Genetic Architecture of Growth and Body Composition in Unique Chicken Populations

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A resource population was established by crossing one modern broiler sire from a commercial broiler breeder male line with dams from two unrelated highly inbred lines; F_1 birds were intercrossed to produce two F_2 populations. A variety of phenotypic measurements related to growth, muscling, internal organs, and skeleton were recorded for the F_2 populations and contemporary pure inbred and broiler birds. Based on the means and phenotypic distributions of the F_2 populations compared to their parental lines, the effective number of genes affecting each trait and heterosis were estimated and discussed relative to the known genetic selection history for each trait. The results suggest that a high number of genes with small epistatic effects are involved in determining the phenotype for traits that broilers were traditionally selected for, and a lower number of genes with major effects are involved in determining the phenotype for traits related to fitness. The estimated number of genes and the phenotypic distributions of the different traits suggest that a quantitative trait loci (QTL) search might be more effectively applied for traits with a low number of involved genes and a high phenotypic distribution among the F_2 birds than for traits that show a lower phenotypic distribution and a high number of genes.

Selection for Growth and Fitness

Geneticists have made rapid genetic improvements through the use of intense selection for specific biological traits, leading to continuous improvements in body weight (BWT), growth rate, and meat yield in meat-type birds. Marketing age (the time when broilers reach 2000 g) continues to be reduced by 1 day every generation/year (Havenstein et al. 1994a,b). As a result, contemporary meat-type chickens reach marketing weight at about 42 days of age, whereas about 52 days were required to reach a similar BWT 10 years ago. Ironically, accompanying the success of intense genetic selection, there has been a reduction in the overall fitness of modern broiler chickens (Emmerson 1997; Julian 1998; Marks 1996). The increase in physiological disorders such as obesity, ascites, sudden death syndrome, and leg problems, as well as a reduction in overall immunocompetency have become important issues. This reduction in fitness is mainly because of a tremendous increase in body mass without parallel improvements in the internal organs, vascular system, and skeleton to support such a rapidly growing and large body mass (Dunnington and Siegel 1996; Katanbaf et al. 1988a). The most negatively affected birds are those characterized by the otherwise desirable traits of rapid growth and muscle accretion.

Growth and meat yield traits in poultry, as well as fitness traits, are controlled by many genes (quantitative trait loci, QTL). The total effect of the QTLs is influenced by many genes that might interact with each other (gene × gene or gene × genotype interactions) and the environment that might interact with the genotype (environment × genotype interaction) (Cahaner 1990). Hence quantitative traits have low to medium heritability. Moreover, production and fitness traits are negatively correlated (Pinard-van der Laan et al. 1998). Multitrait selection to improve fitness and simultaneously increase growth rate and meat yield is therefore difficult to accomplish by traditional, direct phenotypic selection. Thus selecting individuals with additional information about their genotype for markers associated with QTLs for fitness and growth (marker-assisted selection, MAS) is preferred. To accomplish MAS, it is essential to detect linkages between DNA markers and QTL associated with the traditional selection

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 93:107–118

traits (growth and muscle mass) as well as fitness traits (increasing heart capacity and spleen weight, improving the skeleton, and reducing the fat content) for which populations were not routinely selected. Because the negative genetic correlation between growth and fitness is not absolute, it is possible to select for genotypes with high fitness characteristics and high yield using MAS. However, the relative advantage of MAS over phenotypic selection depends on the heritability of the traits and the cost of phenotyping versus genotyping. In general, fitness traits are very expensive to measure because they require specialized facilities (e.g., disease resistance) or cannot be readily measured on live animals (e.g., internal organs).

DNA Markers and Resource Populations

Successful QTL identification using molecular markers depends on the availability of suitable markers and the use of a resource population with sufficient genetic variation to detect linkage between a segregating QTL and a genetic marker. More than 800 highly polymorphic microsatellite markers are available in the chicken genome (Groenen 2001; Groenen et al. 2000), which allows scanning for markers linked to QTL of interest by using a genomewide search. Two morphologically expressed genes that are easily identified at hatching (*polydactyly* and *naked-neck*) were recently mapped by using a genomewide microsatellite search in chickens (Pitel et al. 2000). However, when the trait has a polygenic inheritance pattern (as have most QTLs), a more complicated experimental design than single-gene morphologically expressed traits is required. To ensure sufficient genetic variation, two genetically distant parental lines for the trait(s) of interest must be crossed and F_2 or backcross populations produced (Hillel 1997). Studies to identify markers associated with traits of economic interest in poultry are few to date, and the ability to identify such associations has been limited because of limited variation in the traits of interest within the resource populations. Using backcross and F_2 crosses derived from two chicken lines divergently selected for level of antibody response to *Escherichia coli* (Yonash et al. 2001), a cross between two inbred parental chicken lines differing in susceptibility to Marek's disease (Vallejo et al. 1998; Yonash et al. 1999), an F_2 cross of two mouse lines divergently selected for a high or low fat content (Horvat et al. 2000), or an F_2 cross between genetically distant wild boar and Large White pigs (Knott et al. 1998), a high number of loci/QTLs associated with each trait was found. In other studies, however, the resource population was based on crossing two parental lines that both were previously selected for high BWT (commercial broiler lines). Despite the very high number of genetic markers that were used and the large population size, the number of QTLs that were detected was very limited (van Kaam et al. 1999a,b). Many lines and breeds are available in chickens (Pisenti et al. 1999), each with their unique characteristics, making it feasible to develop a cross expressing maximum genetic variation for the traits of interest.

Effective Gene Number

The majority of techniques in animal breeding are based on phenotypic selection. Estimating the number of genes contributing to the variance of quantitative characters within and between populations is essential to studying the mechanisms of heredity and breeding. A method of estimating the number of loci contributing to a quantitative trait based on phenotypic data was proposed by Wright (described in Castle 1921). The method makes use of inbred line means and phenotypic variances of their F_1, F_2, and backcrosses. Wright (1968) reviews the basic concept and limitations. He assumed additivity, that all loci are unlinked and have an equal contribution, and that positive additive alleles are fixed in one parental line and negative additive alleles in the other. Failure to meet these assumptions biases the estimator downward (Lande 1981). Wright's equation is therefore often referred to as providing the "minimum number of effective loci." Falconer and Mackay (1996), Park (1977a,b), and Zeng et al. (1990) extended the equation to include a cross between divergently selected lines, and Lande (1981) to include a cross between outbred populations. Wright (1968) and Ollivier and Janss (1993) adjusted the basic formula for dominance effects.

