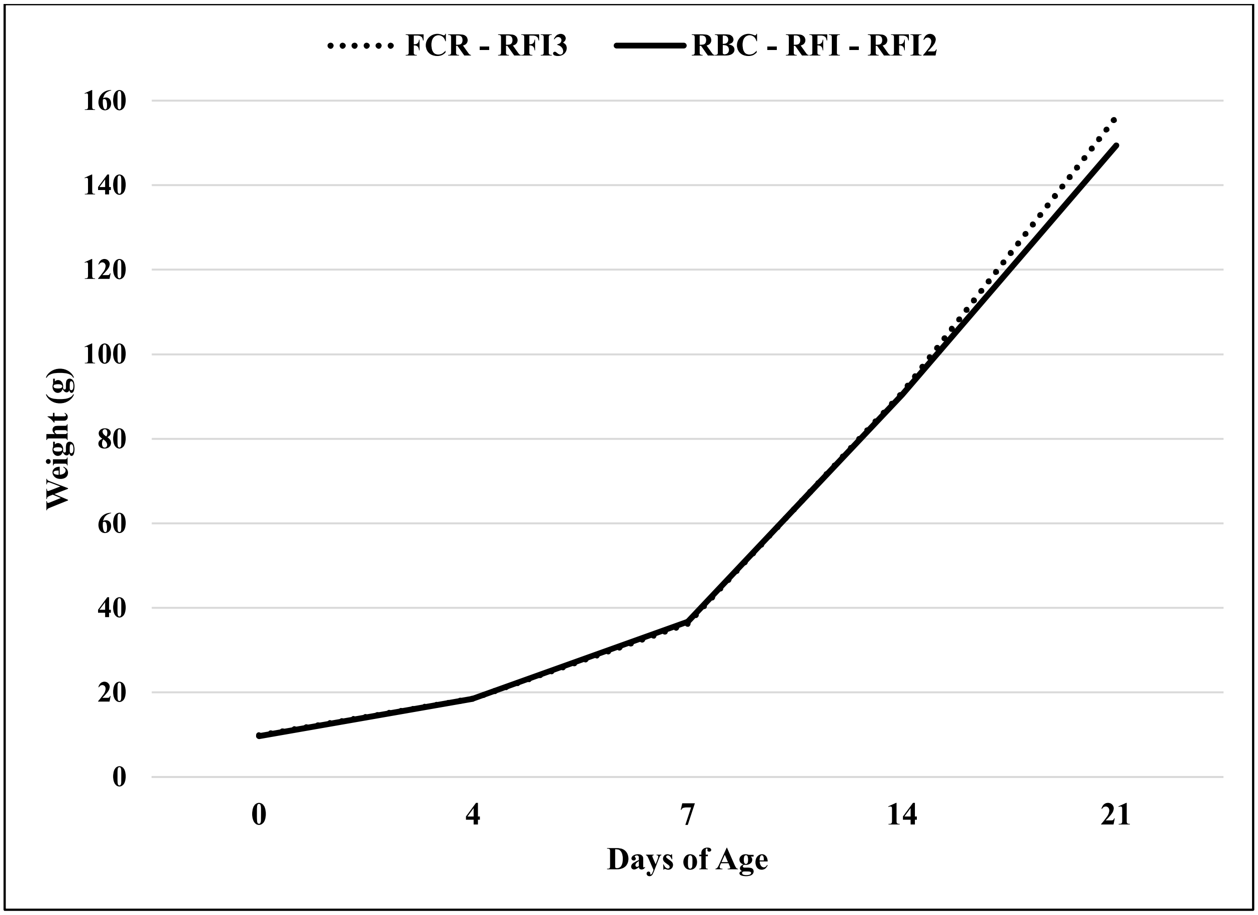

Figure 2. Average growth curves between 0 and 21 days of age in Japanese quail selected for FCR and RFI3 compared to the average growth curves of RBC, RFI, and RFI2 Japanese quail

