Changes in Body Composition and Adipocyte Cellularity of Male Broilers Subjected to Varying Degrees of Early-Life Feed Restriction

A. K. ZUBAIR and S. LEESON

Department of Animal and Poultry Science, University of Guelph, Guelph, Ontario, Canada, N1G 2W1

ABSTRACT

Three experiments were conducted to determine growth performance, body composition changes, and adipocyte characteristics of male broilers subjected to early-life feed restriction. The purpose of Experiment 1 was to determine 42-d growth performance and body composition changes. Treatments used were full-fed control and 50% physical feed restriction during the period 6 to 12 d of age. Experiment 2 was conducted to determine the adipocyte characteristics during and after feed restriction to 42 d of age. An additional treatment involved gradual refeeding following the feed restriction period. Experiment 3 was designed to test the effect of feeding different types of dietary fat during realimentation on the abdominal fat pad (AFP) size, and lasted until 18 d of age. Three types of fats were tested, namely animal-vegetable (A-V) blend, flax oil, and animal tallow, each represented by full-fed and feed-restricted treatments.

Complete compensatory growth by feed-restricted birds relative to controls was not achieved by 42 d in either Experiments 1 or 2. Early feed restriction resulted in lower body fat percentage at 12 d (P < 0.05), although by 42 d a higher rate of fat deposition mainly by hypertrophy of adipocytes resulted in no difference in fatness. Gradual reintroduction into ad libitum feeding did not alter such adipocyte hypertrophy nor improve compensatory growth response during refeeding. There was consistent improvement in feed efficiency associated with early-life feed restriction (P < 0.05). The use of different types of dietary fat did not effect the AFP when expressed as percentage body weight. Birds that were fed A-V blend during the refeeding period had bigger AFP (grams per bird), a situation that is attributable to differences in body weight. Attainment of growth compensation by the feed-restricted broilers apparently requires a more prolonged growth period or a less severe feed restriction program than that used here. Saturation of dietary fat has no effect on realimentation characteristics of the broiler.

(Key words: broiler, adipose tissue, feed restriction, carcass composition)

INTRODUCTION

Research into methods of lowering carcass fat continues to receive attention because of the need to produce lean meat. Studies by Wilson and Osbourn (1960) and Auckland and Morris (1971) demonstrated compensatory growth in poultry, following a period of growth retardation imposed by early undernutrition. This means that there is potential to underfeed broilers for some time, without affecting weight at normal market age. Plavnik and co-workers in a series of studies confirmed the phenomenon of compensatory growth and reported consistently lower carcass fat in broilers and turkeys subjected to early undernutrition (Plavnik and Hurwitz, 1985; 1988a,b; 1991; Plavnik et al., 1986). Such improvement in carcass composition in “restricted-refed” broilers is attributed to suppression or delay in adipocyte proliferation as a result of the feed restriction (Ballam and March, 1979; Cartwright, 1991; Jones and Farrell, 1992b). Success in reducing body fat deposition was, however, not achieved by a number of other workers who also used early feed restriction strategies (Bean et al., 1979; Pokniak and Cornejo, 1982; Pokniak et al., 1984; Summers et al., 1990; Yu et al., 1990). This may be due to differences in degrees of feed restriction and to the very high feed intake and associated adipocyte hypertrophy that is often exhibited by restricted-refed broilers (March et al., 1982; Zubair and Leeson, 1993, 1994a,b).

Studies with mammalian species have shown that the use of polyunsaturated fatty acids (PUFA) as opposed to saturated fatty acids in the diet has potential for suppressing fat synthesis. This was attributed to the inhibition of fatty acid synthetase enzyme in the liver (Herzberg and Rogerson, 1988; Tomlinson et al., 1988; Blake and Clarke, 1990; Clark, et al., 1990a,b). The fact that the inhibition of lipogenesis was demonstrated in the liver makes it a very attractive hypothesis for application in broiler chickens because about 50% of lipogenesis occurs in the liver (Nir and Lin, 1982).
Vegetable oils containing high levels of PUFA, such as soybean oil, have been reported to inhibit lipogenesis (Leveille et al., 1975; Tanaka et al., 1983; Donaldson, 1985) and depress body fat content in the broiler chicken (Keren-Zvi et al., 1990; Pinchasov and Nir, 1992). To the contrary, Olomu and Baracos (1991) and Scaife et al. (1994) found no effect of dietary PUFA in reducing body fat content in broiler chickens. The effect of such dietary PUFA on fat synthesis in restricted-refed birds is unknown.

