GROWTH AND ORGAN DIFFERENCES BETWEEN CHICKEN LINES SELECTED FOR DIVERGENT GROWTH RATES

by

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Thank you to the staff, students, and professionals who assisted with the weekly study. Without our "disassembly" line, this thesis would not be possible.

This thesis is dedicated to my incredible family. Your love and support made this possible. I am forever grateful.

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ABSTRACT

Selecting chicken for enhanced meat production has altered the relative growth of organs in modern broiler lines, when compared with heritage lines. In this five week study, we compared the growth and feed efficiency of a heritage line, UIUC, with a modern production line, Ross 708. During this period, the body mass and feed efficiency of the modern strain was higher than that of the heritage line, indicating that the Ross 708 birds are more efficient at converting feed to body mass. The relative growth of the breast, heart, liver and intestine were also compared during these five weeks. The breast muscle of the heritage line constituted 9% of the total body mass at five weeks, while the breast mass of the modern line comprised 18% of the total body mass. In contrast, the relative size of the heart decreased after day fourteen in the modern line, suggesting that selection for increased breast muscle has translated to decreased relative heart muscle mass. The mass of the liver reached its peak earlier in the modern line than the heritage line, possibly improving nutrient utilization. Finally, the jejunum and ileum segments of the intestine were 20% longer in the modern line, indicating a potential increase in nutrient absorption.

Chapter 1

INTRODUCTION

The chicken was domesticated approximately 7000-10,000 years ago in Asia (Komiyama, et al., 2004) from the jungle fowl (Fumihito, et al., 1994; Liu, et al., 2006; Kanginakudru, et al., 2008). While early selection focused largely on egg laying, the advent of industrial scale agriculture in the early 20th century triggered intensive genetic selection to improve the chicken's meat (broiler) production traits. This significant improvement was achieved by selection for increased feed efficiency and growth rate of the bird. In 1950, broilers took 16 weeks to reach marketable weight, while by 1990 this was reduced to 6-7 weeks (Thomas, et al., 1958; Warren, 1958; Griffin and Goddard, 1994; Konarzewski, et al., 2000). This selection played an important role in the high productivity of the U.S broiler industry, which produced approximately 36 billion pounds of chicken meat in 2007 (Service, 2008).

Selection for rapid growth in broilers has affected many of the major organ systems including the muscle, digestive, skeletal, nervous, cardiovascular, integumentary and immune systems. For example the nervous and digestive systems have changed to produce a bird with an insatiable appetite. The overall metabolism of the modern broiler has evolved, yielding birds that are highly efficient at converting feed to body mass along with increased muscle yield (Griffin and Goddard, 1994), possibly resulting from early maturation of the muscle tissue (Wick, et al., 2003; Reddish, et al., 2005). In addition, undesirable traits have arisen, presumably due to the stress induced by such rapid growth. These include sudden death due to cardiovascular failure (Olkowski, et al., 2008), ascites (Morris, 1992), reduced adaptive immune function (Cheema, et al., 2003), poor reproductive performance (Reddy and Siegel, 1976; Hocking, 1993) and skeletal problems (Lilburn, 1994; Rath, et al., 2000; McDevitt, et al., 2006).

These different traits provide unique opportunities to understand the effects of human directed evolution. As an experimental model, the broiler offers an excellent system for observing how selection for rapid growth has affected specific tissues and organs along with providing insight into how changes in one organ system can have pleiotropic effects on others. Finally, a better understanding of how human selection has affected the chicken should allow for further improvements in the genetic stock of this invaluable food source.

Comparative studies between different strains of chickens have been useful for recognizing the morphological and physiological adaptations in response to distinct selective pressures. One approach is to compare growth properties between modern broiler lines and heritage lines that have not been selected for rapid growth (Havenstein, et al., 1994a; Havenstein, et al., 1994b; Qureshi and Havenstein, 1994;

Havenstein, et al., 2003a; Havenstein, et al., 2003b). The heritage line serves as a baseline for characterizing the changes that have occurred in broilers over time. The present study makes use of a heritage broiler, UIUC, developed by Dr. H.M. Scott (Schoettle, et al., 1956a; Schoettle, et al., 1956b; Waterhouse and Scott, 1962) and maintained at the University of Illinois, Urbana Campus (UIUC). The UIUC heritage birds we examined are the progeny of males from a New Hampshire line crossed with females carrying the Columbian feather pattern (to allow feather sexing). The New Hampshire line used to generate the males has been inbred since the late 1940s. The Columbian female line was originally derived from a cross between Barred and White Plymouth Rocks and has also been inbred since the late 1940s.

Here we describe a morphological comparison between the modern broiler line, Ross 708 and the UIUC heritage line.

Chapter 2

MATERIALS AND METHODS

Feather sexed male chicks from two sources; a heritage line from the University of Illinois (UIUC), and a commercial line from Allen Family Foods (Ross 708) were selected for this experiment. Birds were housed in Pettersime starter batteries until 3 weeks of age when chickens were transferred to Pettersime grower batteries for the remainder of the 5 week study. Chickens received continuous light and were allowed *ad libitum* access to feed and water for the duration of the experiment. Southern States commercial starter ration was fed to these birds until 4 weeks of age, at which time a commercial finisher diet was administered. A total of 120 birds of each line were allocated into six replicate groups of 20 chicks. Because chicks of the two lines were shipped from different locations, initial measurements were collected from six randomly selected birds as detailed below on day 2 post-hatch. Starting on day 7 post-hatch and continuing weekly until day 35, four birds from each of the twelve battery cages were weighed and euthanized via cervical dislocation. Individual organs were weighed and measured; including all three sections of the small intestine (duodenum, jejunum, and ileum), the heart, the liver, and left half of the breast muscle (pectoralis major and minor; which was doubled to determine total breast mass of each individual bird). Three inches on the distal end of the duodenum, three inches of the central section of the jejunum, and three inches of the distal end of the ileum (using Meckel's Diverticulum as a landmark distinguishing between the jejunum and ileum) were also preserved in liquid nitrogen for future studies. Analysis of variance, t-tests and R^2 values were determined using the JMP statistical package. Allometric relationships were determined based on the following relationship (Huxley, 1972):

$$M_0 = \alpha(M_I^{\beta})$$

Where M_0 and M_I are the mass of the organ and the mass of the bird, respectively, α is a constant reflecting the relationship between the mass of the organ and the total mass of the bird, and β is the rate of change of the organ with changes in the total mass. This is simplified to the linear equation:

$$\ln(M_0) = \ln(\alpha) + \beta(\ln(M_I))$$

The University of Delaware College of Agriculture and Natural Resources Agricultural Animal Care and Use Committee approved all animal procedures employed in this study.

Feed conversion ratio was defined by average weight gain in grams to average kilograms of feed intake of all birds in an individual pen.

Chapter 3

RESULTS

The modern broiler Ross 708 line grew to an average of 1.8 kg by the completion of this five week study, while the UIUC heritage line averaged only1 kg over the same time period. Comparative growth characteristics between these two lines reveal many differences in traits, particularly in relative organ mass and allometric growth of organs.

3.1 Overall Body Mass

At day 2 post-hatch, there was no significant difference between the mean mass of the Ross 708 and UIUC lines (Table 3.1; Figure 3.1). However, by day 7 the mass of the Ross 708 birds significantly exceeded that of the UIUC birds (Ross 708 Mean=149g, 95%: 142-157g; UIUC Mean = 91 g, 95%: 86-97g). From day 7 through the completion of the experiment at day 35 post-hatch, the Ross 708 birds increased in mass by a rate of 59 grams per day, while the UIUC birds increased by only 32 grams per day (Figure 3.1). Thus, the modern line deposited mass at a rate 1.8 times that observed in the birds of the heritage line.

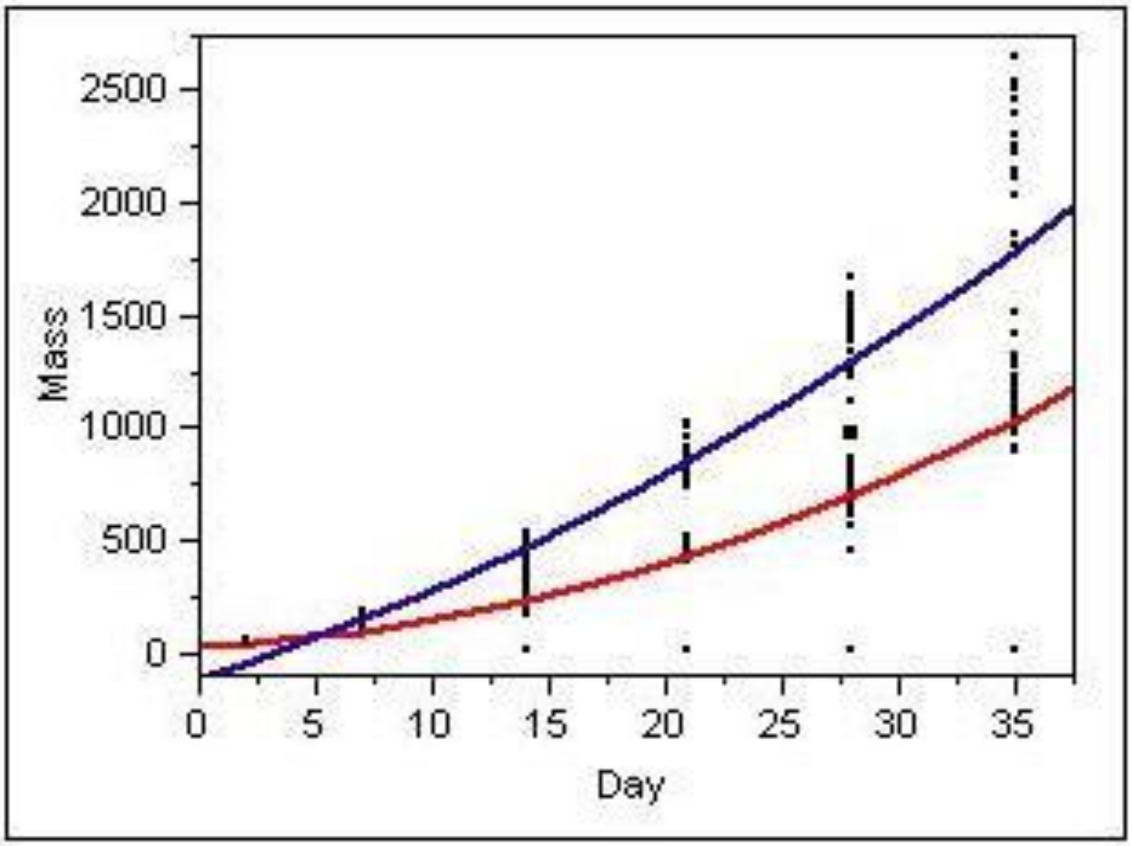
Table 3.1: Average Body Mass by Day

Average mass, in grams, of the heritage line (UIUC) and the modern broiler line (Ross 708). Day 2 values represent the average of six birds, while the remaining time points represent averages of 24 birds per strain. *indicates values that are significantly different (P < 0.05) between UIUC and Ross 708.