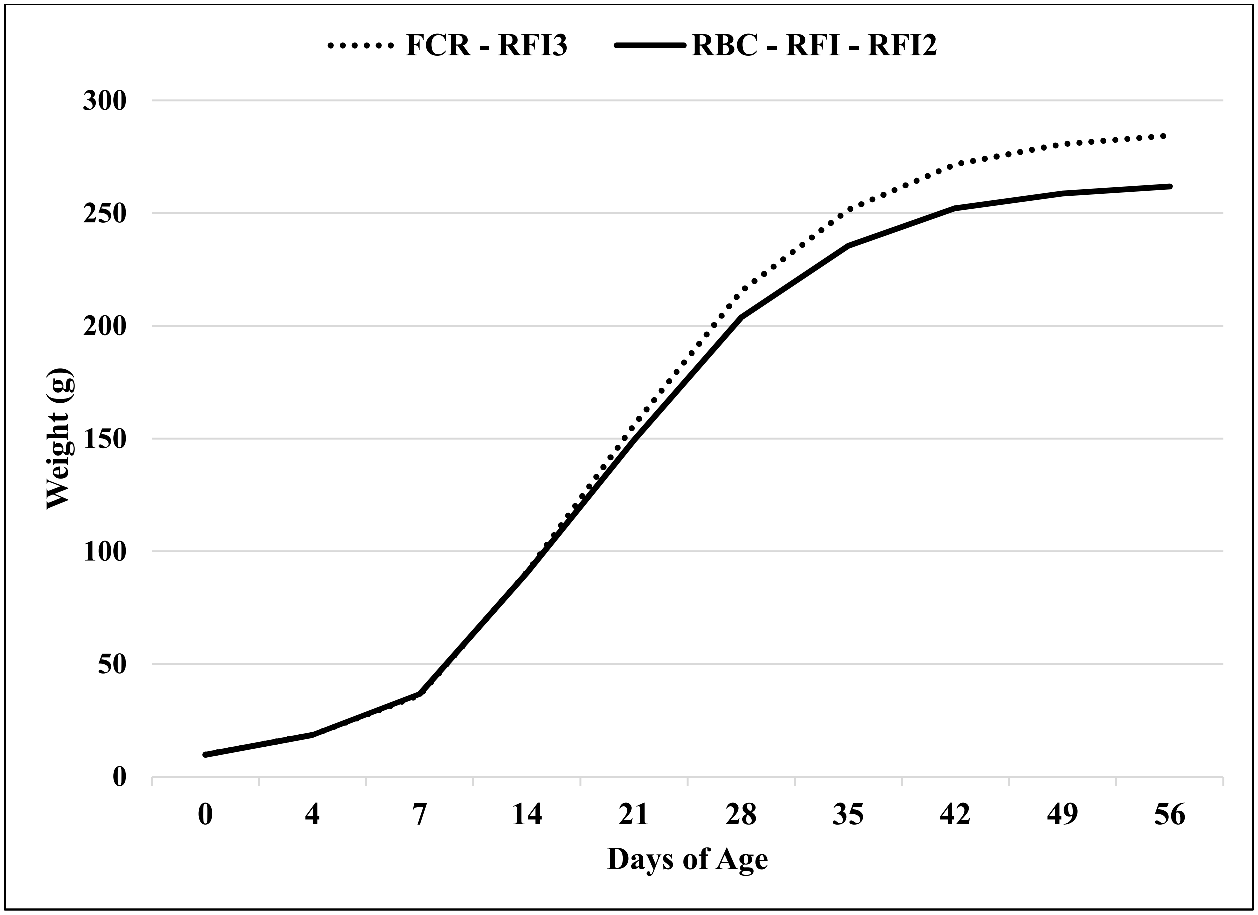

Figure 3. Average growth curves of Japanese quail between 0 and 56 days of age selected for FCR and RFI3 compared to the average growth curves of RBC, RFI, and RFI2 Japanese quail

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Chapter 5

General Synthesis

The objective for this set of experiments was to investigate how selection for traditional and alternative feed efficiency strategies impacted traits related to the growth and development of meat-type birds. A Japanese quail line exposed to chronic high 4-week body weight was selected as a model for the commercial broiler. Four sub-lines were independently selected for their respective feed efficiency strategy (FE). Feed efficiency strategies of interest included two traditional strategies, feed conversion ratio (FCR) and residual feed intake (RFI), along with two strategies recently proposed as alternatives to RFI. The proposed RFI strategies, RFI2 and RFI3 were developed to identify maintenance and growth-related efficiencies at the bird level in addition to the population level. Identifying these efficiencies at the bird level is hypothesized to reduce the level of bias found in traditional RFI and allow geneticists to determine maintenance and growth efficiencies independently from each other. Prior to these sets of experiments, the proposed RFI strategies have only been evaluated through simulation. Therefore, it was of interest to determine how practical application of these strategies in a selection study would respond in comparison to the traditional FE metrics used in commercial animal breeding.

Independent FE strategies were selected over 4 generations. During this time complete pedigree and FE records were collected between 14 and 28 days of age on 4,748 individuals. Estimates of genetic parameters revealed moderately low heritability's for FCR (0.22 + 0.06) and RFI (0.12 + 0.05), indicating genetic progress should be expected at similar rates for both FE strategies. Phenotypic correlations showed how improvements in FCR and RFI impact FE component traits differently. Phenotypic correlations for d14 body weight, d28 body weight, weight gain, and mid metabolic body weight in FCR lines varied from 0.09 to -0.67, while phenotypic correlations for these traits in the RFI were close to zero. The phenotypic correlation for feed intake in the RFI line was greater (-0.67) than that found in the FCR line (0.21). These findings demonstrate selection for RFI will strongly favor individuals with lower FI levels, irrespective of the other production traits. Whereas, selection for FCR will slightly favor individuals with lower feed intake but will primarily be influenced by growth traits such as weight gain (WG).