Although many studies have determined body composition of “restricted-refed” broilers at the end of the growth period, there is very little information on such developmental changes during growth. Experiments were carried out to determine the effect of early feed restriction on growth response, changes in body composition, and adipocyte cellularity in male broiler chickens. The effect of dietary saturated vs polyunsaturated fatty acids (PUFA) on fat deposition in restricted-refed male broilers was also investigated.

**MATERIALS AND METHODS**

**Experiment 1**

The objective of Experiment 1 was to determine the growth characteristics and changes in body composition during and after early feed restriction. Two treatments were involved, namely a full-fed control treatment (FF) and a feed-restricted treatment (FR). Each treatment was represented by six replicates of 30 chicks each, kept in 2.44 x 1.83 m floor pens. Room temperature was maintained at 32.5 °C up to 5 d and then gradually reduced by about 0.5 °C/d each day until 24 °C was reached. At 5 d of age, all chicks were wing-banded and individually weighed. Feeding during the pre-experimental period of 0 to 5 d was *ad libitum* for all chicks. Feed intake for the chicks in the FR treatment during the restriction period of 6 to 12 d was limited to 50% of the voluntary feed intake of the full-fed control chicks. This was determined by monitoring the daily feed intake of the control chicks. *Ad libitum* feeding was resumed for all chicks during the remaining period of the experiment, up to 42 d. A conventional broiler starter diet (Diet 1, Table 1), was fed from 0 to 21 d of age. This was followed by grower and finisher diets for the periods 21 to 35 d and 35 to 42 d (Diets 2 and 3, Table 1), respectively. All diets were formulated to meet minimum nutrient requirements established by NRC (1994).

All birds were weighed individually on Days 6, 10, 12, 17, 21, 28, 35, and 42. After each weighing, two representative birds with body weight close to the pen average were selected per pen, and euthanatized by cervical dislocation. All carcasses were kept frozen at –20 °C until required for analysis of body composition. Each carcass was placed in a beaker into which water was added to a depth of 3 cm and then covered with aluminum foil. The carcasses were autoclaved for 1 h and then homogenized in a Waring commercial blender. The homogenate was freeze-dried to constant weight in aluminum containers, and then reground with a mechani-
cal grinder\textsuperscript{5} to give homogeneous consistency. Samples were analyzed in duplicate for crude fat, ash, and crude protein by ether extraction and macro-Kjeldahl, respectively (Association of Official Analytical Chemist, AOAC, 1980).

**Experiment 2**

Experiment 2 was carried out with the objective of monitoring adipocyte characteristics during and after early feed restriction. In addition to the two treatments as used in Experiment 1, a third treatment (FRR) that involved gradual return to \textit{ad libitum} feeding following the 6-d feed restriction was included. Three hundred and sixty male broiler chicks of commercial strain were used in the 42-d experiment, with each treatment represented by four replicates of 30 chicks each. Feeding program, housing, and general management practices were as described in Experiment 1. After the 6-d 50\% feed restriction (6 to 12 d), gradual return to \textit{ad libitum} for chicks in FRR treatment was based on feeding them the same quantities that were consumed by the FF chicks at comparable body weights (in the 6 to 12 d period) from 12 to 21 d. All birds were weighed individually on Days 6, 12, 17, 21, 35, and 42. After weighing on each day, two representative birds were selected per pen, and killed by cervical dislocation. The abdominal fat pad (AFP) was removed and weighed separately for each bird.

One gram of the AFP was used from each bird for the determination of adipocyte diameter and number according to the procedure extensively described by Di Girolamo \textit{et al.} (1971), and previously applied to chicken adipocytes by Simon and Leclercq (1982) and Hermier \textit{et al.} (1989). Briefly, the procedure involves incubating adipose tissue with collagenase enzyme in appropriate buffer medium at 37 C for 80 min. The adipocytes are isolated from the dissociated tissues and purified by washing three times with collagenase enzyme in appropriate buffer medium at 37 C for 80 min. The adipocytes are isolated from the dissociated tissues and purified by washing three times with the buffer, followed by staining with methylene blue. Adipocyte diameter (for at least 200 cells per bird) is calculated using the formula of Goldrich \textit{et al.} (1967) as applied to chicken adipocytes by Hermier \textit{et al.} (1989). Total AFP adipocyte numbers were calculated from the results of lipid density, mean adipocyte volumes, and lipid contents of the abdominal fat tissues.

