

Genetics of Lipid Deposition in the Japanese Quail

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Summary. The research presented here was designed to investigate the mode of inheritance of fat and lean tissue deposition, and the relationship between them and body weight in Japanese quail. Heterotic effects were found for weight, size, and number of adipocytes in the abdominal fat depots, weight of the sartorial fat depot and percentage carcass fat with means for the hybrids being lower than those for the parental lines. General inferences concerning the importance of non-additive genetic variation for lean and body weight were precluded due to inconsistencies observed among mating combinations. Thus, although heterosis and recombination effects were general for characteristics associated with fat deposition, the situation for body weight and lean was unique to the populations involved. It may be hypothesized that heterosis in the efficiency of feed utilization is reflected by the heterosis for fat deposition which explains why hybrids utilize feed better than their parental lines.

Key words: Heterosis – Abdominal fat deposition – Sartorial fat deposition – Breast weight – Japanese quail – Recombination

Introduction

The body weight of an animal is a function of the size of its component parts. In animals used for food consumption, some of the component parts are considered edible, while others are waste products. This creates a dilemma for geneticists when high body weight is included among the selection criteria. For example, it is well known that age at market weight is an integral component in determining the efficiency of broiler production. This age has been reduced by 50 percent

during the past three decades with much of the reduction attributable to intensive artificial selection for heavier juvenile body weights. A response concomitant to this selection has been an increase in the size of the abdominal fat depot. Fat, in this form of obesity, is unacceptable to the consumer and to the processor and thus becomes a waste product.

Carcass composition may be modified by diet, but the extent of this alteration is variable and suggests that significant reductions in abdominal fat deposition by nutrient restriction alone is limited and may involve interactions with nonnutritional factors (Cunningham and Morrison 1976; Pfaff and Austic 1976; Griffiths et al. 1977).

Although studies with laboratory animals and humans suggest that obesity may be caused by either hyperplasia and/or hypertrophy of fat cells (Kirtland and Gurr 1979; Bulfer and Allen 1979), the genetic relationship between fat deposition and growth rate has not been fully assessed in any species. The minimization of adipose tissue accumulation without a corresponding reduction in the growth rate of broilers would be advantageous to both the consumer and the poultry producer. Furthermore, since breast muscle contributes greatly to the amount of lean meat, a goal in the production of poultry should be an increased breast weight with a minimum of adipose tissue.

The research reported here was designed to investigate the mode of inheritance of fat deposition and breast weight, and the relationship between them and growth rate of Japanese quail (*Coturnix coturnix japonica*). Studies with this pilot organism could provide a basis for subsequent studies in the chicken, since both may be placed in the same family on the basis of immunological distance (Mainardi 1959) and when crossed can produce viable (but sterile) hybrids (Wilcox and Clark 1961).

Materials and Methods

Stocks and Matings

The populations used in this study consisted of five lines of quail. Two of the lines (A, D) had undergone over 20 generations of selection for high mating frequency, two (B, E) had undergone over 20 generations of selection for low mating frequency, while the remaining line (C) was the randombred control population which served as the base for the selected lines (Cunningham and Siegel 1978). These lines will be referred to as parental lines in this paper.

An F₁ generation and associated parental line chicks were obtained from matings involving S₂₁ generation parents. Quail from the initial F₁ generation and the S₂₂ were used as parents to produce a contemporary flock (the source of all data except the cellularity data) which consisted of a repeat of the parental lines, the F₁ generation, the F₂ generation and the backcross generation. Each backcross was obtained from mating F₁ males to females from the respective parental lines (Table 1).

Husbandry and Traits Measured

Eggs were incubated and chicks were hatched in a Petersime model S6-Ph incubator-hatcher unit. Chicks were removed from the hatcher the day after hatching and their toes clipped to identify each mating combination. Chicks were reared in sexually intermingled flocks in modified chick battery brooders to 4 weeks of age, at which time they were sexed and wingbanded. The females were transferred to growing batteries where they remained until sacrificed at 8 weeks of age. Males were transferred to another unit for use in another experiment.