Heterosis in the Chicken

Application of heterosis to agricultural production is widely used. Commercial livestock are generally produced by crossing breeds, strains, or lines. In the broiler industry, by using three- or four-way crosses of the breeding stocks to produce the commercial product, breeders control the release of primary lines (pure stocks) and take advantage of interactions between genes (Fairfull 1990, van Tijen 1977). Because of these interactions, the performance of the line crosses is often better than their midparental values—heterosis. However, the physiologic and genetic bases of heterosis are not entirely understood (Griffing 1990).

Objectives

This study documents the establishment of unique resource populations to study growth, composition, and fitness traits in chickens. Details of the average growth and internal organ weights of chickens from a contemporary outbred meat-type line are compared to those of two inbred lines, unselected for growth traits, and their F_2 crosses. The inheritance characteristics of these traits are examined and an estimate of the number of genes contributing to the genetic differences between the lines is made. This information establishes a base for future studies to utilize these genetic crosses for QTL identification.

Materials and Methods

Experimental Animals

The Iowa Growth and Composition Resource Population (IGCRP) was established by crossing two modern broiler sires from a primary breeder's broiler male line with 5–10 dams each from two highly inbred lines. The inbred lines were developed from more than 50 generations of full-sib matings. One inbred line was originally composed of U.S. commercial Leghorn layers (line Ghs6.6), and the second line is the Fayoumi (line M15.2), a native line that was imported from Egypt. These lines are more than 99% inbred (Zhou and Lamont 1999). The F_2 offspring evaluated in this study were all grand-progeny of a single broiler sire founder, with the other sires grand-progeny being maintained for line propagation. About 280 F_1 chicks from the one sire were produced in four hatches. Two F_1 male offspring of the same sire, one from each genetic cross (F_1 Leghorn and F_1 Fayoumi), were randomly selected and each mated with 20 half-sib F_1 females (from the same genetic cross), producing about 720 F_2 offspring in three hatches. During each generation, four broiler sires were mated with

Table 1. Trait measurements and abbreviations

Trait, units	Abbreviation[a]
Body weight, g	BWT
Body weight gain, g	WTG
Breast muscle weight, g	BRT
Abdominal fat weight, g	FAT
Drumstick weight, g	DRM
Heart weight, g	HRT
Liver weight, g	LVR
Spleen weight, g	SPL
Shank length, cm	SHL
Shank weight, g	SHW
Shank weight to length ratio, g/cm	SHR

[a] % sign is added when calculated as a percentage of BWT at 8 weeks of age (relative weight).

three to five unrelated broiler females, and one inbred male from each of the two inbred lines was mated with three to five full-sib inbred females of the same line.

All hatched chicks (F_1, F_2, inbred Leghorn, inbred Fayoumi, and broilers) were wing-banded for individual pedigree identification. Contemporary stocks (broilers, inbreds, and crosses) were grown in a single house, but separated by screen wall dividers to prevent undue stress and competition as a result of the dramatic differences in body size of the different genetic stocks. Birds were grown under standard management conditions from hatch to 8 weeks of age and had ad libitum access to water and feed.

Phenotypic Measurements

Body weight (BWT) was recorded for all F_2 ($n = 720$), contemporary pure inbred (Leghorn, $n = 50$; Fayoumi, $n = 50$), and broiler birds ($n = 50$) at hatch and in 2-week intervals up to 8 weeks of age. Daily weight gain (WTG) was calculated for each interval as the average daily change in BWT between two consecutive BWT measurements. At 8 weeks of age, all F_2, contemporary pure inbred, and broiler birds were euthanized by cervical dislocation and body composition measurements were recorded. These measurements included breast muscle weight (BRT) (pectoralis major and pectoralis minor), drumstick weight (DRM) (bone and muscle), shank weight (SHW) and shank length (SHL), abdominal fat weight (FAT), spleen weight (SPL), liver weight (LVR), and heart weight (HRT), and the shank weight to shank length ratio (SHR) was calculated (Table 1). All traits were also expressed as a percentage of body weight at 8 weeks of age. Sex was determined by macroscopic inspection of the gonads.

Statistical Analysis

To account for heterogeneous variances between the different genetic groups, data were subjected to a four-way analysis of variance (ANOVA) using the MIXED procedure (SAS Institute 2000b), with the genetic cross (G) and sex (S) as fixed effects and dam (D) within genetic cross and hatch (H) as random effects, according to the model

$$Y = \mu + G + D(G) + S + H + G \times S + S \times H + e,$$

where Y is the dependent variable, μ is the grand mean, and e is the random error term. To account for heterogeneous variances, both $D(G)$ and e were allowed to have different variances for different genetic crosses. The interactions of hatch by genetic cross or by dams within genetic cross were not included in the model because of the smaller number of pure-line birds that were used in this study and which were obtained in two hatches only. Least-square means for each trait were calculated and compared using the Tukey–Kramer testing procedure (SAS Institute 2000b).

For each trait, heterosis was calculated as the difference between the F_2 least-square mean and the contemporary midparents value of the pure lines:

$$\overline{F2} - \left(\frac{\overline{BR} + \overline{INB}}{2}\right), \quad (1)$$

where $\overline{F2}$ is the F_2 population mean, $\overline{BR}$ is the pure broiler population mean, and $\overline{INB}$ is the pure inbred (Leghorn or Fayoumi) population mean. Heterosis was also expressed as a percentage from the expected midparent pure line values:

$$100 \cdot \left[\left(\frac{2 \cdot \overline{F2}}{\overline{BR} + \overline{INB}}\right) - 1\right]. \quad (2)$$

The significance levels of the heterosis were estimated using the Contrast test (SAS Institute 2000b).

The number of genes contributing to the variance was estimated using methodology developed by Wright (1968) and adjusted to meet the requirements of the present work. Data were transformed using the natural log prior to estimating the gene numbers. The basic formula to evaluate the number of loci (n) contributing to the quantitative trait is

$$n = \frac{(\overline{BR} - \overline{INB})^2}{8\sigma^2_G}, \quad (3)$$

where σ^2_G is the genetic variance resulting from differences in gene frequencies of the parental population.

Because the inbred lines that were used are 99% inbred, the phenotypic variation within the line is essentially environmental variation (σ^2_E). The F_2 phenotypic variation is composed of ($\sigma^2_G + \sigma^2_E$). Hence the genetic variation can be estimated by subtracting the phenotypic variance of the F_2 cross from the phenotypic variance of the contemporary inbred birds:

$$\sigma^2_G = \sigma^2_{F_2} - \sigma^2_{INB}. \quad (4)$$

The phenotypic variance was calculated for each trait and genetic cross by two-way ANOVA including sex and hatch, the first as a fixed effect and the second as a random effect, and their interaction as a random effect using JMP (SAS Institute 2000a). These calculated phenotypic variances included all other effects listed in the model above, but were adjusted for the variance caused by differences between males and females and the different hatches.