\footnote{\textsuperscript{5}Autio Co., Astoria, OR 97103.}
\footnote{\textsuperscript{6}Nikon Co., Nippon Kogaku K.K., Chiyoda-Ku, Tokyo 100, Japan.}
\footnote{\textsuperscript{7}Petersime Incubator Co., Gettysburg, OH 45528.}
\footnote{\textsuperscript{8}Sigma Chemical Co., St. Louis, MO 63178-9916.}
\footnote{\textsuperscript{9}Varian Instruments Co., Mississauga, ON, Canada, L5N 5R9.}
\footnote{\textsuperscript{10}J & W Scientific, Folsom, CA 95630-4714.}

**Experiment 3**

This experiment was conducted to test the effect of different types of dietary fat on fat accretion in restricted-refed male broiler chickens. Two hundred and forty male broiler chicks of commercial strain were randomly allocated to one of the six treatments, giving 40 chicks per treatment. Each treatment was represented by four replicates of 10 chicks each, housed in a cage within a Petersime brooder.\textsuperscript{7} The cage temperature was maintained as described for Experiment 1. At 5 d of age, all chicks were wing-banded, individually weighed, and randomly allocated to one of the six treatments. Feed intake of the chicks in Treatments 2, 4, and 6 during the period 6 to 12 d was restricted to 50\% of the amount voluntarily consumed by their full-fed counterparts in Treatments 1, 3, and 5. The diet fed to all birds up to 12 d of age contained 3.63\% animal-vegetable (A-V) blend as the source of supplemented fat (Diet 1, Table 1). Feeding during the period 13 to 18 d was \textit{ad libitum} for all treatments, with diets containing different types of fats. Chicks in Treatments 1 and 2 received Diet 1, which contained 3.63\% A-V blend, whereas this was substituted with an equal amount (3.63\%) of flax oil (Diet 4) or beef tallow (Diet 5) in the case of Treatments 3 and 4, and 5 and 6, respectively (Table 1). All other components of the Diets 1, 4, and 5 were the same. The experiment was terminated on Day 18.

All chicks were group-weighed at 6, 12, 15, and 18 d of age. Feed intake over the periods 6 to 12 and 12 to 18 d of age was recorded, also on a group basis. Two representative chicks with body weight close to the group average were selected from each cage on Day 18 and killed by cervical dislocation. The AFP was removed and weighed separately for each chick. Total lipids were extracted from 3 g of each AFP using dimethyl ether as outlined by AOAC (1980). Samples of the extracted fats were dissolved in toluene, after which Meth-Prep II\textsuperscript{8} was added at the rate of 50 \(\mu\text{L}/\text{mL}\) of the dissolved fats. After 30 min at room temperature, 2 \(\mu\text{L}\) of the prepared samples were injected into a Varian 3400 Gas Chromatography\textsuperscript{9} equipped with DB225 Column\textsuperscript{10} (0.54 gas diameter \(\times 30\) min 180 C initial temperature, increased by 3 C/min to 22 C final temperature) and flame ionization detection. Peak areas were measured using a Varian 654 Data System\textsuperscript{9} and used to determine the percentages of each fatty acid in relation to the total of identified fatty acids.

Statistical analysis of the data from Experiment 1 was carried out by Student’s \(t\) test, whereas all other data were analyzed by ANOVA (SAS Institute, 1991). Those variables having a significant \(F\) test were compared using Duncan’s multiple range test (Duncan, 1955). The data of total cell number from Experiment 2 was transformed using natural logarithm and subjected to regression analysis.
RESULTS

Experiment 1

Growth performance and body weight gain of broiler chicks during the feed restriction and realimentation periods are presented in Figure 1 and Table 2, respectively. As expected, early 50% feed restriction resulted in significantly (P < 0.01) smaller body weight gain for the feed-restricted chicks than for the controls during the period of 6 to 12 d of age. Body weight gain during the realimentation period of 12 to 42 d was similar for the two groups (Table 2); however, growth compensation by the feed-restricted birds relative to the full-fed birds was not achieved by 42 d of age when the experiment was terminated (Figure 1).