DAY	**UIUC**	**ROSS 708**
2	38.4	36.4
7*	91.7	149.3
14*	233.6	431.8
21*	450.3	855.9
28*	699.2	1411.3
35*	1046.6	1804.2

Figure 3.1: Total Body Mass Comparison Between the Heritage and Modern Lines Throughout the 35-day Experiment

This image shows the difference in overall body mass over the full 35-day experiment. From day 7 to the end of the experiment (day 35), the modern day Ross 708 birds, represented by the blue line, grew at a rate of 59 grams per day, to a final average weight of 1804.2 grams. During the same time frame, the heritage line, represented by the red line, grew at a rate of 32 grams per day to a final average weight of 1046.6 grams.



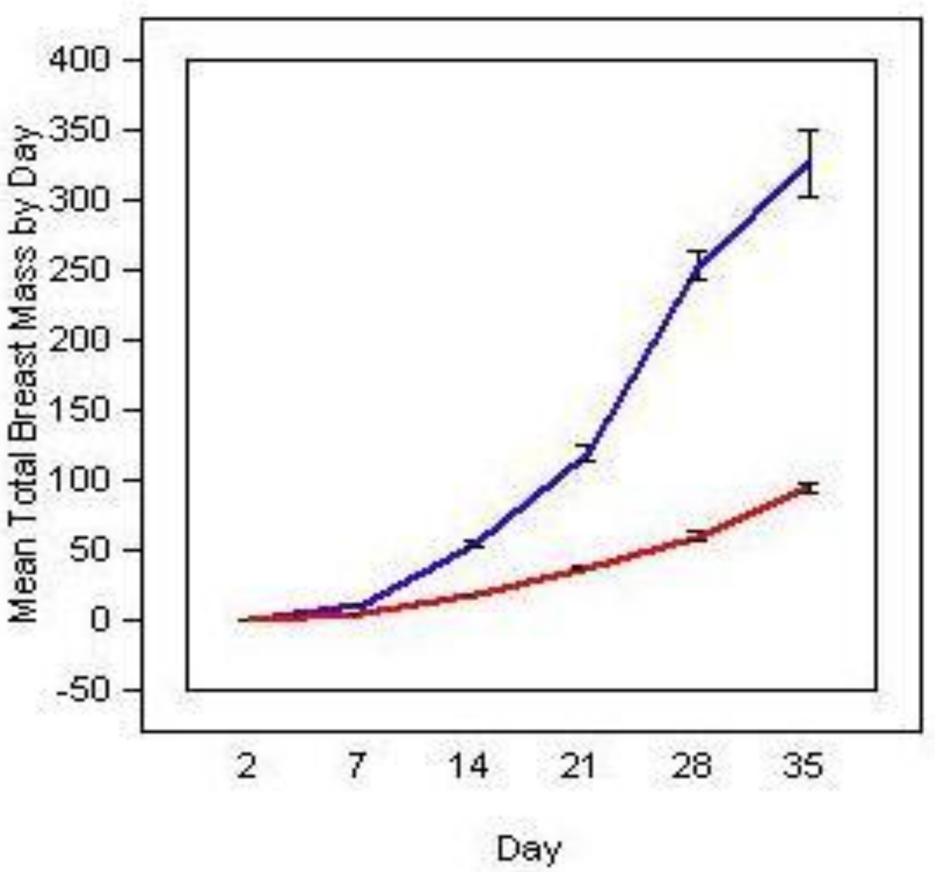
3.2 Breast Muscle

The major effect of broiler selection has been an increase in overall muscle mass of the chicken, and this is particularly evident in the breast muscle (Figure 3.2). During the course of this experiment, the breast muscle of the UIUC birds gained 1.6 grams per day while the Ross 708 birds increased by 6.1 grams per day. Hence, while the total body mass of the Ross 708 strain increased 1.8 times faster than the UIUC strain, the breast muscle of the Ross 708 birds increased 3.8 times faster than that of the UIUC birds.

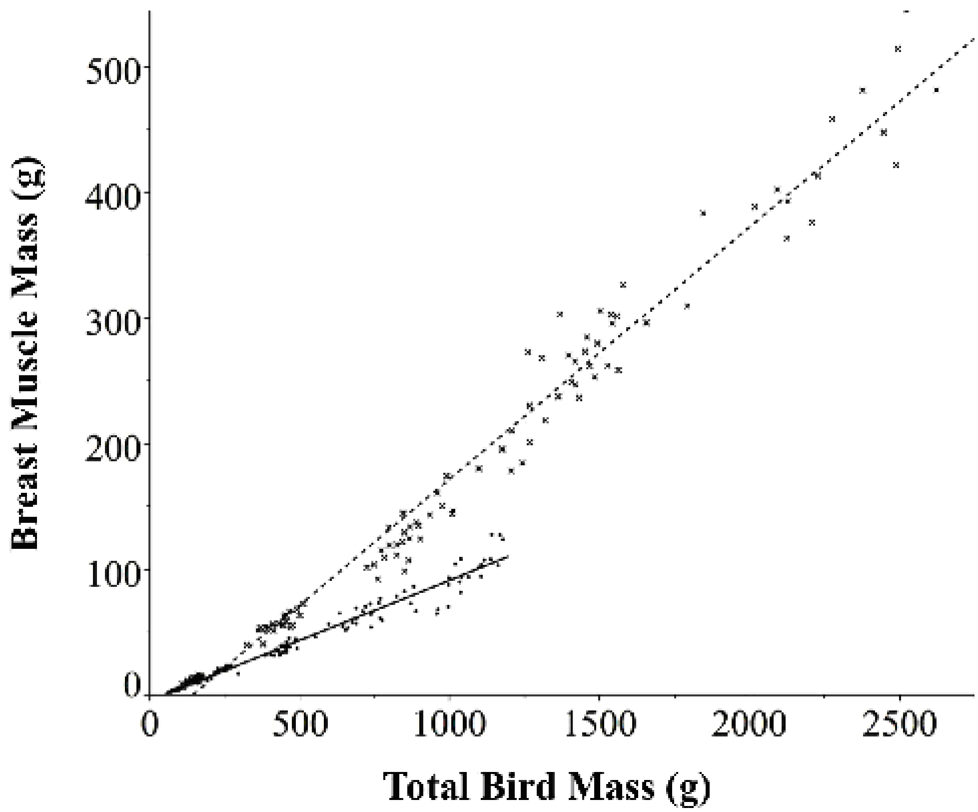
Plotting the breast muscle mass as a function of bird mass (Figure 3.3) revealed that this relationship was distinct when compared between the two strains. The equations describing the Ross 708 and UIUC birds differed (UIUC: Breast = -5.2 + 0.10 Mass; r^2 = 0.97; Ross: Breast = -29.1 + 0.20 Mass; r^2 = 0.97) with the Ross 708 slope twice that of the UIUC.

Further comparison revealed an additional difference between the two strains. By day 14, the breast muscle of the UIUC strain constitutes 9% of the body mass, and this percentage remained constant through the completion of this trial (Figure 3.4). In contrast, by day 14, the Ross 708 breast muscle constitutes 14% of the body mass. Instead of reaching a plateau at day 14, this ratio continues to increase through day 35, when the breast muscle reaches 18% of the total body mass. A major difference occurred in breast muscle development following day 14, after which the UIUC birds maintained a constant allocation of resources to breast muscle production, while the Ross 708 birds continued to incorporate additional resources into this tissue. This distinction in resource allotment was supported by analysis of the allometric relationships between breast muscle mass and total body mass. Both the UIUC and Ross 708 strains exhibited positive allometry in breast muscle mass over the five week study (Figure 3.5, Table 3.2). However, comparison of the normalized breast muscle mass plots between the two strains indicates that breast muscle growth differed between the strains after day 14; the Ross 708 birds exhibited an allometric exponent of 1.25, while the UIUC birds decreased this relative growth rate to 1.09. The allometric exponents are consistent with the hypothesis that there is an increased incorporation of resources in breast muscle development after day 14 in the modern day Ross 708 birds, compared to the UIUC line.