If the inbred population is taken as the base, and it is assumed that there is a constant (and equal for all loci) degree of deviation from the expected midparent value (D) measured by

$$D = \frac{\overline{F2} - \overline{INB}}{\overline{BR} - \overline{INB}}, \quad (5)$$

the expected number of genes (N) is

$$N = [1.5 - 2D(1 - D)] \times n \quad (6)$$

(Wright 1968). When the mean of the F_2 is equal to the average of the two parental lines, N will equal n.

Results

All measurements, units, and abbreviations are summarized in Table 1. Significance levels [$P(F)$] are presented in Table 2 for all traits. Sexual dimorphism between males and females was significant for most traits. However, the magnitude of that difference varied between the different genetic crosses, leading to significant sex × genetic cross interactions for most traits (Table 2). Least-square means, maximum and minimum values, and the heterosis levels (based on least-square means) of each genetic cross over sexes are presented in Tables 3–5 for BWT and WTG, body composition, and body composition measures as a percentage of BWT8, respectively. Growth curves and the distribution of individual phenotypic measurements, by population, are illustrated in Figures 1–5.

Table 2. Significance levels [*P*(*F*)] derived from a four-way ANOVA

Trait[a]	Age (weeks)	Cross[b]	Sex	Sex × cross
Absolute weight				
BWT	0	<0.001	NS[c]	NS
	2	<0.001	0.004	0.050
	4	<0.001	0.002	<0.001
	6	<0.001	0.003	<0.001
	8	<0.001	<0.001	<0.001
WTG	0–2	<0.001	0.002	<0.001
	2–4	<0.001	0.002	<0.001
	4–6	<0.001	0.002	<0.001
	6–8	<0.001	0.002	<0.001
BRT	8	<0.001	<0.001	<0.001
DRM	8	<0.001	<0.001	<0.001
FAT	8	<0.001	NS	NS
HRT	8	<0.001	<0.001	<0.001
LVR	8	<0.001	<0.001	<0.001
SPL	8	<0.001	<0.001	<0.001
SHL	8	<0.001	0.002	<0.001
SHW	8	<0.001	<0.001	<0.001
SHR	8	<0.001	<0.001	<0.001
Relative weight[d]				
%BRT	8	<0.001	0.011	<0.001
%DRM	8	<0.001	<0.001	0.004
%FAT	8	<0.001	0.106	0.006
%HRT	8	<0.001	<0.001	0.067
%LVR	8	<0.001	0.050	0.100
%SPL	8	<0.001	<0.001	0.090
%SHL	8	<0.001	<0.001	<0.001
%SHW	8	<0.001	<0.001	<0.001
%SHR	8	<0.001	NS	0.002

[a] See Table 1 for trait abbreviations and measurement units.

[b] Genetic cross: broiler, Fayoumi, Leghorn, and their F_2 crosses.

[c] $P > .20$.

[d] Relative weight = 100(organ weight/body weight at 8 weeks).

Table 3. Body weight (BWT), daily weight gain (WTG), data range (minimum and maximum), and heterosis of the five different genetic populations at different ages

Trait[a]	Age (weeks)	Population	Mean	Data range		Heterosis		
				Minimum	Maximum	Absolute[b]	Percentage[c]	*P*(*t*)[d]
BWT	0	Broiler	37[a]	32.3	46.9			
		Leghorn	26[c]	20.3	30.4			
		Fayoumi	28[c]	24.1	30.5			
		F_2 Leghorn	37[a]	31.2	42.5	5.5	17.5	<.001
		F_2 Fayoumi	34[b]	27.4	40.0	1.5	4.6	.016
BWT	2	Broiler	328[a]	172	416			
		Leghorn	80[d]	67	106			
		Fayoumi	80[d]	53	109			
		F_2 Leghorn	206[b]	128	282	2.0	1.0	.346
		F_2 Fayoumi	200[c]	138	284	−4.0	−2.0	.101
BWT	4	Broiler	1091[a]	758	1367			
		Leghorn	187[c]	157	249			
		Fayoumi	182[c]	113	356			
		F_2 Leghorn	604[b]	382	907	−35.0	−5.5	<.001
		F_2 Fayoumi	593[b]	387	923	−43.5	−6.8	<.001
BWT	6	Broiler	2047[a]	1431	2583			
		Leghorn	340[c]	252	397			
		Fayoumi	338[c]	215	443			
		F_2 Leghorn	1024[b]	595	1509	−169.5	−14.2	<.001
		F_2 Fayoumi	1010[b]	681	1545	−182.5	−15.3	<.001
BWT	8	Broiler	3214[a]	2466	3987			
		Leghorn	515[c]	407	661			
		Fayoumi	492[c]	318	704			
		F_2 Leghorn	1575[b]	998	2311	−289.5	−15.5	<.001
		F_2 Fayoumi	1545[b]	1013	2316	−308.0	−16.6	<.001
WTG	0–2	Broiler	20.7[a]	9.9	26.9			
		Leghorn	3.8[c]	2.9	5.7			
		Fayoumi	3.7[c]	1.7	5.9			
		F_2 Leghorn	12.1[b]	6.1	17.2	−0.2	−1.2	.362
		F_2 Fayoumi	11.8[b]	7.4	17.7	−0.4	−3.3	.020
WTG	2–4	Broiler	54.3[a]	38.9	70.1			
		Leghorn	7.7[c]	5.9	10.9			
		Fayoumi	7.3[c]	4.3	11.6			
		F_2 Leghorn	28.5[b]	15.7	46.6	−2.5	−8.1	<.001
		F_2 Fayoumi	28.2[b]	16.5	45.6	−2.6	−8.4	<.001
WTG	4–6	Broiler	67.4[a]	43.4	92.0			
		Leghorn	10.9[c]	6.8	10.9			
		Fayoumi	11.0[c]	4.0	12.4			
		F_2 Leghorn	30.0[b]	11.9	53.8	−9.2	−23.4	<.001
		F_2 Fayoumi	29.7[b]	5.4	48.6	−9.5	−24.2	<.001
WTG	6–8	Broiler	84.7[a]	52.2	115.1			
		Leghorn	12.8[c]	4.2	17.9			
		Fayoumi	10.9[d]	7.5	17.5			
		F_2 Leghorn	39.1[b]	20.8	59.3	−9.7	−19.8	<.001
		F_2 Fayoumi	38.4[b]	17.7	60.8	−9.4	−19.7	<.001

[a] See Table 1 for trait abbreviations and measurement units.

[b] Deviation (in measurement units) of the F_2 mean from the mid value of their founder lines.

[c] Deviation (%) calculated as a percentage from the mid value of their founder lines.

[d] Significance levels of contrasting F_2 mean to the mid value of their founder lines.