The affect of early 50% feed restriction on body composition of male broilers is presented in Figure 2. The percentages of protein and fat for the full-fed control birds increased steadily with age. In contrast, early feed restriction resulted in a significantly (P < 0.01) lower percentage fat for feed-restricted birds than for their full-fed counterparts during the restriction period. Thereafter, the percentage body fat for the feed-restricted birds increased, becoming significantly (P < 0.01) higher than for the full-fed birds after 5 d of realimentation at 17 d of age. Proportional content of the birds then declined and by 42 d of age there was no difference in body fat percentage between the two groups of birds. Percentage body protein was not different between treatments except at 21 d of age when the full-fed birds had significantly (P < 0.05) more percentage protein than did their feed-restricted counterparts.

Experiment 2

Effect of early feed restriction and refeeding on weight gain and feed efficiency of broilers from Experiment 2 are presented in Table 3. As in Experiment 1, birds subjected to early feed restriction with or without gradual refeeding gained significantly (P < 0.01) less weight during the experimental period of 6 to 42 d than did the full-fed controls, and so there was not complete growth compensation by birds in either of the two feed-restricted treatments. Birds subjected to feed restriction and gradual refeeding gained significantly (P < 0.05) more weight during the period of 21 to 42 d than did those without gradual refeeding. Overall feed efficiency for the period of 6 to 42 d was similar for the two restricted treatments, and in both cases significantly (P < 0.01) superior than for the full-fed control birds.

TABLE 2. Effect of early feed restriction on body weight gain of male broilers (means ± SEM), Experiment 1

<table>
<thead>
<tr>
<th>Treatment</th>
<th>6 to 12 d (g/bird)</th>
<th>12 to 42 d (g/bird)</th>
<th>6 to 42 d (g/bird)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Full-fed</td>
<td>188 ± 4</td>
<td>2,144 ± 27</td>
<td>2,332 ± 29</td>
</tr>
<tr>
<td>2. Restricted (6 to 12 d)</td>
<td>66 ± 1</td>
<td>2,182 ± 26</td>
<td>2,248 ± 27</td>
</tr>
</tbody>
</table>

*P < 0.05.
**P < 0.01.
Mean adipocyte cell diameter measured at different ages during feed restriction and realimentation are presented in Figure 3. Mean adipocyte diameter for birds from the two feed-restricted treatments were significantly (P < 0.01) smaller than for full-fed control birds after 6 and 16 d feed restriction, respectively. During the refeeding period, the average cell diameter for the birds subjected to 6-d feed restriction (6 to 12 d) increased from 17 microns at 12 d to about 26 and 30 μ at 17 and 21 d of age, respectively, and in both cases these values were not different from those of the full-fed control birds. Mean adipocyte diameter for the birds subjected to 6 d feed restriction followed by more gradual refeeding also showed some increase over the same period (12 to 21 d), but cell size was significantly smaller than for the other two treatments at 21 d of age, presumably due to their extended feed restriction period. Ad libitum feeding after 21 d for this group of birds resulted in similar cell size as did the other two treatments at 35 d of age, with no difference between the three treatments thereafter.

Results of total adipocyte number in the abdominal fat pad are presented in Figure 4. There were significantly (P < 0.05) fewer abdominal fat cells per bird for the two restricted treatments from 12 d of age and this trend continued to the end of the experiment at 42 d of age. The relationship between age and cell number during the realimentation period (12 to 42 d) are presented in Figure 5. The rate of increase in fat cell number after the restriction period represented by the slopes of the regression equations with the P value of 0.663 was not different between treatments. Total fat cell number per abdominal fat pad therefore remained lower in the case of feed-restricted birds when compared to their full-fed counterparts at 42 d.

### Experiment 3

Effect of feeding different types of dietary fat on the AFP size of broiler chicks subjected to early feed

<table>
<thead>
<tr>
<th>Treatment</th>
<th>6 to 12 d</th>
<th>12 to 21 d</th>
<th>21 to 42 d</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Full-fed</td>
<td>220a</td>
<td>423a</td>
<td>1,570b</td>
<td>**</td>
</tr>
<tr>
<td>2. Restricted (6 to 12 d)</td>
<td>93b</td>
<td>417*</td>
<td>1,595b</td>
<td>**</td>
</tr>
<tr>
<td>3. Restricted (6 to 21 d)</td>
<td>95b</td>
<td>417*</td>
<td>1,645a</td>
<td>**</td>
</tr>
<tr>
<td>Significance</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td></td>
</tr>
</tbody>
</table>

**Means with no common superscript differ significantly.

*P < 0.05.