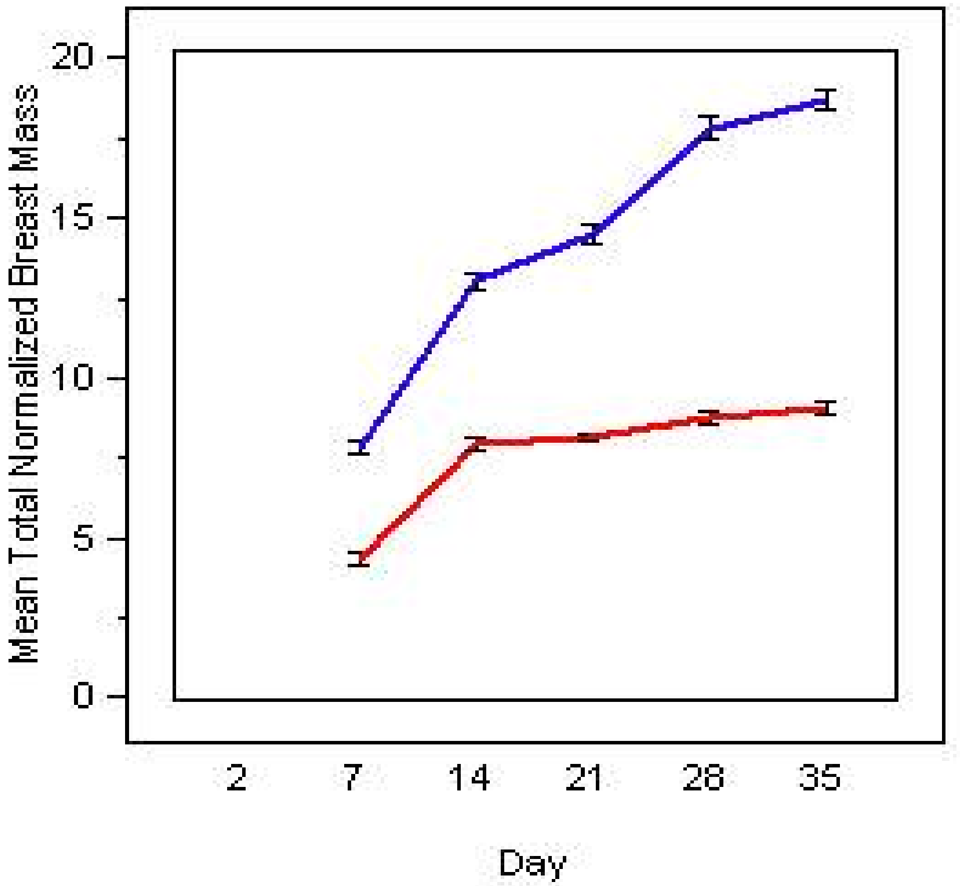
Figures 3.2: Mean Total Breast Mass by Day
The breast mass of the Ross 708 line (blue) grows 3.8 times faster than the heritage, UIUC, line (red).



Figures 3.3: Total Breast Mass Compared to Total Body Mass for Each Strain
Plotting breast mass versus total body mass shows the significant difference between the two strains, with the Ross 708 line (represented by the dashed line) exhibiting a slope twice that of the heritage, UIUC, line.



Figures 3.4: **Normalized Breast Muscle Mass**
The breast muscle mass of these birds was divided by the body mass of the bird to determine the percentage of body mass made up by the breast muscle. The UIUC line appears to plateau around 9%, while the breast mass of the Ross 708 birds continues to contribute more mass to the overall body mass of the bird.



Figures 3.5: Allometric Relationship Between Breast Muscle Mass and Total Body Mass

The natural logarithm (Ln) of breast muscle mass is plotted against the natural logarithm (Ln) of total body mass. With the dashed line representing the Ross 708 birds, and the solid line representing the UIUC birds, it is evident that both lines exhibit positive allometry over the full five week study.

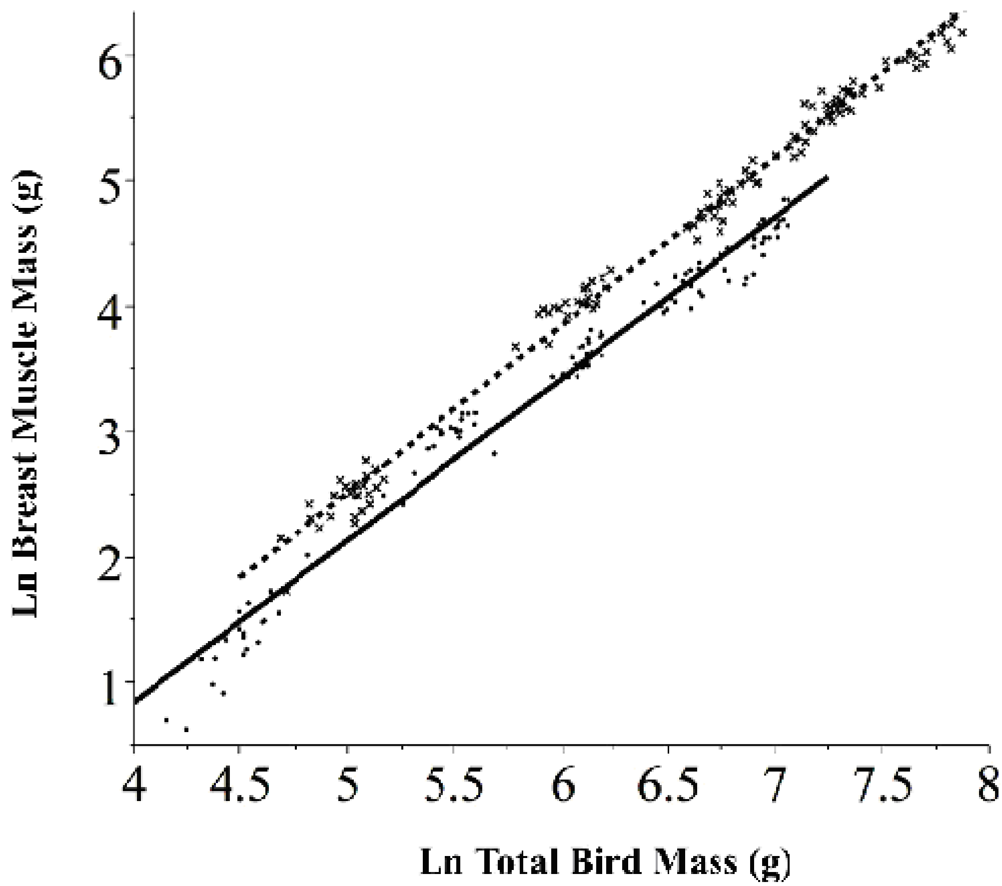


Table 3.2: Allometric Relationships in Breast Muscle
Both strains exhibit positive allometry throughout the complete 35 day experiment. However, analysis of data from day 14 to day 35 reveals that the two strains differ in breast muscle growth after day 14.

Days	Strain	Intercept	Allometric Exponent	R^2
2-35	UIUC	-4.3	1.30	0.98
2-35	ROSS 708	-4.2	1.34	0.99
2-14	UIUC	-6.0	1.64	0.97
2-14	ROSS 708	-4.9	1.47	0.98
14-35	UIUC	-3.1	1.09	0.97
14-35	ROSS 708	-3.6	1.25	0.98

3.3 Heart

The heart mass of each broiler strain continuously increased in size throughout this five week study, as seen in Figure 3.6. The UIUC heart grew at a rate of 240 milligrams per day, while the Ross 708 heart grew at 316 milligrams per day (Figure 3.6). However, as seen in Figure 3.7, a difference is noted between the two strains when comparing relative heart size. The heart of the UIUC birds grew at a rate of 7 milligrams per gram of body mass, while the heart of the Ross 708 birds grew at a rate of 5 milligrams per gram of body mass. Also, when UIUC and Ross 708 birds of equivalent mass were compared, the UIUC hearts were larger than those of the Ross 708 strain (Figure 3.8) (Range of Bird Mass 502-1207g; UIUC Heart mass =6.6 g; 95%: 6.2-7.0; Ross 708 Heart Mass = 5.3 g; 95%: 5.0 – 5.6).

Comparing the normalized heart mass (Figure 3.7) of the UIUC strain across day 2 to 35 showed no statistically significant difference between the normalized heart mass at day 2 (0.85%; 95%: 0.75-0.95) and day 35 (0.72%; 95% :0.68 -0.78). In contrast, the normalized Ross 708 heart was significantly smaller at day 35 (0.55%; 95%: 0.51-0.58) compared with day 2 (0.75%; 95%: 0.68 – 0.82). Furthermore, the plot of normalized heart mass for the Ross 708 birds indicates that between day 14 and 21 the contribution of heart mass to overall body mass decreased (0.77% to 0.60%).

Overall, the UIUC heart exhibited isometric growth (allometric exponent = 0.98) while the Ross 708 heart exhibited slight negative allometric growth (allometric exponent = 0.88) between day 2 and 35. Between day 2 and day 14, the allometric exponent of both strains was close to 1.0 (UIUC = 1.05; Ross = 0.98), while between day 14 to 35 the heart exhibited negative allometric growth in both strains (UIUC = 0.9; Ross 708 =0.8), with the Ross 708 birds growing at an even slower rate compared to overall body mass, than the UIUC line.

Figure 3.6: **Average Heart Mass by Day**

The Ross 708 birds (blue) have larger hearts than the UIUC birds (red) at each experimental time point. The heart of the Ross 708 birds grew at an average of 316 milligrams per day, while the UIUC line grew at approximately 240 milligrams per day.