[a,b,c,d] Means with no common superscripts differ significantly ($P < .05$).

Body Weight and Gain Means

In general, the populations differed from each other in BWT and WTG at all ages, with the pure broiler chicks being heavier than the two inbred lines, which did not differ from each other, and the F_2 crosses being intermediate with similar means (Table 3). Because of the smaller egg size of the inbred dams (data not shown), the inbred birds hatched with significantly lower BWT0 than the F_2 and broiler populations, which had similar means. This led to a significant positive heterosis of 17.5 and 4.6% for the F_2 Leghorn and F_2 Fayoumi, respectively (Table 3). Birds of all genetic crosses increased their WTG over time; however, this increase was greater for the broiler line, lower for the inbred lines, and intermediate for the F_2 crosses (Figure 1B). This led to an increase in the growth advantage of the broiler population in BWT over the other crosses with time and enlarged the gap between the observed F_2 values and their expected means (based on the mean of the two founder lines), causing a significant negative heterosis estimate. At 8 weeks of age, the broiler BWT was more than sixfold higher than the inbred lines and twofold higher than the F_2 crosses. The two F_2 crosses did not differ significantly and had −16% average heterosis (Table 3).

Body Composition Means

The absolute body composition measurements are summarized in Table 4. As expected, the body composition measurements are highly associated with body mass; therefore all measurements were calculated as a percentage of the bird's live BWT on the day of euthanasia (Table 5 and Figures 2–5).

As expected from their selection history, pure broiler chickens were superior to the F_2 crosses and the inbred lines for %BRT and %DRM. However, for internal organs and shank measurements, significantly lower proportional values were found for the broiler population relative to the other populations. The broiler population had the lowest proportion of HRT, LVR, SPL, SHW, SHL, and SHR (Table 5).

For all relative body composition measurements, except %FAT, the F_2 crosses had lower means than their expected value based on the mean of their contemporary founder lines, leading to a significant negative heterosis (Table 5). Fat deposition, represented by the percentage of abdominal fat, was higher in the broiler population than in the inbred lines.

Table 4. Means and data range (minimum and maximum) of body composition measurements of the five different genetic populations at 8 weeks of age

Trait[a]	Population	Mean	Data range		Heterosis		
			Minimum	Maximum	Absolute[b]	Percentage[c]	$P(t)$[d]
BRT	Broiler	524.4[a]	394	678			
	Leghorn	49.3[d]	5.9	66			
	Fayoumi	43.3[d]	5.3	68			
	F_2 Leghorn	200.0[b]	111	314	−86.9	−30.3	<.001
	F_2 Fayoumi	191.5[c]	119	318	−92.4	−32.5	<.001
DRM	Broiler	155.9[a]	115	199			
	Leghorn	22.1[c]	17	28			
	Fayoumi	21.1[c]	14	28			
	F_2 Leghorn	69.3[b]	42	111	−19.7	−22.1	<.001
	F_2 Fayoumi	68.0[b]	40	101	−20.5	−23.2	<.001
FAT	Broiler	63.25[a]	33.9	91.5			
	Leghorn	5.64[c]	0.0	11.7			
	Fayoumi	6.13[c]	0.0	10.3			
	F_2 Leghorn	51.38[b]	15.3	104.1	16.9	49.2	<.001
	F_2 Fayoumi	49.77[b]	8.4	96.8	15.1	43.5	<.001
HRT	Broiler	12.22[a]	8.4	17.7			
	Leghorn	2.77[e]	2.2	4.3			
	Fayoumi	3.19[d]	2.5	4.2			
	F_2 Leghorn	6.31[c]	3.6	10.7	−1.2	−15.8	<.001
	F_2 Fayoumi	6.70[b]	3.5	11.5	−1.0	−13.0	<.001
LVR	Broiler	69.3[a]	47.4	106.2			
	Leghorn	13.4[d]	10.9	16.4			
	Fayoumi	16.9[c]	12.3	22.9			
	F_2 Leghorn	36.5[b]	20.2	67.3	−4.9	−11.7	.002
	F_2 Fayoumi	38.4[b]	16.3	63.5	−4.7	−10.9	.003
SPL	Broiler	3.22[a]	2.2	4.4			
	Leghorn	1.18[d]	0.8	1.6			
	Fayoumi	1.41[c]	0.7	2.2			
	F_2 Leghorn	2.40[b]	1.2	4.4	0.2	9.1	.003
	F_2 Fayoumi	2.53[b]	1.1	4.3	0.2	9.3	.008
SHL	Broiler	9.85[a]	8.9	11.0			
	Leghorn	6.60[d]	6.0	7.2			
	Fayoumi	6.21[e]	5.4	7.1			
	F_2 Leghorn	8.78[b]	7.4	10.5	0.6	6.7	<.001
	F_2 Fayoumi	8.56[c]	7.4	9.9	0.5	6.6	<.001
SHW	Broiler	59.71[a]	44.1	80.5			
	Leghorn	11.36[d]	8.8	14.1			
	Fayoumi	9.77[d]	6.3	13.2			
	F_2 Leghorn	31.09[b]	18.0	54.1	−4.4	−12.5	<.001
	F_2 Fayoumi	28.47[c]	16.2	47.4	−6.3	−18.0	<.001
SHR	Broiler	6.00[a]	4.79	7.64			
	Leghorn	1.72[d]	1.42	1.99			
	Fayoumi	1.56[d]	1.13	1.89			
	F_2 Leghorn	3.52[b]	2.26	5.28	−0.3	−8.8	<.001
	F_2 Fayoumi	3.30[c]	2.19	4.84	−0.5	−12.7	<.001

[a] See Table 1 for trait abbreviations and measurement units.

[b] Deviation (in measurement units) of the F_2 mean from the mid value of their founder lines.

[c] Deviation (%) calculated as a percentage from the mid value of their founder lines.

[d] Significance levels of contrasting F_2 mean to the mid value of their founder lines.

[a,b,c,d,e] Means with no common superscripts differ significantly ($P < .05$).

Surprisingly, the highest %FAT was found in the two F_2 populations, yielding a very high level of heterosis (Table 5).

Variance

The F_2 populations formed from crossing two genetically and phenotypically distant lines (meat-type chickens and light-bodied inbred lines) were expected to express a high level of variance. Therefore the data distribution of the F_2 crosses is expected to cover the entire range of the phenotypic distribution of the two founder lines. However, a single pure-broiler grandsire was used to generate the F_2 population analyzed in this study, and thus the total genetic variation within the outbred population (broilers) might not be completely represented in the F_2 crosses.