**P < 0.01.
TABLE 4. Effect of type of dietary fat on abdominal fat pad (AFP) weight in restricted-fed male broiler chicks, Experiment 3

<table>
<thead>
<tr>
<th>Treatment</th>
<th>AFP weight (g/bird)</th>
<th></th>
<th>AFP weight (% BW)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day 12</td>
<td>Day 15</td>
<td>Day 18</td>
<td>Day 12</td>
</tr>
<tr>
<td>1. Full-fed (AV1)</td>
<td>2.5b</td>
<td>3.4ab</td>
<td>5.9a</td>
<td>0.9a</td>
</tr>
<tr>
<td>2. Restricted (AV)</td>
<td>0.6b</td>
<td>2.5bc</td>
<td>4.6b</td>
<td>0.4b</td>
</tr>
<tr>
<td>3. Full-fed (FO)</td>
<td>2.5a</td>
<td>3.5a</td>
<td>4.0bc</td>
<td>0.9a</td>
</tr>
<tr>
<td>4. Restricted (FO)</td>
<td>0.7b</td>
<td>2.1c</td>
<td>4.3bc</td>
<td>0.4b</td>
</tr>
<tr>
<td>5. Full-fed (TL3)</td>
<td>2.2a</td>
<td>2.9bc</td>
<td>4.6ab</td>
<td>0.8a</td>
</tr>
<tr>
<td>6. Restricted (TL)</td>
<td>0.7b</td>
<td>2.2c</td>
<td>3.4c</td>
<td>0.4b</td>
</tr>
</tbody>
</table>

Source of variation | Probability
Feeding | ** | ** | NS | ** | NS | NS |
Fat | NS | NS | NS | NS | NS | NS |
Feeding × fat | 0.43 | 0.81 | 1.13 | 0.1 | 0.27 | 0.25 |

*Means with no common superscript differ significantly (P < 0.05).
**Means with no common superscript differ significantly (P < 0.01).
1Animal-vegetable blend.
2Flax oil.
3Beef tallow.
*P < 0.05.
**P < 0.01.

restriction and realimentation is presented in Table 4. There was a significant effect of feed restriction on AFP expressed as grams per bird or as percentage of body weight. This difference was not observed after 6 d of ad libitum feeding at 18 d of age. There was a significant (P < 0.05) effect of type of dietary fat on AFP size at 18 d, with chicks that received the high PUFA diet having a smaller AFP size than those that received the diet containing A-V (Diets 4 and 1, respectively; Table 1). There was no significant interaction of feed restriction and type of dietary fat.

The fatty acid profiles of the diets used in Experiment 3 generally reflected those of the fats used in formulating the diets (Table 5). Fatty acid profiles of the AFP are also presented in Table 5. Generally, across treatments, the most predominant fatty acids in the AFP are C16:0, C18:0, C18:1, and C18:2. Contrary to the results of body weight and feed efficiency, fatty acid composition of the AFP was affected only by dietary fat type fed during the period of 12 to 18 d, regardless of the previous level of feeding; therefore, the results are presented according to fat type. There was a significantly (P < 0.01) higher proportion of

TABLE 5. Effect of type of dietary fat on fatty acid profile of diets and abdominal fat pad of male broilers on 18 d, Experiment 3