Feed and water were provided ad libitum. The diet consisted of 30% protein and 2975 kcal/kg energy. Lighting was continuous to four weeks of age, after which the photo-

Table 1. Mating combinations with males listed first and dam second

1. Parental line matings and F ₁ crosses			
a. Sire line	Dam line		
	A	B	C
A	AA	AB	AC
B	BA	BB	BC
C	CA	CB	CC
b. Sire line	Dam line		
	C	D	E
C	CC	CD	CE
D	DC	DD	DE
E	EC	ED	EE
2. F ₂ crosses – reciprocal cross of AB × BA, BA × AB etc.			
3. Backcrosses involved mating F ₁ males to parental line dams (eg. AB × C)			

Table 2. Traits measured (+) in various mating combinations

Age (wks)	Trait	Parental lines	F ₁	F ₂	Back-crosses
8	Body wt (g)	+	+	+	+
	Left and right sartorial fat depot				
	wt (mg)	+	+	+	+
	wt (mg/100 g body wt)	+	+	+	+
	Carcass fat (%)	+	+	+	+
	Breast wt (g) ^a	+	+	+	+
	Abdominal fat depot				
	wt (mg)	+	+	+	+
	wt (mg/100 g body wt)	+	+	+	+
	no. cells/depot × 10 ⁶	+	+		
	no. cells/g × 10 ⁶	+	+		
	cell diameter (μg)	+	+		

^a Measurements obtained for mating combinations AB and DE

period consisted of 16 hours of light, followed by 8 hours of darkness.

At 8 weeks of age, five females were selected at random from each parental line, F₁ cross, F₂ cross, and backcross, and sacrificed for various measurements (Table 2). Feed was removed from the birds approximately 14 hours prior to sacrifice by cervical dislocation and defeathering. The left and right sartorial fat depots and the abdominal fat depots were removed and weighed to the nearest mg. Carcasses were tagged and stored at 0 °C for subsequent determinations of total body fat. Grinding and mixing of individual carcasses were made in a Waring blender with an Eberbach cup. Samples of each carcass were taken at random and their lipid content determined by using a modification of the A.O.A.C. (1970) ether extraction procedure which utilized a Goldfish apparatus. To estimate the amount of lean meat, breast weight in g were obtained at the time of the sacrifice for birds from certain matings. The rationale for this measurement is the highly positive correlation between breast weight and lean body weight (Plotkin and Soller 1980).

Cellularity of the abdominal fat pad was measured in the initial F₁ crosses and their respective parental lines by a modification of Method III described by Hirsch and Gallian (1968). Raw counts obtained from the Coulter Channelyzer were used to obtain the number of cells per g of tissue and the total number of cells in the depot. Data obtained from the Logarithmic range Expander were used to calculate cell diameter.

Statistical Analyses

Data were analyzed by analysis of variance using the statistical model:

$$Y_{ij} = \mu + C_i + e_{ij}$$

where Y_{ij} is the measure of the jth individual in the ith mating combination (C). For traits involving cellularity of adipose

tissues, $i=1, 2 \dots 4$ and $j=1, 2 \dots t$; for all other measurements $i=1, 2 \dots 8$ and $j=1, 2 \dots t$. Percentages were transformed to arc sine $\sqrt{\%}$ prior to analysis (Snedecor and Cochran 1967). All other measurements were analyzed as measured, and as logarithms (Carte and Siegel 1970), with the exception of the cellularity data, which were analyzed as measured. The mean channel for cellularity was determined using a weighted average (Chilko 1979).

Comparisons were made among mating groups using Duncan's multiple range test (Kramer 1956) and nonorthogonal linear contrasts (Scheffe 1970). Duncan's multiple range test was used for a comparison among the parental lines. For the Scheffe test, seven contrasts were made within the matings involving each pair of lines. Using lines A and B as an example, the contrasts showing the sire line first and dam line second were:

- (1) AA-BB
- (2) AB-BA
- (3) (AA + BB)-(AB + BA)
- (4) (AA + AB + BA + BB)-2 (ABAB + BABA)
- (5) (ABAB-BABA)
- (6) (AB + BA)-(ABAB + BABA)
- (7) (AA + AB + BA + BB)-2 (BAAA + ABBB)

Contrast 1 evaluates differences between parental lines, contrasts 2 and 5 measure reciprocal effects, contrast 3 appraises nonadditive genetic effects, and contrasts 4, 6, and 7 estimate recombination loss. Differences between female progeny of reciprocal crosses (contrasts 2 and 5) have a confounding of maternal and sex-linked effects since in the Japanese quail the female is heterogametic (ZW). In most cases where the F_1 shows consistent heterosis, contrast 6 may be biased since a comparison of the F_1 to the F_2 would be biased by the latter.