In general, the phenotypic variances within the F_2 crosses, calculated based on the log-transformed data, were higher than the phenotypic variances within the inbred lines and the broiler population for all traits, except BWT0 (Table 6). Although the phenotypic distributions of %DRM, %HRT, %LVR, and %SHW confirmed the original expectation that the F_2 distribution covers the entire range of phenotypic distributions for the parental lines, the distributions of BWT8 and %SHL were much smaller than expected (Figures 2A and 4B, respectively). The phenotypic data for %BRT and %SHR for the F_2 birds partially overlapped that of their parental lines (Figures 2B and 4C, respectively). In the instance of %FAT, there was a clear overdominance situation with a very wide phenotypic distribution in the F_2 (Figure 5).

Differences Between the Two Genetic Crosses

Despite the similar BWT of the two inbred lines, they differed significantly for many of their characteristics (Tables 3–5). In general, these differences were inherited in their F_2 crosses. Similar to the two inbred lines, which did not differ significantly from each other, their F_2 crosses had similar means for BWT, except for BWT at early ages (0 and 2 weeks of age) (Table 3). For body composition, however, the relationships of data between lines and crosses were not consistent. The two inbred lines had similar means for some traits and differed significantly for others. The relative differences between the two F_2 crosses were not always in agreement with the relative differences between the two pure inbred lines (Tables 4 and 5).

Effective Gene Number

Based on equation (6), the effective number of genes (N) was estimated for each one of the two genetic backgrounds (Fayoumi and Leghorn). Phenotypic variances and gene numbers are summarized in Table 6. Because of the higher growth rate of the broiler stock compared to the inbred lines (Figure 1A), the differences between the pure broilers and the inbred birds in BWT increased with age. After a sharp increase in the phenotypic variance from hatch to 2 weeks of age in all five lines and crosses, the phenotypic variation within the two inbred lines decreased constantly, whereas the phenotypic variation increased within the two F_2 crosses and increased steadily from hatch to 4 weeks of age within the broiler population, and decreased thereafter (Table 6). Because of the very large differences in BWT between the pure parental lines at all ages, and the large difference in the phenotypic variance between the F_2 crosses and the inbred lines, this led to a high estimated gene number for BWT at all ages except hatch date (Table 6). At 8 weeks of age the estimated gene numbers for BWT were 29 and 56 for the Leghorn and Fayoumi crosses, respectively (Table 6). The estimated gene numbers for the different relative organ weights were much lower, and varied from almost 0 to 43 (Table 6).

Table 5. Means and data range (minimum and maximum) of body composition measurements calculated as a percentage of 8-week body weight

Trait[a]	Population	Mean	Data range		Heterosis		
			Minimum	Maximum	Absolute[b]	Percentage[c]	$P(t)$[d]
%BRT	Broiler	16.3[a]	15.04	18.85			
	Leghorn	9.9[d]	9.30	10.83			
	Fayoumi	9.2[e]	8.33	10.18			
	F_2 Leghorn	12.7[b]	10.25	16.01	−0.40	−3.1	.004
	F_2 Fayoumi	12.4[c]	10.04	15.55	−0.35	−2.7	.013
%DRM	Broiler	4.86[a]	4.12	5.31			
	Leghorn	4.14[c]	3.73	4.40			
	Fayoumi	4.14[c]	3.63	4.40			
	F_2 Leghorn	4.38[b]	3.55	5.40	−0.12	−2.7	<.001
	F_2 Fayoumi	4.40[b]	3.50	5.30	−0.10	−2.2	.004
%FAT	Broiler	2.00[b]	1.26	3.05			
	Leghorn	1.07[c]	0.00	2.07			
	Fayoumi	1.22[c]	0.00	1.81			
	F_2 Leghorn	3.26[a]	1.21	6.23	1.73	112.4	<.001
	F_2 Fayoumi	3.25[a]	0.54	6.37	1.64	101.9	<.001
%HRT	Broiler	0.379[d]	0.275	0.517			
	Leghorn	0.513[b]	0.406	0.719			
	Fayoumi	0.621[a]	0.502	0.736			
	F_2 Leghorn	0.398[d]	0.307	0.634	−0.05	−10.8	<.001
	F_2 Fayoumi	0.430[c]	0.305	0.749	−0.07	−14.0	<.001
%LVR	Broiler	2.20[c]	1.60	3.09			
	Leghorn	2.55[b]	2.09	3.20			
	Fayoumi	3.28[a]	2.59	4.22			
	F_2 Leghorn	2.31[c]	1.63	4.05	−0.06	−2.7	.181
	F_2 Fayoumi	2.49[b]	1.50	3.93	−0.25	−9.1	<.001
%SPL	Broiler	0.103[d]	0.063	0.152			
	Leghorn	0.225[b]	0.180	0.269			
	Fayoumi	0.282[a]	0.220	0.356			
	F_2 Leghorn	0.154[c]	0.085	0.279	−0.01	−6.1	.031
	F_2 Fayoumi	0.164[c]	0.088	0.300	−0.03	−14.8	<.001
%SHL	Broiler	0.32[c]	0.26	0.37			
	Leghorn	1.22[a]	1.07	1.57			
	Fayoumi	1.21[a]	0.99	1.42			
	F_2 Leghorn	0.57[b]	0.38	0.79	−0.20	−26.0	<.001
	F_2 Fayoumi	0.57[b]	0.41	0.78	−0.20	−25.5	<.001
%SHW	Broiler	1.86[c]	1.52	2.22			
	Leghorn	2.11[a]	1.85	2.27			
	Fayoumi	1.91[bc]	1.71	2.07			
	F_2 Leghorn	1.97[b]	1.48	2.62	−0.01	−0.8	.136
	F_2 Fayoumi	1.84[c]	1.40	2.52	−0.04	−2.4	.005
%SHR	Broiler	0.189[e]	0.16	0.22			
	Leghorn	0.320[a]	0.29	0.35			
	Fayoumi	0.308[b]	0.27	0.36			
	F_2 Leghorn	0.224[c]	0.17	0.29	−0.03	−12.0	<.001
	F_2 Fayoumi	0.214[d]	0.17	0.27	−0.03	−13.9	<.001

[a] See Table 1 for trait abbreviations and measurement units.

[b] Deviation (in measurement units) of the F_2 mean from the mid value of their founder lines.

[c] Deviation (%) calculated as a percentage from the mid value of their founder lines.

[d] Significance levels of contrasting F_2 mean to the mid value of their founder lines.

[a,b,c,d,e] Means with no common superscripts differ significantly ($P < .05$).