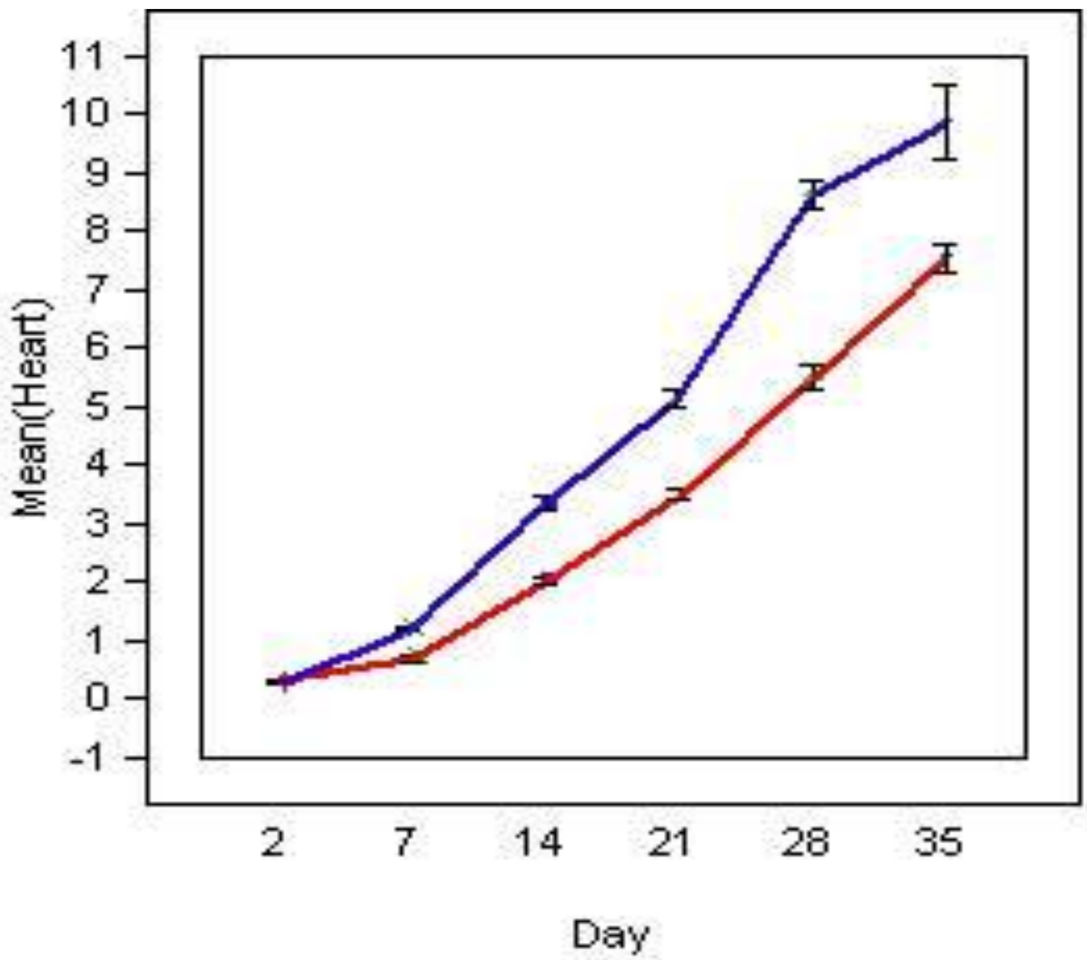


Figure 3.7: Average Normalized Heart Mass by Day
The heart mass of each bird was divided by its total body mass, giving the percentage of body mass made up by the heart. A significant difference is observed after day 14, showing that the heart mass of the Ross 708 birds (blue) drops drastically in comparison to the overall body mass, while the UIUC line (red) exhibits a much less drastic drop in normalized heart mass.

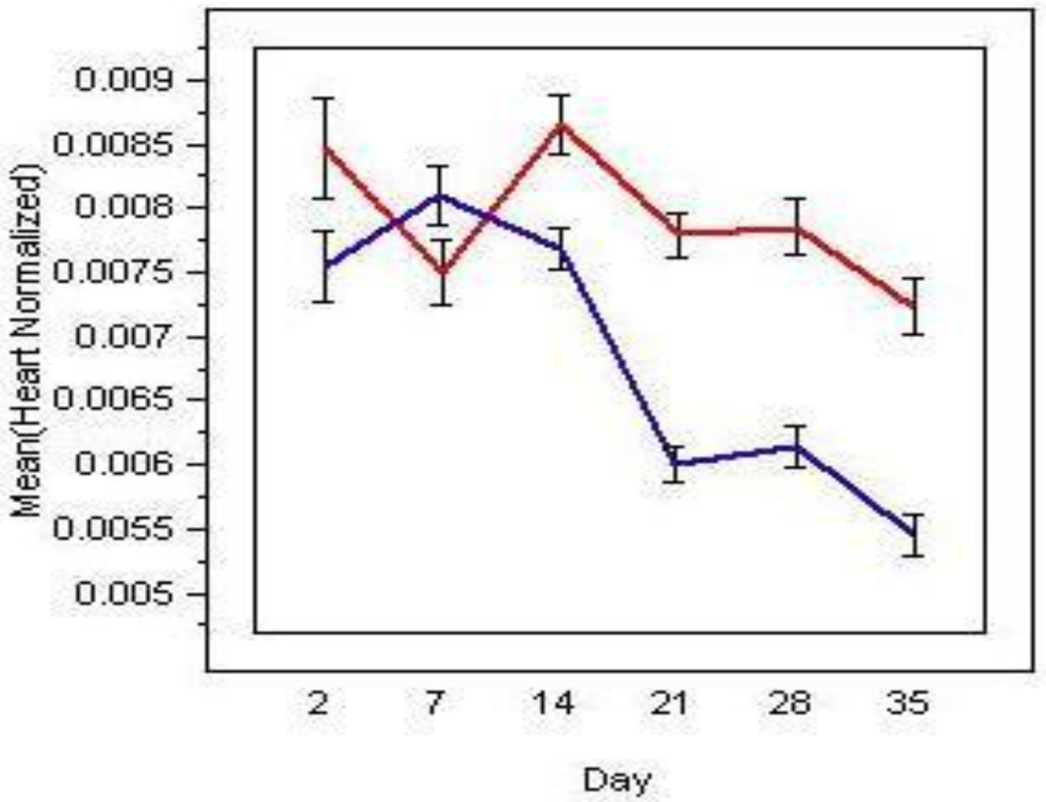
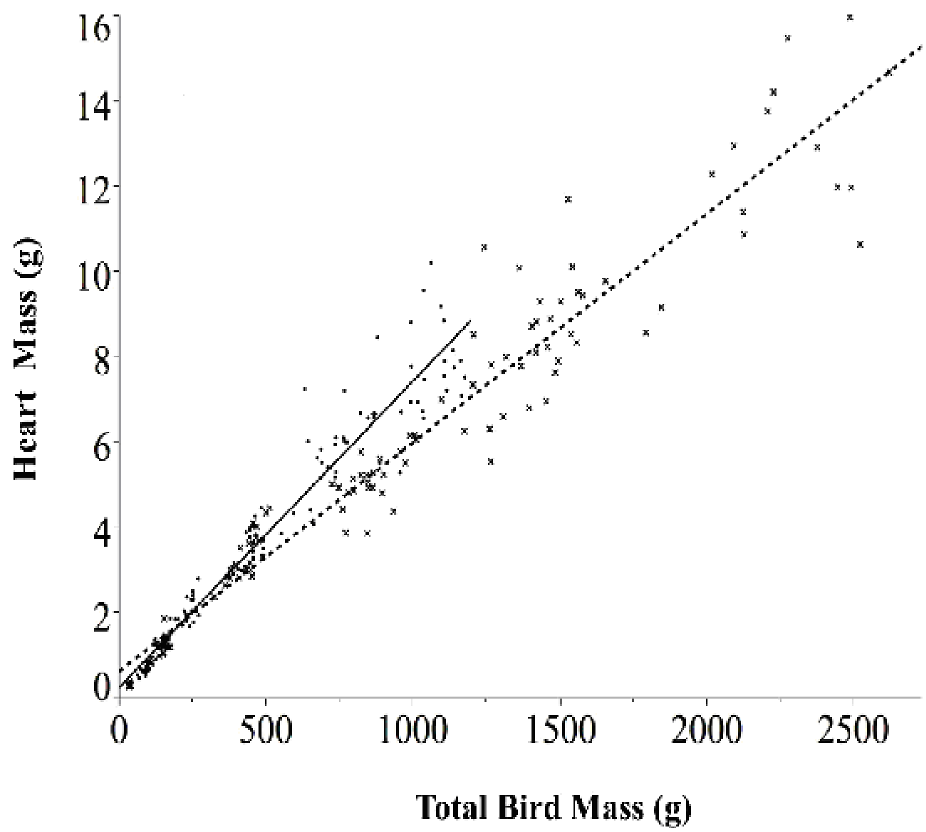


Figure 3.8: **Heart Mass vs. Total Body Mass**
The heart mass of each bird is plotted against the overall mass of the bird, to determine the difference between strains at similar weights. As seen, when birds of equal mass (502g-1207g) are evaluated, the UIUC strain possess larger hearts (UIUC: 6.6g; Ross 708: 5.3g).



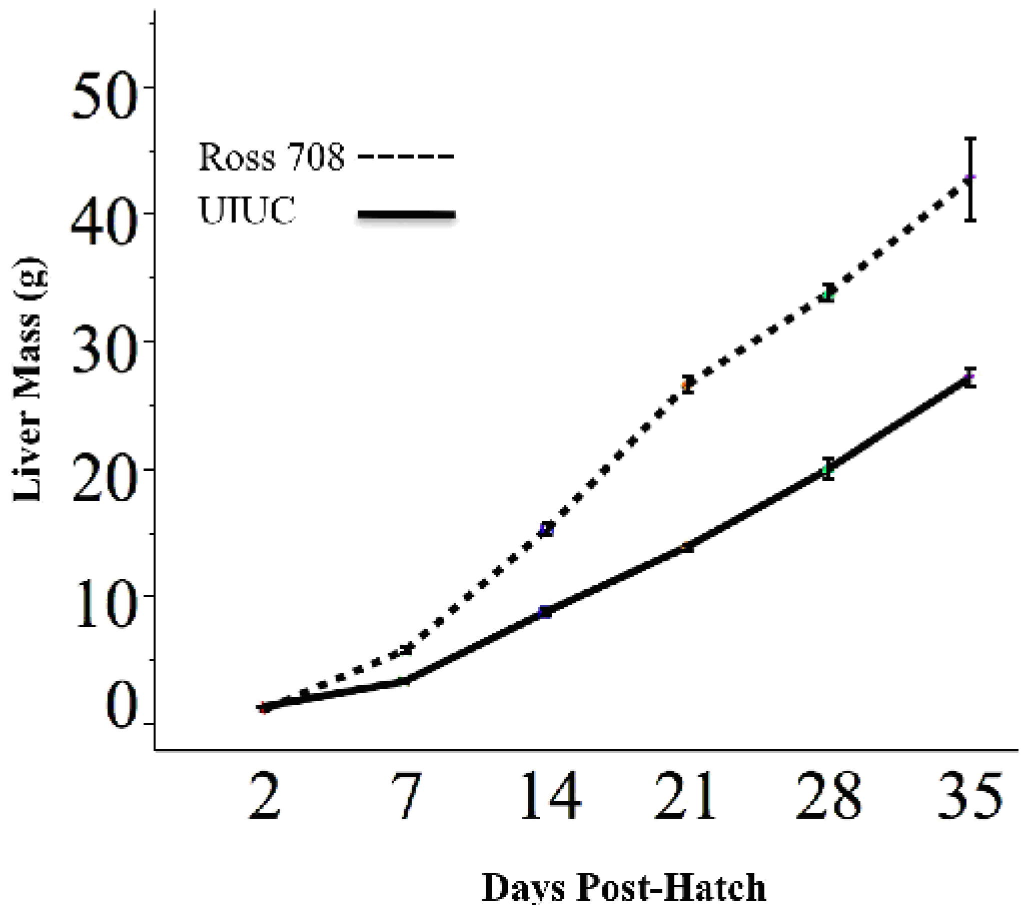
3.4 Liver

The liver of the UIUC strain grew at a rate of 800 milligrams per day while the Ross 708 liver grew 1300 milligrams per day (Figure 3.9). However, the relative liver growth rate in the two strains was similar: 24 milligrams per gram of body mass. Unlike breast muscle mass, comparable sized UIUC and Ross 708 birds had comparable sized livers (compare Figures 3.3 and 3.10). The normalized liver mass peaked at 3.8% (+/- 0.1%) of the total body mass for both strains, after which there was a decrease in the relative contribution of the liver to overall mass (Figure 3.12). This peak was noted on day 7 in the Ross 708 birds, but day 14 in the UIUC birds.