Results and Discussion

Body, breast, abdominal fat depot, and sartorial fat depot weights were analyzed by analysis of variance, both as absolute values and when transformed to logarithms. Since rankings of means were the same for both data sets, only the nontransformed data will be presented.

Body Weight

Mean body weights at 8 weeks of age are presented in Table 3. The F_1 and F_2 reciprocal crosses were pooled since there were no significant differences among them, suggesting that sex-linked and maternal effects were unimportant. This is consistent with the observations of Sefton and Siegel (1974) who found little evidence for maternal effects at this age.

Females from lines A and D were significantly heavier than those from lines B and C which is consistent with previous observations for these lines (Cunningham and Siegel 1978). None of the remaining differences between parental lines were significant.

Table 3. Mean body and breast weights in g at 8 weeks of age

Gen ^a	Mating combination					
	AB	AC	BC	CD	CE	DE
<i>Body wt</i>						
P ₁	139	139	129	127	127	145
P ₂	129	127	127	145	132	132
F ₁	139	129	128	130	128	131
F ₂	135	132	117	136	121	129
B ₁	137	119	120	129	119	131
B ₂	127	126	128	143	121	124
<i>Breast wt</i>						
P ₁	25.1					27.3
P ₂	26.2					25.4
F ₁	25.4					24.4
F ₂	25.3					21.8
B ₁	27.3					25.3
B ₂	28.4					24.5

^a Matings denoted with AB as an example, are P₁ (A × A), P₂ (B × B), F₁ (reciprocal crosses), F₂ (reciprocal crosses), B₁ (BA × A), and B₂ (AB × B). Reciprocal crosses were pooled in the F₁ and F₂ generations because they were not significantly different

Contrasts 2 through 7 were not significant. Heterosis was low (Table 4) ranging from -5 to 4 percent, suggesting that it is population dependent. This was consistent with the magnitude of recombination effects which ranged from 2 to 6 percent (Table 5). Although these observations were not unlike those noted for the

Table 4. Percentage heterosis^a for various traits measured at 8 weeks of age

Trait	Mating combination					
	AB	AC	BC	CD	CE	DE
<i>Body wt</i>						
	4	-3	0	-5	-1	-1
<i>Breast</i>						
wt	-1					-7
% body	-5					-6
<i>Sartorial fat depot</i>						
wt	-51	-77	-91	-63	-67	-80
% body	-56	-75	-92	-60	-66	-79
<i>Abdominal fat depot</i>						
wt	-28	-37	-74	-50	-54	-68
% body	-35	-34	-76	-49	-53	-63
cells/g	22	-21	-32	-21	-8	-10
cells/depot	-20	-42	-75	-42	-46	-38
cell diam.	-18	-12	-18	-6	-15	-9
<i>% carcass fat</i>						
	-13	-10	-38	-21	-21	-26

^a Estimated as the percentage deviation of the mean for the F₁ reciprocal crosses from the mean of the parental lines

Table 5. Percentage recombination effects^a for various traits measured at 8 weeks of age

Trait	Mating combination					
	AB	AC	BC	CD	CE	DE
<i>Body wt</i>	2	3	6	2	6	5
<i>Breast wt</i>	4					8
<i>% body</i>	6					3
<i>Sartorial fat depot wt</i>						
<i>% body</i>	58	57	34	48	46	9
	58	61	29	46	61	4
<i>Abdominal fat depot wt</i>						
<i>% body</i>	88	59	10	37	6	29
	88	144	5	37	0	25
<i>% carcass fat</i>	19	22	3	21	11	22

^a Estimated as the mean percentage deviation of the F_2 from the parental lines and the F_1 crosses (contrast 4) and the backcrosses from the parental lines and the F_1 crosses (contrast 7)

domestic fowl where heterosis for body weight is erratic (Kan et al. 1959; Cock and Morton 1963), they were surprising in that the populations used in this experiment were closed for over 20 generations and had inbreeding coefficients in excess of .25. Inbreeding is known to decrease the body weight of chickens (eg., Glazener et al. 1951; Blow and Glazener 1953) and Japanese quail (Sittman et al. 1966), suggesting that body weight may be influenced by heterosis.