Discussion

Variance in the F_2 Cross

To maximize the number of progeny tested within family and line, and because the total number of birds that can be accurately tested is limited, one broiler grandsire was used to generate the entire population for the present study. Therefore the phenotypic distributions of the different traits might be affected by the genetic contribution of this grandsire. Pure broiler contemporaries of the F_1 that were produced by crossing the same single grandsire to random broiler females, however, did not differ in mean or variance of tested traits from the larger contemporary pure broiler population produced using other broiler sires. Thus the selected broiler grandsire well represented the entire broiler population. The F_2 populations were generated by crossing one F_1 sire for each genetic cross (Fayoumi and Leghorn) with about 20 half-sib females representing all families within the line.

Body Weight

In theory, selection for traits with moderate to high heritabilities would narrow the genetic variation, and a close-to-zero value or equilibrium (in case of dominance) of the genetic variance would be quickly approached. The reduction in the genetic variation would lead to a dramatic reduction in the heritability coefficient and therefore response to selection would slowly diminish, or the population would reach a selection limit (Falconer and Mackay 1996). After 84 generations of selection for body weight in mice, Bünger and Herrendörfer (1994) found that realized heritability declined from 0.361 to 0.0004. Surprisingly, despite intense selection programs, heritability for BWT in broiler populations has not dramatically changed during the last few decades and is found to vary from 0.4 to 0.6 (Chambers 1990). Commercial poultry populations are characterized by large effective population size, whereas laboratory animals, such as mice, have low effective population size. Thus the dramatic reduction in heritability (genetic variation) reported in mice (Bünger and Herrendörfer 1994) may be due to inbreeding and genetic drift rather than due to selection. Because of stringent genetic selection, BWT of modern meat-type chickens at marketing age (40–42 days) is four- to fivefold its level 50 years ago (Havenstein et al. 1994b). No domestic species other than chickens exhibits such a range of body size, perhaps with the exception of dogs, for which the genetic selection period has been much longer than for chickens. Moreover, the phenotypic distributions for BWT of the contemporary meat-type chicken population and its ancestors 50 years ago do not overlap, indicating that intensive selection accomplished more than simply increasing the frequency of the desired genotype, but rather produced "new" genotypes with levels of performance much beyond their ancestors. The increase in genetic variance of quantitative traits from the accumulation of new mutations has been known for some time (Falconer and Mackay 1996; Hill 2000, Notter 1999). After 50 generations of divergent selection for 6-weeks body weight in a highly inbred mouse line, Keightley (1998) calculated an increase of 0.23–0.57% in body weight heritability per generation from new mutations. However, it is unlikely that these "new" genotypes are only because of random mutations that took place simultaneously in stocks of all commercial genetic programs. It is likely that selection increased the frequency of new combinations of rare alleles and genes, which gave rise to the higher-performing genotypes (resulting from the sum of many genes with small additive effects and/or epistatic effects). This combinatorial effect may explain why the phenotypic variation found among F_2 birds for BWT was less than expected. Theoretically an F_2 cross between

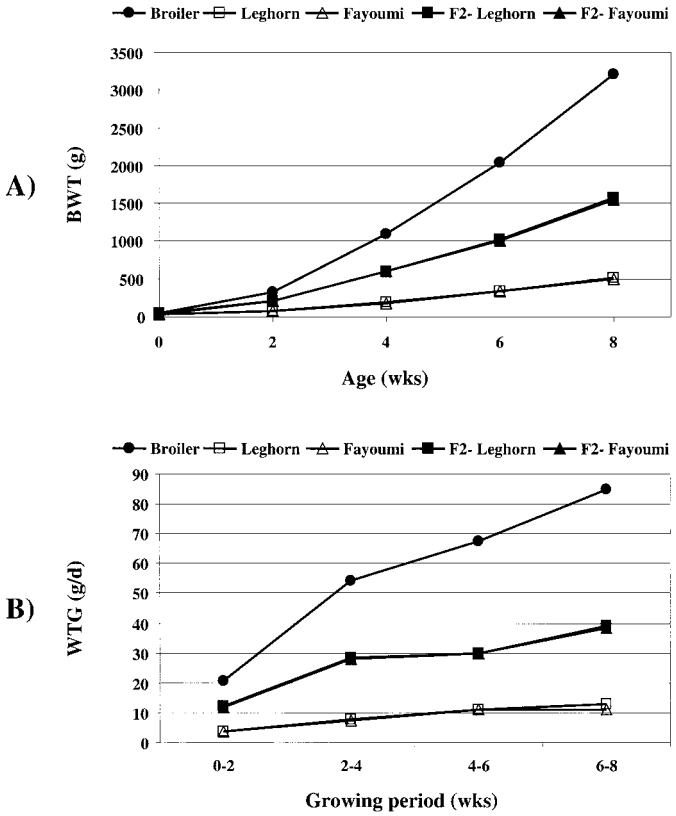

Figure 1. **(A)** Means of cumulative body weight (BWT) and **(B)** daily weight gain (WTG) of outbreds (broilers), inbreds (Leghorn and Fayoumi), and their F_2 crosses at different ages.

two genetically distant lines is expected to reveal high genetic variation, causing a wide phenotypic distribution that completely overlaps with the phenotypic values of the two founder lines. However, if a large number of loci are involved in determining the phenotype, a very large number of progeny are required to have individual representatives of the entire range of the genetic variation. The probability of a specific combination of alleles can be calculated by 0.5^{2L}, where L is the number of unlinked loci affecting the trait. Therefore more than 1000 animals must be produced to generate a single animal with the specific most desirable combination of alleles derived from only five loci. These combinations of alleles, a result of more than 50 generations of commercial selection for body weight, cannot be restored in the numbers measured in the F_2 cross, resulting in the limited distribution as it was measured in this experiment. If all loci affecting BWT are linked, some F_2 individuals (genotypes) with a similar performance level as their parental lines would be expected, because combinations of different alleles, optimized for high growth through long-term selection, would be inherited as one unit. The data therefore provide evidence that most genes for growth are not closely linked to each other. The high number of unlinked loci affecting BWT make it difficult to utilize MAS to improve broiler growth. Moreover, in the present study, only inbred females were used to produce the F_1 cross, and thus the mitochondria are contributed primarily from the inbred birds. This lack of broiler mitochondrial contribution to the F_2 might result in a decreased distribution of highly energy-dependent traits, causing a decrease in F_2 trait distribution.

Shank Length

Shank length measurement in poultry is characterized by high heritability (Abdellatif 1989; Buss 1990; Rizzi et al. 1994). Shanks that are long relative to their weight are considered a source of leg problems in heavy-bodied chickens. Therefore meat-type birds have been successfully selected for proportionally shorter shanks for many generations. Indeed, the lowest mean for %SHL in the present study was found among the pure broiler population (Table 5 and Figure 4B). Direct selection to reduce shank length in broilers has dramatically altered the %SHL, despite its high genetic correlation with BWT (Chambers 1990). The large differences between the two parental lines and the selection history of this trait suggest that many genes contribute to shank length. These allelic combinations cannot be restored in the F_2 cross (similar to the situation for BWT), leading to the dramatic separation in the phenotypic values between the meat-type chickens, inbreds, and their F_2 crosses.