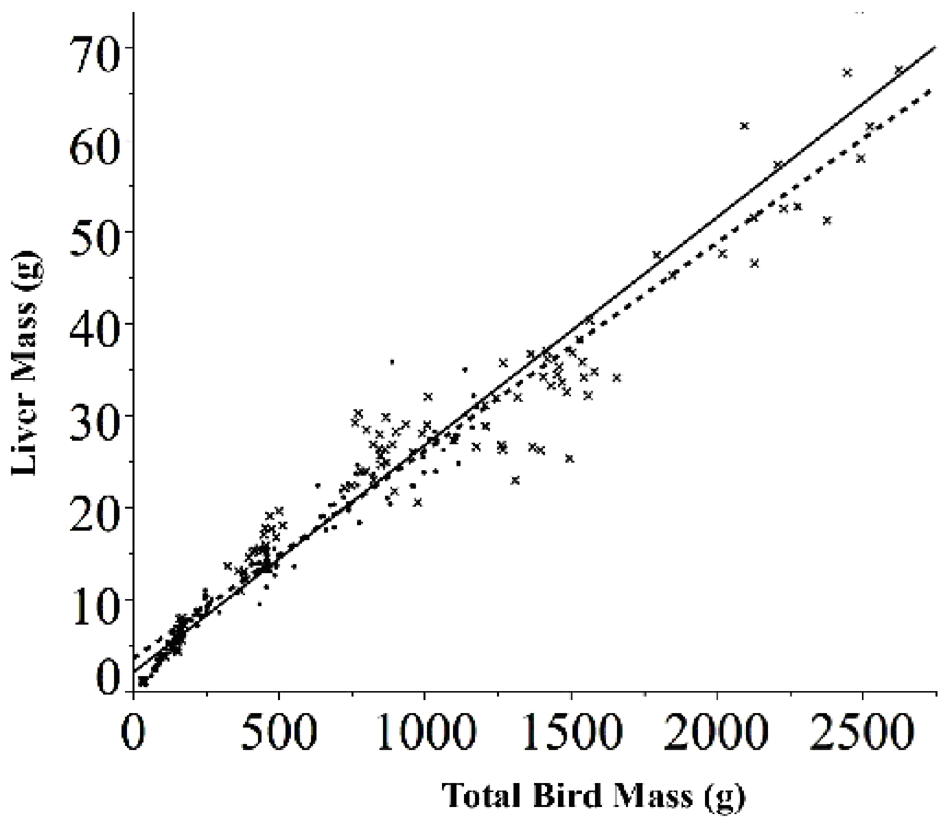
Overall, the liver exhibited negative allometric growth with respect to body mass. However, the relationship differed before and after day 14 (Figure 3.11). Prior to this time, the liver grew with slight positive allometry in both strains (exponent =1.05 +/- 0.02). This relationship became negative (UIUC exponent = 0.76 +/- 0.02; Ross 708 exponent = 0.72 +/-0.02) after day 14 indicating that the rate of growth of the liver was slower than the overall growth of the bird.

These results show that liver growth was similar between the UIUC and Ross 708 birds. The difference in the age at which the strains reached their maximal normalized liver weight (day 7 for Ross 708; day 14 for UIUC) may reflect the faster growth rate of the Ross birds. However, the drop in normalized liver mass, and the change in allometric relationships after day 14 suggests a dramatic shift in relative growth stimulation of the liver for both strains between day 7 and 14.

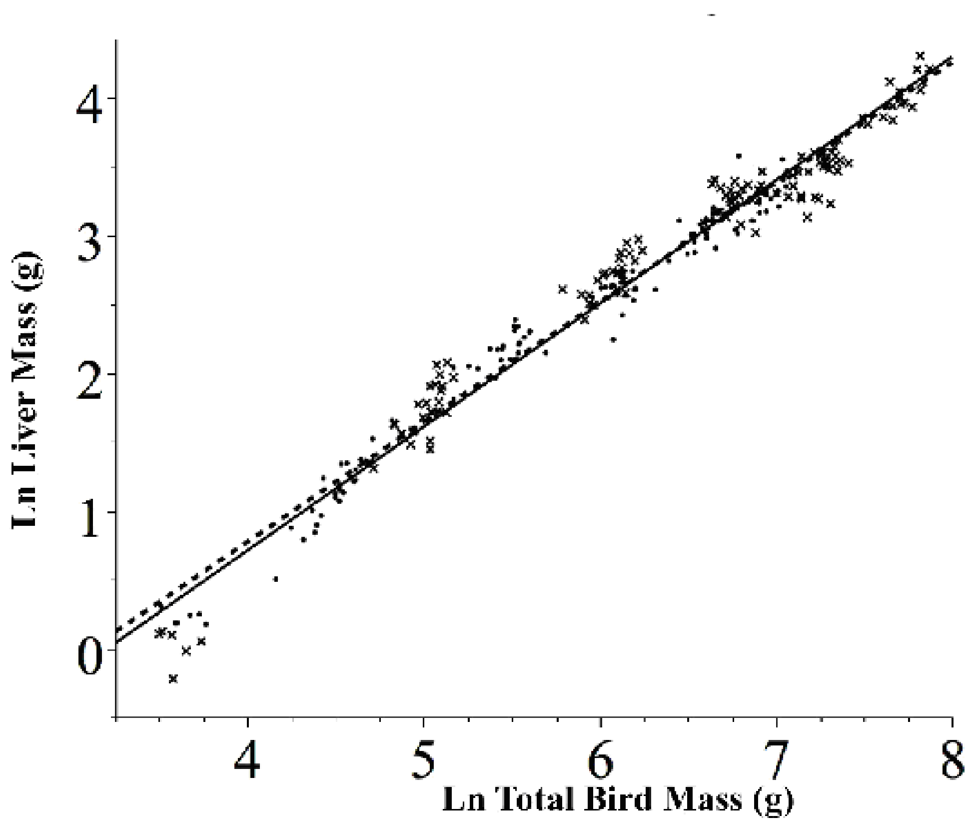
Figures 3.9: Liver Mass by Day
The liver mass of each bird was plotted by day to determine the overall size differences between the two strains. The Ross 708 line, represented by the dashed line, is significantly larger than UIUC line (solid line) when comparing birds at the same age.



Figures 3.10: Liver Mass by Total Body Mass
When the liver mass of equal sized birds is compared, the liver masses are similar, exhibiting no difference between the two strains.

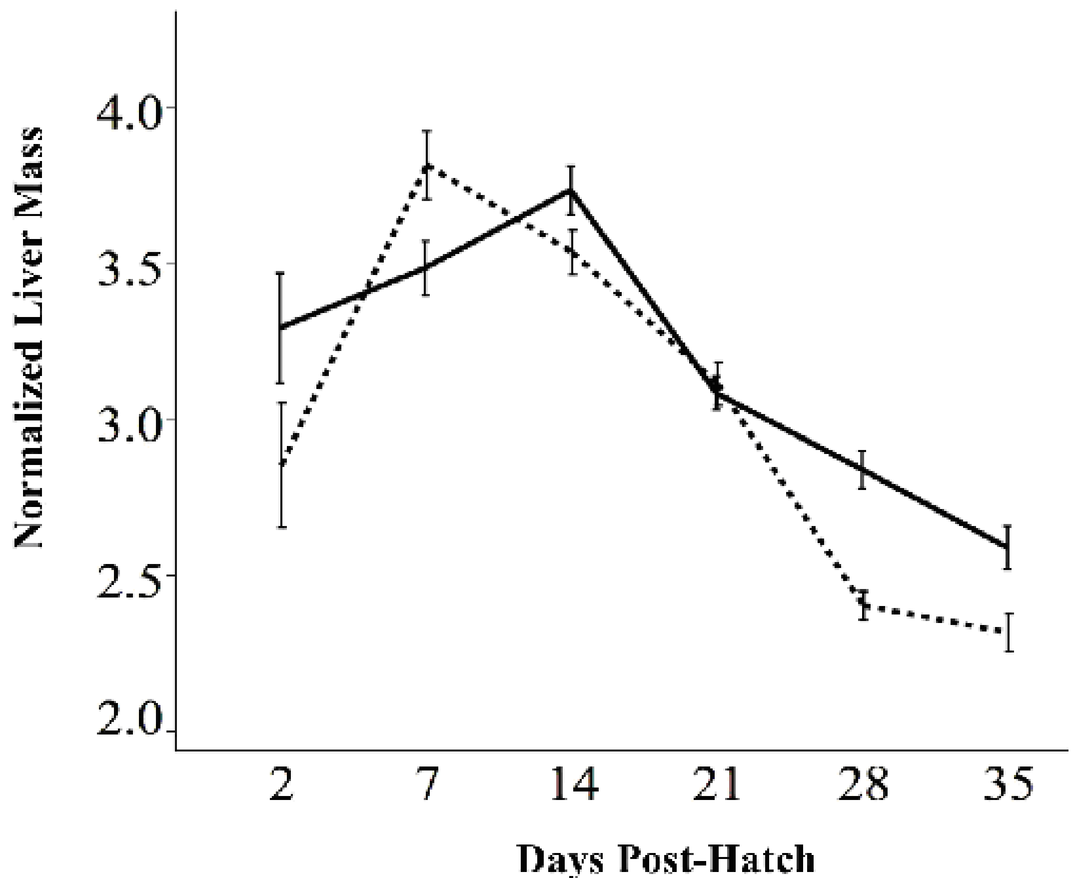


Figures 3.11: Allometric Relationship Between Liver Mass and Total Body Mass
The natural logarithm (Ln) of liver mass is plotted against the natural logarithm (Ln) of total body mass. The allometric exponent of liver to body mass is slightly complex, exhibiting positive allometry in the beginning of the experiment and switching to negative later.