Breast Weight

Breast weight was measured for mating combinations AB and DE and means are presented in Table 3. The results obtained were similar either when breast weight was expressed on an absolute basis or when it was expressed as a percentage of live body weight. Of the contrasts made using Scheffe's analysis, only one (contrast 4 for the DE mating combination) was significant ($DD + DE + ED + EE - 2(DEDE + EDED)$). Heterosis ranged from -1 to -7 percent (Table 4) and recombination effects from 3 to 8 percent (Table 5). The magnitude of the values was quite similar to that found for live body weight (Table 4) and similarly suggests that the degree of heterosis observed for breast weight is parental population dependent.

Sartorial Fat Depot

The weight of the sartorial fat depot at 8 weeks of age followed a pattern where the F_1 crosses had values that

were smaller than the midparent means of their respective parental lines (Table 6). Contrasts for the weight of the sartorial fat depot revealed significant differences in all cases except contrasts 1 and 6 in the DE and CE mating combinations, respectively. This indicates a role of the parental line (contrast 1), maternal effects and/or sex-linked effects (contrasts 2, 5) and recombination effects (contrasts 4, 6, 7). Most important, however, was that in all cases the means for the F_1 crosses were significantly lower than those of their respective midparent means. When the means were expressed as the percentage deviation of the F_1 crosses to the midparent values of the parental lines, heterosis ranged from -50 for the AB to -91 for the BC mating combinations, providing considerable evidence for nonadditive genetic effects for the weight of the sartorial fat depot (Table 4). Furthermore, recombination effects were of a considerable magnitude for all matings except that involving the DE combination (Table 5).

When sartorial weight was expressed as a percentage of body weight, the percentage of heterosis and of recombination was similar to that noted for the sartorial fat depot weight per se (Tables 4, 5).

Abdominal Fat Depot

The weight of the abdominal fat depot at 8 weeks of age followed a pattern where F_1 crosses had values that

Table 6. Mean sartorial and abdominal fat depot weights in mg at 8 weeks of age

Gen ^a	Mating combination					
	AB	AC	BC	CD	CE	DE
<i>Sartorial wt</i>						
P_1	57	57	187	100	100	151
P_2	187	100	100	151	154	154
F_{1q}	25	21	17	39	65	48
F_{1r}	65	15	9	55	19	15
F_{2q}	221	88	54	140	62	23
F_{2r}	67	70	83	64	30	10
B_1	108	66	33	116	17	246
B_2	131	79	38	190	15	57
<i>Abdominal wt</i>						
P_1	297	297	847	644	644	1,636
P_2	847	644	644	1,636	1,222	1,222
F_{1q}	370	371	318	510	429	604
F_{1r}	455	225	69	633	428	308
F_{2q}	1,160	714	329	1,509	1,654	322
F_{2r}	559	518	573	712	326	173
B_1	1,198	532	278	985	333	1,607
B_2	775	685	519	1,491	233	565

^a Matings denoted, with AB as an example, are P_1 ($A \times A$), P_2 ($B \times B$), F_{1q} ($A \times B$), F_{1r} ($B \times A$), F_{2q} ($AB \times BA$), F_{2r} ($BA \times AB$), B_1 ($BA \times A$) and B_2 ($AB \times B$)

were smaller than the midparent means of their respective parental lines (Table 6). These findings were consistent with the results obtained for the size of the sartorial fat depot indicating a similar mode of inheritance for both of these fat depots. Scheffe's contrasts indicate that, with few exceptions, the weight of the abdominal fat depot was influenced by parental line effects (contrast 1), maternal and/or sex-linked effects (contrasts 2, 5). Considerable heterosis was evident (contrast 3) with the percentage of heterosis ranging from -28 to -74 (Table 4), while recombination effects were considerable for all but the BC and CE mating combinations (Table 5). When the weight of the abdominal fat depot was expressed as a percentage of body weight, the general pattern again followed that observed when sartorial fat depot weights were expressed as a percentage of body weight.