<table>
<thead>
<tr>
<th>Type of fat</th>
<th>C16:0</th>
<th>C16:1</th>
<th>C18:0</th>
<th>C18:1</th>
<th>C18:2</th>
<th>C18:3</th>
<th>C20:0</th>
<th>PUFA1</th>
<th>SAT2</th>
<th>PUFA:SAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-V Fat*</td>
<td>23.1</td>
<td>1.1</td>
<td>7.7</td>
<td>40.1</td>
<td>26.1</td>
<td>3.0</td>
<td>0.3</td>
<td>29.1</td>
<td>70.4</td>
<td>0.41:1</td>
</tr>
<tr>
<td>Flax oil</td>
<td>10.0</td>
<td>0.6</td>
<td>3.0</td>
<td>16.3</td>
<td>32.5</td>
<td>38.2</td>
<td>0.4</td>
<td>70.7</td>
<td>29.4</td>
<td>2.4:1</td>
</tr>
<tr>
<td>Tallow</td>
<td>25.2</td>
<td>1.4</td>
<td>12.5</td>
<td>30.6</td>
<td>25.7</td>
<td>6.0</td>
<td>0.4</td>
<td>31.1</td>
<td>69.2</td>
<td>0.45:1</td>
</tr>
<tr>
<td>A-V Fat</td>
<td>17.3b</td>
<td>2.9b</td>
<td>43.5A</td>
<td>19.9b</td>
<td>13.7</td>
<td>0.2b</td>
<td>3.2</td>
<td>13.9b</td>
<td>86.9</td>
<td>0.16:1b</td>
</tr>
<tr>
<td>Flax oil</td>
<td>19.0b</td>
<td>4.6ab</td>
<td>20.3B</td>
<td>22.0b</td>
<td>13.8</td>
<td>14.9A</td>
<td>4.1</td>
<td>28.7a</td>
<td>70.9</td>
<td>0.40:1a</td>
</tr>
<tr>
<td>Tallow</td>
<td>25.4a</td>
<td>6.8a</td>
<td>17.9B</td>
<td>32.7a</td>
<td>12.6</td>
<td>0.2B</td>
<td>2.4</td>
<td>12.8b</td>
<td>86.5</td>
<td>0.15:1b</td>
</tr>
<tr>
<td>Significance</td>
<td>*</td>
<td>*</td>
<td>**</td>
<td>*</td>
<td>*</td>
<td>**</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>SD</td>
<td>5.57</td>
<td>3.57</td>
<td>21.32</td>
<td>12.26</td>
<td>4.87</td>
<td>6.00</td>
<td>4.03</td>
<td>5.4</td>
<td>18.2</td>
<td>11:1</td>
</tr>
</tbody>
</table>

*Means with no common superscript differ significantly (P ≥ 0.05).
**Means with no common superscript differ significantly (P ≥ 0.01).
1Polyunsaturated fatty acids.
2Saturated fatty acids.
3Animal-vegetable fat blend.
*P < 0.05.
**P < 0.01.
C_{18:3} in the AFP of chicks that received flax oil than in those that received the diets containing either A-V blend or tallow over the same period. Chicks that received the diet containing A-V blend had significantly (P < 0.01) more C_{18:0} and significantly (P < 0.05) less C_{16:1} and C_{18:1} than those fed tallow. Chicks that received tallow had significantly (P < 0.05) more C_{16:0} in the AFP than did birds receiving the other fats. These differences in individual fatty acid also resulted in significantly (P < 0.05) higher total PUFAs and PUFAs:saturated fatty acid ratio in the AFP of chicks fed flax oil than in the chicks fed A-V blend and tallow.

**DISCUSSION**

**Growth Performance and Feed Efficiency**

Complete growth compensation was not attained by the birds subjected to early feed restriction compared to the full-fed controls in Experiment 1 (Figure 1). This is in agreement with the results of Pinchasov and Jensen (1989), and Yu et al. (1990), but contrary to those of others, (Plavnik and Hurwitz, 1985, 1988 a,b, 1989, 1991; Leeson et al., 1991; Jones and Farrell, 1992 a,b; Zubair and Leeson, 1994a). At the end of the 6-d feed restriction period, feed restricted birds weighed about 130 g less than the full-fed controls. This difference in body weight was reduced to about 80 g by 42 d (Figure 1). Most studies that have reported complete growth compensation either used milder undernutrition programs (Leeson et al., 1991; Plavnik and Hurwitz, 1991; Jones and Farrell, 1992b; Zubair and Leeson, 1994a), or the growth periods were extended to at least 56 d of age (Plavnik and Hurwitz, 1985, 1988 a,b; Plavnik et al., 1986; Jones and Farrell, 1992b). It is not clear at this point whether growth compensation observed in more prolonged growout studies is simply due to early plateau in growth of the full-fed control birds.