Figures 3.12: Normalized Liver Mass by Day

Normalized liver mass (the percentage of total liver mass/total body mass) by day for both strains; shows that both lines peak at approximately 3.8 percent of the total body mass. After this, the liver of both strains decreases in the percent mass it contributes to the overall body mass of the bird.



3.5 Total Intestine

Individual segments of the small intestine (duodenum, jejunum and ileum) were monitored for growth in terms of length and mass; the overall small intestine growth was derived by summation of these individual segments. From day 2 to 35 post-hatch, the length of the small intestine in the UIUC strain increased by 1.8 centimeters per day (r^2=0.63), while the Ross 708 strain increased by 2.5 centimeters per day (r^2=0.63). However, the length of the intestine did not increase linearly over this time (Figure 3.13). Instead, the majority of post-hatch increase in intestine length for both strains occurred between days 2 and 7, when the mean intestine length reached 70% of the final (day 35) mean length (Figure 3.13). Between day 7 and day 14, both strains exhibited a plateau in the lengthening of the intestine, followed by a second elongation period between days 14 and 28. Neither strain exhibited a significant increase in intestinal length between day 28 and day 35. Hence, it is concluded that the elongation of the small intestine during the first 35 days post-hatch exhibits periods of extension interspersed with periods of stasis. If we compare UIUC and Ross 708 birds of equivalent size when their mass is less than 400 grams, there was little difference between the overall intestine lengths. However, when birds greater than 400 grams (range 400g-1200g) were compared, the Ross 708 intestine is longer than comparable sized UIUC birds (Table 3.3). The mean small intestine length of the Ross 708 birds in this group was 135 centimeters (95%: 131 – 141 cm) while that of the UIUC birds was 119 centimeters (95%: 115 - 123 cm).

The analysis of total intestine mass versus age for both strains exhibited an inflection point at day 21 (Figure 3.14). Prior to day 21, the intestinal mass of the UIUC strain increased at 1.0 gram per day (r^2=0.92) while the Ross 708 birds increased at 1.8 grams per day (r^2=0.92). After day 21, the rates dropped to 0.7 grams per day (r^2=0.58) for the UIUC strain and 0.62 (r^2=0.08 – essentially flat) for the Ross 708 strain. The plots of normalized mass (Figure 3.15) of the total intestine by day revealed that the strains were similar, peaking at day 7 and decreasing to a plateau between day 14 and 21, ultimately followed by a continued decrease to the completion of the experiment. From day 7 to day 35, the normalized intestine mass of the UIUC birds was greater than that of the Ross 708 birds. However, when normalized for intestine length, the Ross 708 line had a greater mass per unit of length when compared with the UIUC line (Figure 3.16).

The complex growth of the small intestine, including changing growth rates affecting both length and mass, generated non-linear allometric plots for the intestine (Figure 3.17). There were two distinct segments to these plots; one spanning from day 2 to day 7 (period of maximal lengthening), and the second from day 7 to day 35. From day 2 to 7, a positive allometric exponent was seen for both strains (UIUC =2.0; r^2=0.95; Ross 708 = 1.6; r^2=0.98). During this period, the overall growth rate of the small intestine was greater than overall body growth rate in both strains. However, this relationship became negative from day 7 to 35, with the allometric exponent for the UIUC birds declining to 0.54 (r^2=0.94) and Ross 708 birds to 0.56 (r^2= 0.90).

Figure 3.13: Total Intestine Length
Length measurements for all three segments of the small intestine were summed to determine the total intestine length. The total small intestine of the Ross 708 broiler, represented in blue, is longer than the UIUC line, represented in red.

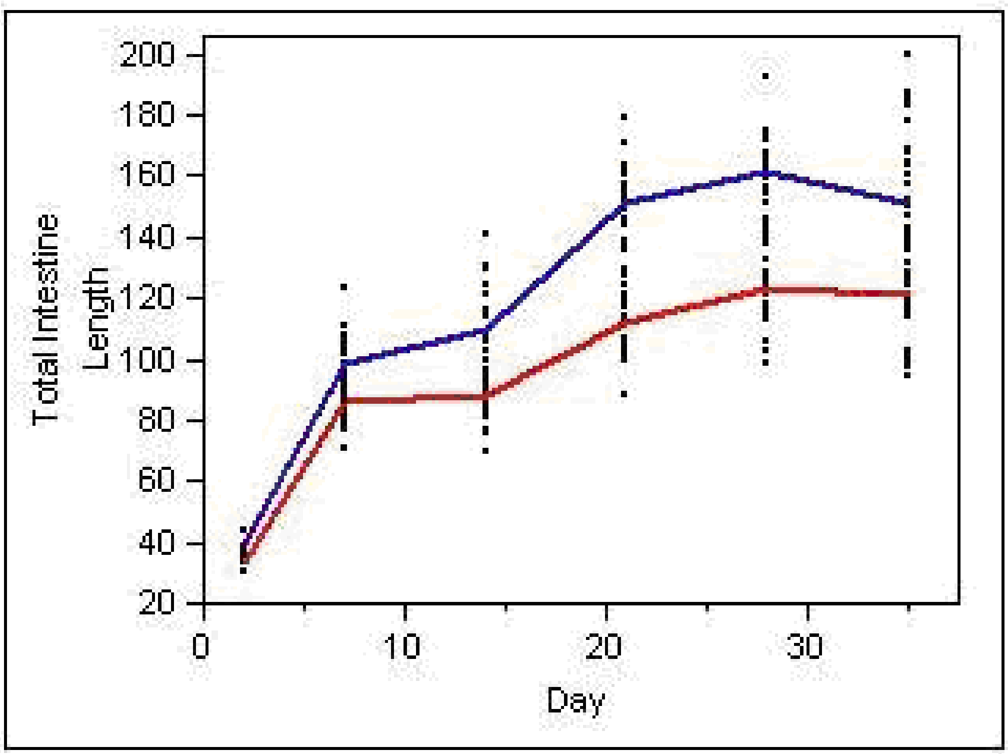


Table 3.3: Intestine Length of Comparable Sized Ross 708 and UIUC Birds
Analysis of intestine length between comparable sized larger birds (400-1200g) from each strain. Asterisks indicate segments which are significantly different among the broiler strains ($P < 0.05$).

	STRAIN	**MEASUREMENT**	**LOWER 95%**	**UPPER 95%**
Total Mass	UIUC	746g	688g	804g
Total Mass	ROSS 708	744g	668g	819g
Total Intestine Length*	UIUC	119cm	115cm	123cm
Total Intestine Length*	ROSS 708	135cm	130cm	141cm
Duodenum Length	UIUC	25cm	24cm	25cm
Duodenum Length	ROSS 708	25cm	24cm	26cm
Jejunum Length*	UIUC	47cm	45cm	49cm
Jejunum Length*	ROSS 708	55cm	53cm	58cm
Ileum Length*	UIUC	47cm	45cm	49cm
Ileum Length*	ROSS 708	55cm	53cm	58cm

Figure 3.14: Total Intestine Mass

Weights for all three segments of the small intestine were summed to determine the total intestine mass. The overall small intestine mass of the Ross 708 broiler, represented in blue, is heavier than the UIUC line, represented in red.

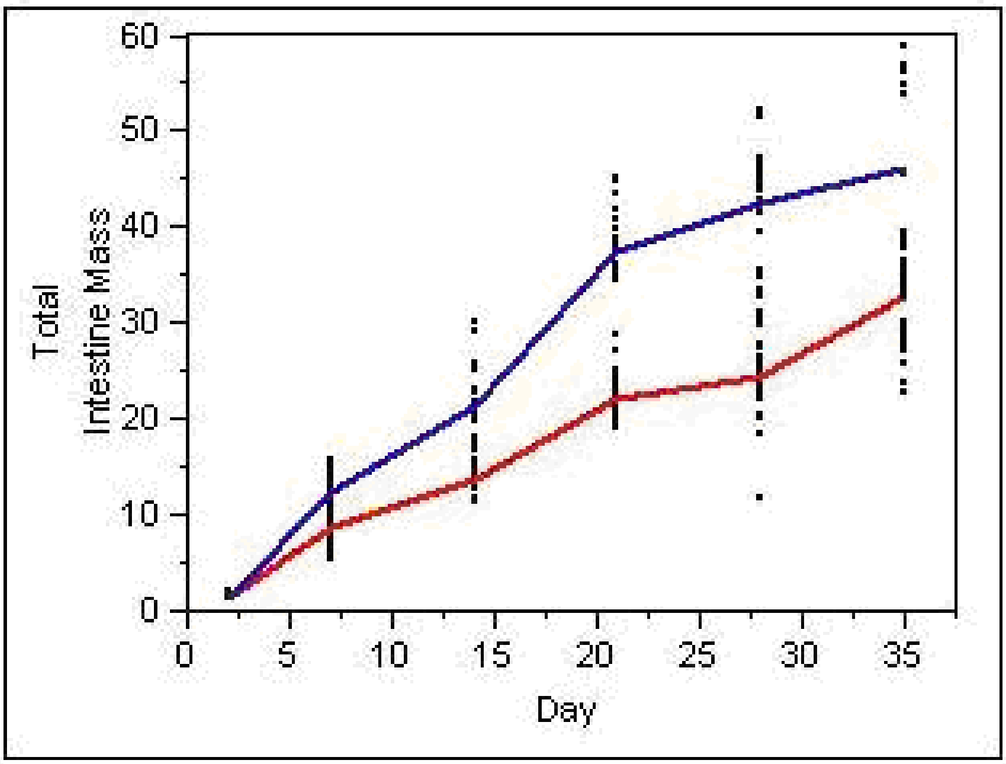


Figure 3.15: Normalized Intestine Mass by Day

The total intestine mass was normalized to overall body mass and plotted by day. Both strains peak at day 7, and continue to decrease in normalized mass until the completion of this experiment. An apparent plateau is noted from day 14 to day 21.