Mean number of adipose cells/abdominal fat pad and the mean diameter of these cells are presented in Table 7. No significant differences were found among parental lines or the reciprocal F_1 crosses of the parental lines for either the size of the abdominal fat cells, the number of cells/g, or number of cells/depot. Although contrast 3, which estimated nonadditivity, was not significant, the F_1 means were consistently less than that of the midparent means of the parental lines (Table 4). In all but one case (cells/g for the AB mating), the percentage heterosis was negative (Table 4).

The results obtained for the various measures involving the abdominal fat depot suggest the presence of heterosis with F_1 values being less than that of the mean of the parental lines. Since considerable energy is required for the deposition of fat, it may be hypothesized that part of the expression that one sees for the heterosis of feed efficiency is a reflection of the hybrid

Table 7. Mean number of adipose cells/abdominal fat depot and diameter of adipose cells

	Mating combination ^a					
	AB	AC	BC	CD	CE	DE
<i>Cells/depot × 10⁶</i>						
P_1	3.5	3.5	5.7	5.1	5.1	3.1
P_2	5.7	5.1	5.1	3.6	6.1	6.1
F_{1q}	2.8	1.6	2.2	1.5	3.1	4.0
F_{1r}	4.6	3.4	0.5	3.6	3.0	2.0
<i>cell diameters (μm)</i>						
P_1	38.4	38.4	44.4	39.8	39.8	39.4
P_2	43.4	39.8	39.5	39.4	41.0	41.0
F_{1q}	33.8	35.7	34.1	36.7	33.8	37.8
F_{1r}	33.4	33.4	34.0	37.7	34.6	35.5

^a Matings denoted, with AB as an example, are P_1 ($A \times A$), P_2 ($B \times B$), F_{1q} ($A \times B$), and F_{1r} ($B \times A$)

Table 8. Mean percentage carcass fat at 8 weeks of age

Gen ^a	Mating combination					
	AB	AC	BC	CD	CE	DE
P_1	6.1	6.1	8.6	6.3	6.3	10.7
P_2	8.6	6.3	6.3	10.7	8.6	8.6
F_1	6.4	5.6	4.7	6.8	5.9	7.1
F_2	7.7	7.7	6.9	9.5	7.0	5.0
B_1	9.0	7.0	5.1	7.5	5.1	9.9
B_2	8.3	6.5	6.2	10.4	4.6	6.2

^a Matings denoted, with AB as an example, are P_1 ($A \times A$), P_2 ($B \times B$), F_1 (reciprocal crosses), F_2 (reciprocal crosses), B_1 ($BA \times A$), B_2 ($AB \times B$). Reciprocal crosses were pooled in the F_1 and F_2 generations because they were not significantly different

offspring laying down less fat than that found in parental lines.

Percentage Carcass Fat

Percentage carcass fat is presented by matings in Table 8. None of the contrasts for this trait was significant. The sign of the percentage of heterosis was consistent with that noted for traits involving abdominal and sartorial fat depots. The degree of heterosis for percentage carcass fat varied according to the mating combination, ranging from -10 to -38 percent (Table 4) which was generally less than that noted for specific fat depots per se. The general pattern for recombination effects (Table 5) was consistent with that just described for heterosis.

General

Heterosis was large in all mating combinations for all traits associated with fat characteristics. In essentially all cases, means of the hybrids were lower than the midparent values for the parental lines. Such was not the case for body weight or lean, which was measured by breast weight. It is well known that the energetic costs associated with fat deposition are high. Thus, it may be hypothesized that the efficiency of feed utilization should be reflected by such heterosis to a degree that is commensurate with the percentage of carcass that is fat.

Although feed efficiency was not measured in this experiment, there is a general consensus that broiler crosses utilize their feed more efficiently than their parental lines. Data to support this view have been provided by Barbato (1980) who observed heterosis using crosses of various chicken lines from hatching to

42 days of age. Furthermore, there is evidence that within chicken mating combinations the percentage heterosis for feed efficiency is greater than that for body weight. It may thus be inferred that the improvement in feed efficiency noted in crosses of various lines may be in part a reflection of heterosis of fat deposition.

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