Improvement in feed efficiency by the feed-restricted birds during the realimentation periods recorded in Experiment 2 (Table 2) was also observed in Experiments 1 and 3. This is in agreement with the results reported by Pokniak et al. (1984), McMurtry et al. (1988), Yu et al. (1990), and Plavnik and Hurwitz (1988 a,b; 1989; 1991). Overall feed efficiency for the period of 6 to 42 d was superior for birds subjected to feed restriction when compared to control birds that were full-fed throughout the experimental period (Table 3). Such improvement in feed efficiency associated with early feed restriction has been attributed to higher metabolic efficiency associated with maintaining a smaller body (Dickerson, 1978; Jones and Farrell, 1992b). Calorimetric studies by Zubair and Leeson (1994b) however showed that lower metabolic rate in restricted-refed broilers does not play a role in any improvement in feed efficiency. Zubair and Leeson (1994b) suggest that higher feed intake relative to the smaller body weight and associated digestive adaptations of restricted-refed broilers seem to be the major contributing factors to improved feed efficiency.

**Body Composition and Adipocyte Cellularity**

During the first 5 d of realimentation in Experiment 1, the feed-restricted birds gained about 41 g of fat per bird, as opposed to 26 g for the full-fed birds (data not included). The feed-restricted birds weighed significantly (P < 0.01) less than full-fed control group birds at 17 d of age, but had a significantly higher percentage body fat such that there was no difference in absolute fat content per bird. This is consistent with results of Pokniak and Cornejo (1982) and Yu et al. (1990), who also showed a high rate of fat deposition during the early phase of realimentation. After 17 d, the percentage body fat in the feed-restricted birds relative to the full-fed birds started to decline and at the end of the growth period (42 d of age), the feed-restricted birds had the same percentage fat content as the control. The ability of early feed restricted birds to exhibit “catch-up” in body fat relative to their full-fed counterparts during early realimentation has also been reported by other workers (Rosebrough et al., 1986; McMurtry et al., 1988). These workers subjected broilers to early feed restriction similar to that used in these studies and reported suppression of hepatic enzymes associated with lipogenesis during the restriction period. This was followed by hyperactivities of the enzymes during the first 10 d of realimentation and a subsequent suppression during the remaining growth period. The reason for the short-term rebound and subsequent decline in hepatic lipogenic enzymes activities seen by others is yet to be adequately explained.

The original idea of using an early feed restriction strategy was based on the proposal that the degree of fatness at an early age may affect adiposity at maturity. Many such studies were intended to elucidate whether early-life nutrition may have subsequent effects on fat cell
development, based on the hypothesis that early under-nutrition may cause suppression or delay in adipocyte hyperplasia (March and Hansen, 1977; Nir, et al., 1988; Jones and Farrell, 1992b). Early 50% feed restriction used in Experiment 2 resulted in no increase in cell size from 6 to 12 d in the case of feed-restricted birds, whereas fat cells of full-fed birds showed about 35% increase in diameter over the same period. On commencement of refeeding at 13 d, there was a dramatic increase in cell size of birds subjected to 6-d feed restriction and immediate return to ad libitum feeding, resulting in similar cell size to their full-fed counterparts after 5 d of full-feeding. This scenario corresponds to high fat deposition during early refeeding that was observed in Experiment 1 (Figure 2) and also reported by others (Pokniak and Cornejo, 1982; Rosebrough et al., 1986; McMurtry et al., 1988; Yu et al., 1990; Zubair and Leeson, 1993).

Results of the current studies show that increase in cell size was significantly suppressed by feed restriction, but this effect was very transitory. Similar results were reported by March et al. (1982), who observed only a transitory effect of feed restriction in lowering adipocyte diameter. Broiler chickens subjected to feed restriction followed by a gradual refeeding also showed more adipocyte hypertrophy in response to full-feeding. However this adaptation was delayed until after 21 d when full-feeding commenced. The restricted-refed birds eventually attained similar mean adipocyte size as the birds in the other two treatments at 35 d, further confirming the very transitory nature of the effect of early feed restriction on fat cell size. Contrary to this finding, Gordon and March (1979) observed that feed restriction suppressed adipocyte growth and that the effect on cell size was still apparent when birds were 42 wk old. Such differences on the effects of early nutrient restriction on fat cell size may be related to the level and duration of undernutrition. Dietary restriction in the study of Gordon and March (1979) was imposed for up to 14 wk, a situation likely to result in suppression of development of not only fat tissue cells, but also of lean tissue.