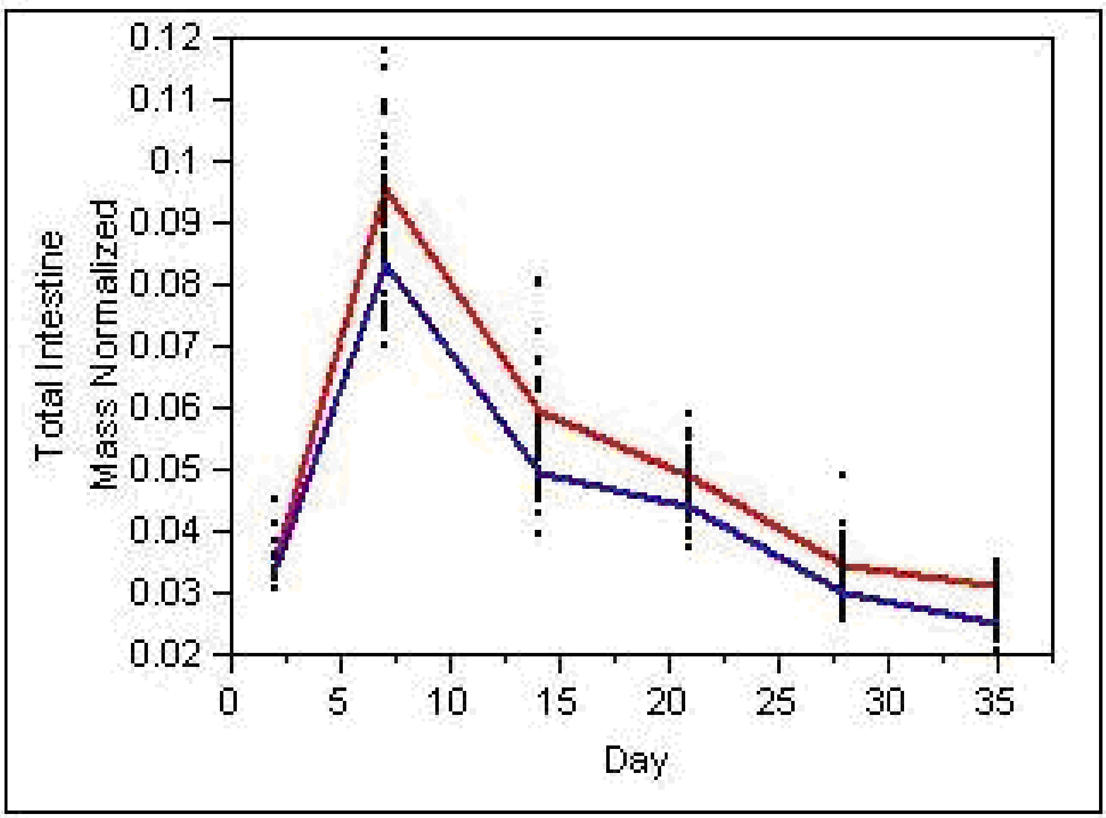


Figure 3.16: Intestine Mass per Unit Length by Day
Total intestine mass was normalized to intestine length and plotted by day. The Ross 708 line, represented by the dashed line, exhibits a greater mass per unit of length than that of the UIUC line (represented by the solid line).

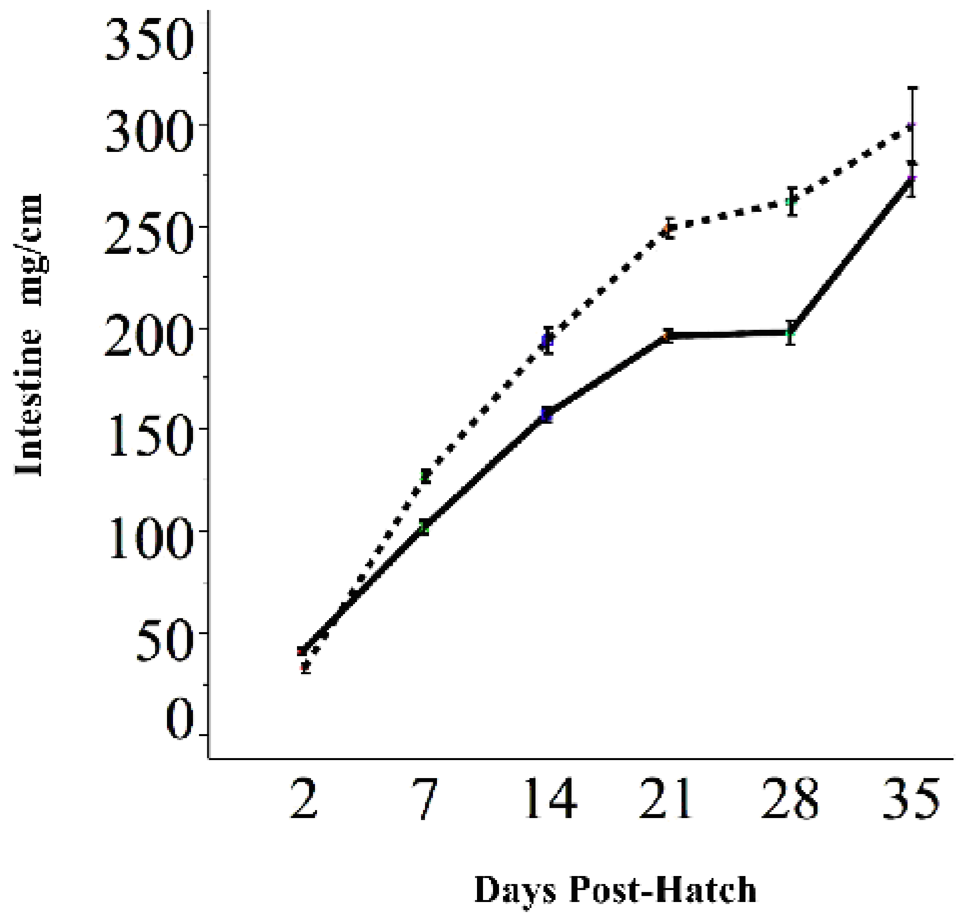
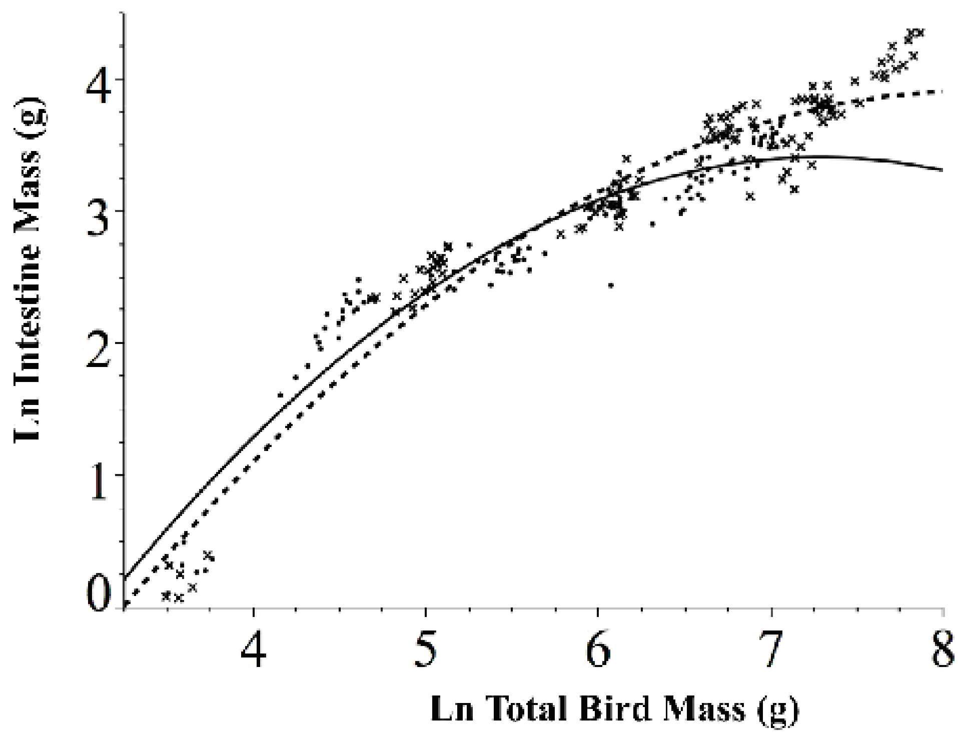


Figure 3.17: Allometric Relationship Between Intestine Mass and Body Mass
The natural logarithm (Ln) of intestine mass is plotted against the natural logarithm (Ln) of total body mass. The allometric exponent of intestine to body mass is complex, exhibiting positive allometry from day 2 to day 7, but becoming negative from day 7 to the completion of the 35 day study.



3.6 Intestine Segments

The individual intestinal segments contributed different growth patterns to the small intestine (summarized in Table 3.4 and Table 3.5). The analysis of the normalized mass and mass per unit length for the individual segments mirror those described for the total intestine.

3.6.1 Duodenum

The duodenal segment was most unique of the three intestinal segments. From day 7 to day 35, it constituted approximately 22% and 19% of the length and 32% and 27% of the mass of the small intestine in the UIUC and Ross 708 strains, respectively. Similar values have been reported for Steggles and Ross crossed broilers (Iji, et al., 2001). In both strains, this segment achieved the highest mass per unit length of the three segments. Over the course of this experiment, the duodenum exhibited the lowest allometric exponent of the three segments (Table 3.4). Between days 2 and 7, the values were 1.7 and 1.5, while from day 7 to day 35 they were 0.51 and 0.49 for the UIUC and Ross 708 strains, respectively. When similar sized birds were compared, the duodenal lengths did not significantly differ between the two lines.