Only two traits measured on this population (BWT and %SHL) can be tested on live birds. Therefore such traits can be efficiently measured on breeding flocks and thus direct selection for them can be strongly applied. It is noteworthy that in both instances the phenotypic distribution of the F_2 populations did not overlap at all with their founder lines (Figures 2A and 4B).

Muscling

The breast muscle is the most economically valuable in meat-type chickens. However, because of the complexity of obtaining phenotypic data, selection to improve breast muscle percentage is lagging behind selection for BWT. Despite the small overlap between the phenotypic distribution of the F_2 populations and the two founder lines, none of the F_2 birds reached the yield level of the highest meat-type chickens or the lowest inbred birds (Figure 2B), indicating that the selection for breast meat yield followed a pattern similar to that of BWT. Conversely, for %DRM, a measurement combining muscle and bone of the upper leg, but for which breeders have not directly selected, the F_2 crosses demonstrate a very high phenotypic variation that covers the entire range of phenotypic variance of the two founder lines (Figure 2C).

Internal Organs

Meat-type chickens have not been directly selected to improve internal organs. Therefore a high level of genetic variation within the broiler population is retained. Thus, as expected, the F_2 cross also revealed a very high level of genetic variation, covering the entire range of the phenotypic distributions of the two founder lines for %HRT and %LVR. However, the F_2 distribution of %SPL only partially covered the phenotypic values of the two founder lines, probably as a result of natural selection because of the involvement of the spleen in the immune system.

Abdominal Fat

Excessive fat has been recognized as an undesirable correlate of selection for rapid growth and high live BWT. The genetic

correlation between abdominal fat and other lipid deposits or total carcass lipids is very high (0.6–0.9) (Chambers 1990). Heritabilities estimated for abdominal fat are very high (0.4–0.8) (Chambers 1990; Le Bihan-Duval et al. 1998) and thus direct response to divergent selection for abdominal fat has been dramatic. Cahaner (1988) found a twofold difference between two lines divergently selected for abdominal fat after only three generations of selection. Both active selection against abdominal fat and for improvement in feed efficiency have reduced the fat content in meat-type chickens. The F_2 cross of the present study revealed a surprisingly high level of heterosis (107%, average of the two crosses) and genetic variation in %FAT (Figure 5). Previous studies that included an F_1 cross between Giant Jungle Fowl and broiler breeder (Wall and Anthony 1995) or an F_1 cross between two lines divergently selected for 27 generations for BWT (Katanbaf et al. 1988b) showed 32 and −22% heterosis for %FAT, respectively, despite the higher differences between the parental lines in %FAT than in the present study. However, the overdominance inheritance pattern measured in the present study is likely because of specific combinations of alleles contributed by the light-bodied inbred and heavy-bodied broiler chickens. Unlike internal organs, which may be restricted by association with each other in size and physiological activity, abdominal fat is a relatively size-unrestricted tissue that can be reduced or expanded dramatically without much influence on other physiological mechanisms.

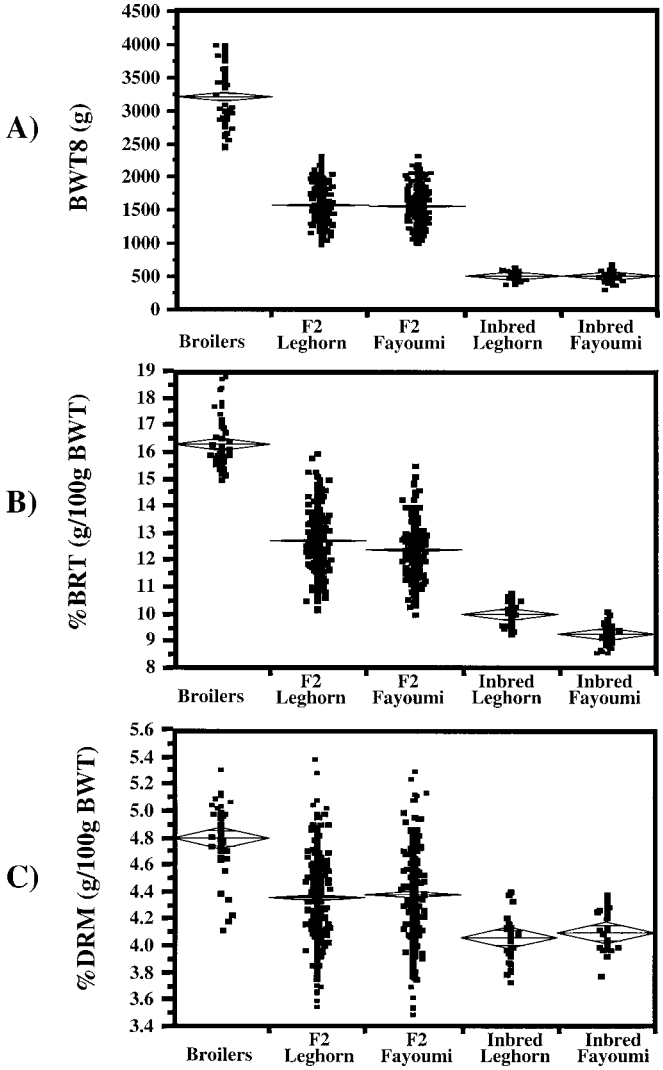

Figure 2. Means and distributions of **(A)** body weight at 8 weeks of age (BWT8), **(B)** breast muscle (%BRT), and **(C)** drumstick (%DRM) as a percentage of BWT at 8 weeks of age of outbreds (broilers), inbreds (Leghorn and Fayoumi), and their F_2 crosses.

Effective Gene Number

Equation (6) can be precise under several assumptions discussed by Wright (1968) that, in practice, are very difficult to satisfy. The estimates of the number of loci involved in determining the genotype are therefore only approximate ones. Thus we will only discuss the order of magnitude of the estimated number of loci and not fine numerical comparisons.

The two F_2 genetic crosses (with Leghorn and Fayoumi), which can be considered as two unrelated genetic crosses, revealed similar estimated gene numbers. As seen from equation (3), the number of genes and the genetic variation are inversely related. With a given distance between the two parental lines, if the original genetic variation is high, then fewer genes are contributing to the difference between the two lines, and if there is very low genetic variation, then there must be a higher number of genes involved. In general, the estimated gene numbers are in agreement with the previous assumptions that were based on the selection history of the different traits in meat-type chickens. The estimated gene number was very high for BWT and %SHL, moderate for %BRT, %HRT, %SPL, and %SHR, and very low for %DRM, %LVR, and %SHW, which were consistent between the two crosses. For most of the traits, the difference in the estimated gene number calculated based on equation (3) or on equation (6) was minimal. However, because of the large deviation of the F_2 populations from the expected midparent values for %FAT (Figure 5), the estimated gene numbers were 4 and 1 for Leghorn and Fayoumi, respectively, based on equation (3), and 21 and 4 according to equation (6). As expected, for all traits except BWT0, the phenotypic variance within the F_2 crosses was higher than their ancestor lines (Table 6).