Total fat cell number at 12 d in Experiment 2 was significantly (P < 0.01) less for feed-restricted birds than for the full-fed controls, due to 50% feed restriction. The increase in fat cell number for the period of 12 to 42 d did not change this trend, such that the lower fat cell number in the case of feed-restricted birds was still apparent at 42 d. This result is in agreement with those of Jones and Farrell (1992b), who also reported fewer fat cells in the AFP of early feed-restricted broilers than in the AFP of those that were full-fed. Similar results have been reported from studies with mammalian species by Hood and Allen (1977), who showed that slow early growth rate resulted in delayed porcine adipocyte hyperplasia, and that it had no effect on total cell number in mature pigs. Rate of increase in fat cell number during the refeeding period of Experiment 2 (12 to 42 d) with the P value of 0.665 obtained from the regression of cell number with age was not different between treatments (Figure 3). Attain-

ment of complete growth compensation apparently requires a more prolonged growth period, up to 56 d of age, as indicated by results of many studies (Plavnik and Hurwitz, 1985, 1988a, 1991; Plavnik et al., 1986; Jones and Farrell, 1992b). It is not clear at this point whether such a prolonged growth period would also result in compensation of fat cell number. Gradual, as opposed to immediate, reintroduction into ad libitum feeding following early feed restriction did not seem to have any effect on adipocyte cellularity, in terms of average cell size and total number. Because no measurement of body fat content was taken in Experiment 2, it is unclear whether gradual refeeding would have any beneficial effect in terms of lowering fat content without affecting body weight.

**Dietary Fat, Abdominal Fat Pad Size, and Fatty Acid Profile**

Type of dietary fat did not influence abdominal fat pad size when expressed as percentage of body weight (Table 4). There was, however, a larger AFP (grams per bird) in birds that were fed A-V blend than in those fed flax oil or animal tallow. This increase in AFP may be simply due to differences in body weight because there was no difference in AFP size as percentage of body weight. This finding is at variance with results of Pinchasov and Nir (1992), who reported significant reduction in AFP size, AFP lipid content, liver size, and liver lipid content due to feeding increasing levels of PUFA as opposed to animal tallow. Current results are however, in agreement with those of Scaife et al. (1994), who reported no significant difference in AFP size of broiler chickens that were fed diets containing increasing levels of PUFA. These differences in response of broiler chickens to feeding different types of fat could be due to differences in the levels of the fats used. Dietary PUFA levels of up to 7% were used by Pinchasov and Nir (1992), a level that is double the 3.6% fats used in this experiment. Duration of feeding the high PUFA diet could also be a contributing factor to differences in response reported by many workers. Pinchasov and Nir (1992) fed a high PUFA diet for 40 d as opposed to only 6 d in this experiment. There was no interaction of feed restriction and type of dietary fat.

The fatty acid profile of the abdominal adipose tissue generally reflected that of the different diets, regardless of prior feed allocation (Table 5). Chicks in Treatments 3 and 4 that were fed diets containing flax oil, for example, had significantly (P < 0.01) higher levels of C18:3, a situation very consistent with the dietary fatty acid profile. Fatty acid profile of the fat derived from AFP of chicks in Treatments 5 and 6, on the other hand, had significantly (P < 0.05) higher levels of C16:0 and C16:1, a trend that is very consistent with the dietary fatty acid profile. These results are in agreement with those reported by Scaife et al. (1994), who reported that fatty acid profile of abdominal adipose tissue reflects that of the diets fed. These authors attributed such similarity in fatty acid profile of diets and adipose tissue in the broiler chickens to the fact that in
monogastric animals, dietary fatty acids are absorbed and deposited in the tissues without significant modification.

Male broiler chickens subjected 50% feed restriction during the period 6 to 12 d of age did not show compensatory growth at 42 d of age in these studies. Such feed restriction resulted in initially lower body fat percentage, a situation that did not continue after refeeding to 42 d of age due to high fat deposition, mainly by hypertrophy of the adipocytes. Gradual reintroduction into ad libitum feeding neither succeeded in altering the adipocyte hypertrophy nor result in better compensatory growth response during refeeding. However, there was consistent improvement in feed efficiency due to early feed restriction. Attainment of growth compensation by the feed-restricted broiler apparently requires prolonged growout.

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