Estimated breeding values (EBVs) were plotted over the 4 generations of selection for each of the selected lines. Similar to the genetic and phenotypic correlations, plots indicated selection for FCR and RFI changed the genetic merit of FE components differently. Selection for FCR significantly reduced the genetic merit of d14 body weight and significantly increased the genetic merit of d28 body weight and WG in comparison to RFI. Genetic merit for FI was reduced in both FCR and RFI; however, the decrease over 4 generations was greater in RFI. Changes in the EBVs of FE component traits in RFI2 and RFI3 illustrated similar patterns to those seen in traditional RFI. The generational changes in the component trait EBVs of RFI2 closely mirrored those found in traditional RFI indicating both FE strategies were targeting the same genes to similar degrees. Changes in EBVs for RFI3 were intermediate to FCR and RFI for WG and d28 body weight but closely followed the downward slope of RFI for FI. Changes in the genetic merit of these component traits implies that selection for RFI3 is targeting growth genes to intermediate degrees of that found in FCR and RFI but targeting FI genes to similar degrees of RFI and RFI2 selection.

Progeny of the fourth generation along with progeny from the RBC were evaluated for FE and its component traits between 14 and 28 days of age. During this period growth and development of supply and demand organs were also evaluated. Measurement of FE during the two-week period revealed improvements in FE occurred across all lines in comparison to the RBC. Similar to the genetic and phenotypic correlations found in the first trial, selection for FCR accomplished FE primarily through improvements in weight gain, resulting in higher ending body weight. In contrast, FE improvements for RFI and RFI2 lines were a result of significant reductions in FI and did not impact body weight or weight gain during the testing period. Line differences for the relative weight of supply and demand organs were not present at d14 but were present at the end of the FE testing period. At d28, the relative weight of supply organs was smaller in traditional and contemporary RFI lines but relative weights for demand organs were larger in comparison to FCR and RBC. Supply organs are known to have disproportionately high maintenance requirements. Therefore, the reduction in the relative weight of supply organs will reduce maintenance requirements. The reduction in maintenance requirements is one of the likely causes for the reduction in FI and improved FE found in RFI type lines.

Progeny from the fourth generation and the RBC were also evaluated for growth curve parameters. Among the 5 lines evaluated in this study, two separate growth curves emerged. Selection for FCR and RFI3 resulted in a growth curve with higher asymptote values along with higher values for point and weight of inflection. The second growth included RFI, RFI2, and RBC lines, indicating selection for RFI and RFI2 could improve FE without altering the growth curve.

Findings of this set of experiments highlights the complexity of selecting for FE. A major factor in the difficulty associated with FE selection is the unclear objective when selecting for FE. Compare FE selection to body weight selection. When the objective of the poultry breeder is to increase body weight the objective is clear because body weight is a single trait. In contrast FE is made up at a minimum of two traits. For this example, we will consider feed intake and weight gain. If the objective is to improve FE the breeder can accomplish this in a variety of ways. The breeder can keep FI constant and focus on only improving weight gain, in contrast the breeder can hold weight gain constant and reduce FI, or the breeder can use an index and put various degrees of weighting on FI and WG. For these reasons, the breeder must have a clear objective when selecting for FE and understand the consequences of each FE metric.

All FE strategies discussed in this document will effectively improve feed efficiency; however, the breeding objective will likely determine which FE metric is most appropriate. Traditionally improvements in FE have been accomplished through increased growth rate and weight gain resulting from FCR selection. Perpetual selection of FCR to improve FE has led to metabolic and skeletal issues brought on through rapid growth rates. In addition to the metabolic and skeletal issues, consumer interest in slower growing poultry has increased. If these trends continue, poultry breeders will need to improve FE without increasing weight gain or body weight. Selection for FCR will be ineffective in this scenario; however, as this document shows selection for RFI is effective at improving FE with minimal impact on weight gain and body weight.

The contemporary RFI models were developed to better explain the variation in feed intake and help the poultry breeder better manage maintenance and production efficiencies. The results of these studies demonstrate that selection for traditional and contemporary RFI models will result in similar outcomes. Future research should involve selection of the random regression coefficients in RFI2 or RFI3, to determine if more targeted selection towards maintenance and growth efficiency is possible. The results of these experiments unveiled how selection for different FE strategies will accomplish improved FE differently through changes in production traits, organ development, and altered growth patterns. In addition, these studies laid the foundation for further exploration in newly proposed RFI models and indicate how the ability to target maintenance and growth efficiencies will impact other biological factors.

Appendix

UNIVERSITY OF ARKANSAS

Office of Research Compliance

To:	Nicholas Anthony
Fr:	Craig Coon
Date:	December 3rd, 2018
Subject:	IACUC Approval
Expiration Date:	April 5th, 2018

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol # **15039:** *General Rearing of Selected Chicken and Quail Populations*.

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond April 5th, 2018 you must submit a newly drafted protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The following individuals are approved to work on this study: Alex Gilley, Katy Estill, Nicholas Anthony, Sara Orlowski, Timothy Lipnack, and Joseph Hiltz. Please submit personnel additions to this protocol via the modification form prior to their start of work.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/tmp