3.6.2 Jejunum

The jejunum constituted 39% and 40% of the length and 39% and 42% of the mass of the small intestine in the UIUC and Ross 708 strains, respectively. Of the three, this segment increased in mass at the highest rate (Table 3.5). Between day 2 and 7, the allometric exponent (Table 3.4) for the jejunum was 2.0 and 1.6, while between day 7 and 35 these values fell to 0.57 and 0.58 for the UIUC and Ross 708 strains, respectively. The length of the jejunum in comparable sized UIUC and Ross 708 birds differed significantly, with the modern strain having a longer segment (Table 3.3).

3.6.3 Ileum

The ileum comprised 39% and 41% of the length and 29% and 31% of the mass of the small intestine in the UIUC and Ross 708 strains, respectively. The ileum increased in length at the same overall rate as the jejunum (Table 3.5). However, the ileum mass increased at a lower rate than the jejunum. Finally, the allometric exponent of the ileum (Table 3.4) was the highest of the three segments, at 2.3 for the UIUC and 1.7 for the Ross 708 birds, between day 2 and day 7. After day 7, the allometric exponent of the ileum decreased to 0.55 and 0.59 for the UIUC and Ross 708 strains, respectively. As with the jejunum, when comparable sized Ross 708 and UIUC birds were analyzed, the Ross 708 line possesses a longer ileum segment. (Table 3.3).

Table 3.4: Allometric Exponents for Total Intestine and Intestine Segments at Each Time Point

	UIUC	ROSS 708	UIUC	ROSS 708	UIUC	ROSS 708
Days Post-Hatch	2-35	2-35	2-7	2-7	7-35	7-35
Duodenum	0.64	0.66	1.7	1.5	0.51	0.49
Jejunum	0.72	0.75	2.0	1.6	0.57	0.58
Ileum	0.72	0.76	2.3	1.7	0.55	0.59
Total Intestine	0.69	0.86	2.0	1.6	0.54	0.56

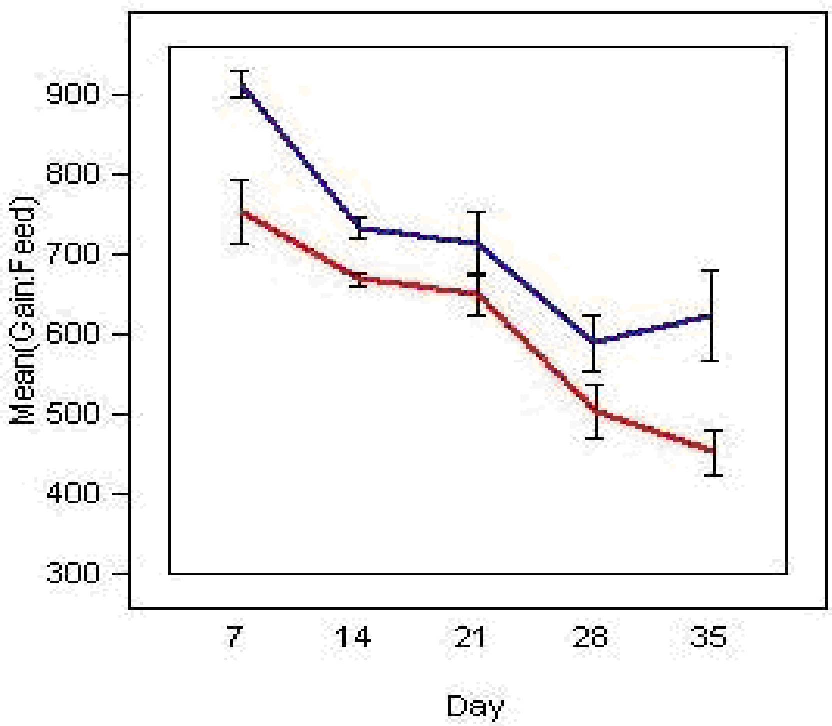
Table 3.5: Growth Rates of Individual Intestine Segments

Segment	UIUC	ROSS 708	UIUC	ROSS 708
Measurement	**mg/day**	**mg/day**	**cm/day**	**cm/day**
Duodenum	247	310	0.3	0.4
Jejunum	343	562	0.7	1.0
Ileum	267	448	0.7	1.1

3.7 Feed Efficiency

Feed efficiency, expressed as grams of weight gain per kilogram of feed consumed, is a measure of the ability of an animal to convert feed into body mass. As seen in Figure 3.17, the Ross 708 line had a greater ($P < 0.05$) feed efficiency than the UIUC line throughout the course of the experiment.

Figure 3.18: Mean Feed Efficiency by Day
The mean feed efficiency is greater in the Ross 708 birds (blue) than the UIUC line (red), with both broiler strains exhibiting a plateau from day 14 to 21.



Chapter 4

DISCUSSION

Following the domestication events of the red jungle fowl, over 8,000 years ago, the chicken is continuously changing in order to meet the needs of the growing commercial poultry market. This selection process is just one example of the dramatic effect human directed evolution has on agriculture. This is evident in the broiler industry by comparing the overall mass of three lines of birds: the Red Jungle Fowl (RJF; Jackson and Diamond, 1995), the UIUC heritage line that is representative of chickens from an early point in the U.S. broiler industry, and the modern Ross 708 line. By 35 days post-hatch, the RJF mass was approximately 300 grams (Jackson and Diamond, 1995), while the UIUC heritage line averaged 1046 grams, and the Ross 708 averaged 1800 grams. If we use the RJF as the baseline, the first several thousand years of selection leading to chicken lines used in the 1950's resulted in a 3-fold increase in body mass at 5 wks post-hatch, while the past 50-60 years increased overall mass approximately 1.8 fold. If we compare the percent body mass devoted to the breast muscle, there is little difference between the RJF and the heritage line, with the breast muscle contributing approximately 9% to the overall mass of the bird in both lines (Jackson and Diamond, 1995 and current work). In contrast, the breast muscle contributed approximately 18% of the mass in the Ross 708 birds. Until the late 1950s, broiler performance was largely improved by selection for increased growth rate (Warren 1958). Apparently, this approach maintained the same allometric relationship between overall growth rate and breast muscle size. The adoption of modern selection approaches, emphasizing feed conversion and body mass, evidently shifted resources to the production of additional breast muscle.

While modern selection has dramatically increased the relative size of the breast muscle, the relative size of the heart muscle has decreased. In the UIUC heritage line, the relative size of the heart remained constant over this five week study. The relative size of the Ross 708 heart was comparable to that of the heritage line for the first two weeks post-hatch, but then decreased significantly after day 14. Presumably, the reduced relative heart size in the modern line yields diminished cardiac capacity, which could play an important role in the increased susceptibility of modern broilers to ascites, sudden death syndrome (SDS) and heart failure (Ononiwu et al., 1979; Jillian, 1998; Maxwell and Robertson, 1998; Olkowski and Classen, 1997; Olkowski et al, 2007). In addition, the coincidental timing of the decrease in relative heart mass and continued increase in breast muscle mass in the modern line suggests that the growth control of these distinct muscles may be linked. Possibly, modern selection has diverted resources originally destined to maintain balanced heart growth into increased breast muscle mass. This could result in cardiovascular problems, as the small relative heart of the modern birds has to work much harder to support the rapid growth of the bird (Konarzewski, Gavin, McDevitt and Wallis, 2000).

The main objectives of broiler selection are complex, but have generally focused on increased muscle mass and decreased time from hatch to market, combined with an increased feed efficiency. A reasonable hypothesis is that the digestive system has also been modified, as increased nutrient uptake would be essential to achieve these objectives. This may be accomplished by an increase in surface area of the small intestine and/or by an alteration in associated transporters and growth factors.

The intestine of both lines exhibited complex post-hatch development, with interspersing periods of stasis and growth. The normalized mass plots were similar, although the UIUC line had a higher normalized intestine mass than the Ross 708 line between day 7 and day 35. The allometric plots were non-linear (Figure 3.16), further demonstrating the complex growth of the intestine. During the first week post-hatch, the intestine exhibited positive allometry, switching to negative allometry after day 7, in both lines. The dramatic switch in relationship between the growth of the intestine and total body mass may reflect the maturation of the digestive track around day 7 post-hatch (Govaerts, et al., 2000). During this period, all three segments experience an increase in overall surface area by enterocyte hypertrophy (Geyra, et al., 2001). Day 7 to day 14 post-hatch likely corresponds to the period when the chick exhausts the yolk sac and subdermal lipid deposits and begins to rely on the intestine to digest and absorb feed-derived nutrients (McGreal, 1956; Jin, et al., 1988; Uni, et al., 1995; Batal and Parsons, 2002; Moran, 2007). The observed morphometric changes likely play an important role in preparing the intestine to assume this responsibility.

Ross 708 birds have a higher feed efficiency than the heritage UIUC line (Figure 3.17), indicating that the modern birds are more efficient at converting feed to body mass. One important aspect of feed efficiency is nutrient absorption, which can be improved by increasing the length of the intestine (Jackson and Diamond, 1996). When equal sized Ross 708 and UIUC birds were compared (Table 3.3), the total intestine length was greater in the modern line compared to the heritage line. While the duodenal segments of both lines did not differ significantly, the jejunum and ileum were approximately 20% longer in the Ross 708 line. Hence, selection for rapid growth may have yielded birds with improved absorption by increasing the relative length of the terminal two segments of the small intestine.

The UIUC heritage line represents a cross (New Hampshire and Plymouth Rocks) typical of those used by the poultry industry in the late 1940s and early 1950s (Warren, 1958). The major objective of this work was to identify morphological changes caused by genetic selection over the past 50 to 60 years, which has yielded the modern broilers. Since the UIUC and Ross 708 birds in our study were raised under identical conditions, the growth and morphometric distinctions noted are largely due to genetic differences between the two lines. A future challenge will be to identify the specific genetic changes that have yielded the various traits of the modern broiler. This will aid geneticists attempting to further improve this vital food resource. In addition, understanding how both natural and artificial selection has changed the chicken genome will further improve our understanding of evolution.

Chapter 5

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