The mean differences between the parental lines (broilers versus Fayoumi and Leghorn) for internal organs were much lower than for BWT. Thus it is easier for environmental effects to cause wider distributions of the different populations and to cover the entire range of data, regardless of the number of genes involved. However, the results do not agree with that assumption, proving that the different distributions of data are not because of different environmental effects, but because of different gene numbers.

Fitness and Growth

The present study clearly demonstrates the advantage of the broiler population in BWT, growth, and meat yield over the two

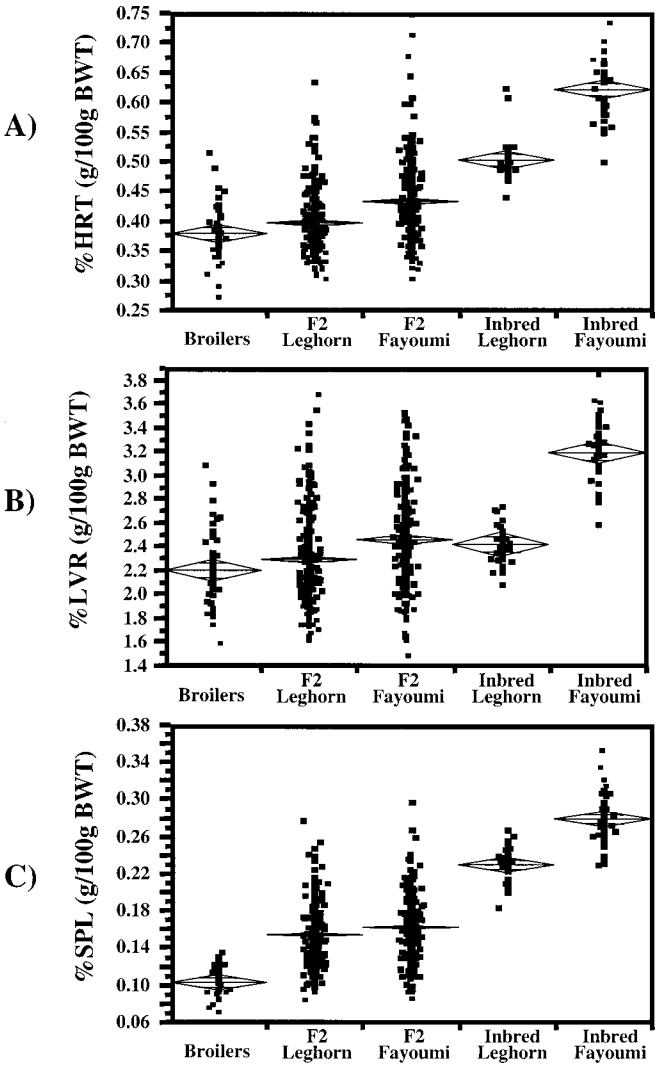

Figure 3. Means and distributions of **(A)** heart (%HRT), **(B)** liver (%LVR), and **(C)** spleen (%SPL) of outbreds (broilers), inbreds (Leghorn and Fayoumi), and their F_2 crosses as a percentage of BWT at 8 weeks of age.

inbred lines. This advantage is because of the rapid genetic improvements resulting from the use of intense selection for these traits in broilers. Despite the genetic correlation between BWT and internal organs that led to improvement in internal organ absolute weight (Table 4), as meat-type chickens were intensively selected for high growth rate, the relative weight of their supporting organs was reduced. Broilers had the lowest %HRT, %LVR, and %SPL (Figure 3). Apparently as a result of rapid genetic improvements through the use of intense selection for growth and meat yield, there has been a reduction in the relative weight of the internal organs needed to support all physiological mechanisms of the increased body mass. This deviation from biological homeostasis, as measured by organ proportions, may have led to the dramatic increase in physiological disorders, such as ascites, sudden death syndrome, heat-related growth depression, and leg problems, as well as the reduction in overall immunocompetency, seen in recent years (Deeb and Cahaner 2001a,b, 2002; Siegel and Dunnington 1997).

Selection for Growth and Fitness

Because of the unfavorable association between fitness and growth, it is essential to detect linkages between DNA markers and QTL associated with traditional selection traits as well as fitness traits to improve animals simultaneously in both categories of traits. The ability to identify associations between markers and traits of economic interest can be considerably improved if the genetic distance between the two founder lines is maximized. The enormous difference in body weight, growth, meat yield, internal organs, and skeletal measurements detected between the broiler population and the inbred lines and the high genetic variation within the F_2 crosses demonstrate the highly informative nature of this population as a resource population for marker-QTL searches. A similar population design has been used to generate the internationally used East Lansing mapping reference population by crossing a Red Jungle Fowl line to highly inbred White Leghorn females (Crittenden et al. 1993).

Gene × Genetic Cross Interaction

Despite the similar body mass values of the two inbred lines, they differ for most of their other phenotypic measurements (Figures 2–5). These differences between the two inbred lines may reflect differences in their origin. The Leghorn birds were sampled from the commercial U.S. layer population, whereas the Fayoumi birds were sampled from a native chicken population from Egypt. Therefore they represent two very different genetic pools. As expected, for most of the traits the mean differences between the two F_2 populations were half of the original differences between the two inbred lines. However, for %LVR and %SPL, the differences between the two F_2 stocks were half their expected values. This suggests that, in this instance, alleles contributed from the meat-type chickens and the inbred birds strongly interact to determine the F_2 level. Moreover, the apparently additive effects of the broiler and inbred alleles affecting all traits (except %LVR and %SPL) are the average effect of many loci that might interact. Because this interaction is random across all loci, the sum will be equal to zero. The high level of genetic variation and potential gene interactions with the genetic background therefore makes these F_2 populations ideal to locate QTLs affecting a variety of traits and to be able to distinguish between QTLs with general effects across the two genetic backgrounds versus QTLs with background-specific effects.

Heterosis

Heterosis was calculated as the deviation of the F_2 mean from the expected midparent value. This broad definition of heterosis is based on the principle that Hardy–Weinberg equilibrium is attained by a single generation of random mating. However, deviation from the expected heterosis based on a single locus model is expected, because the number of loci involved is high and because epistasis is

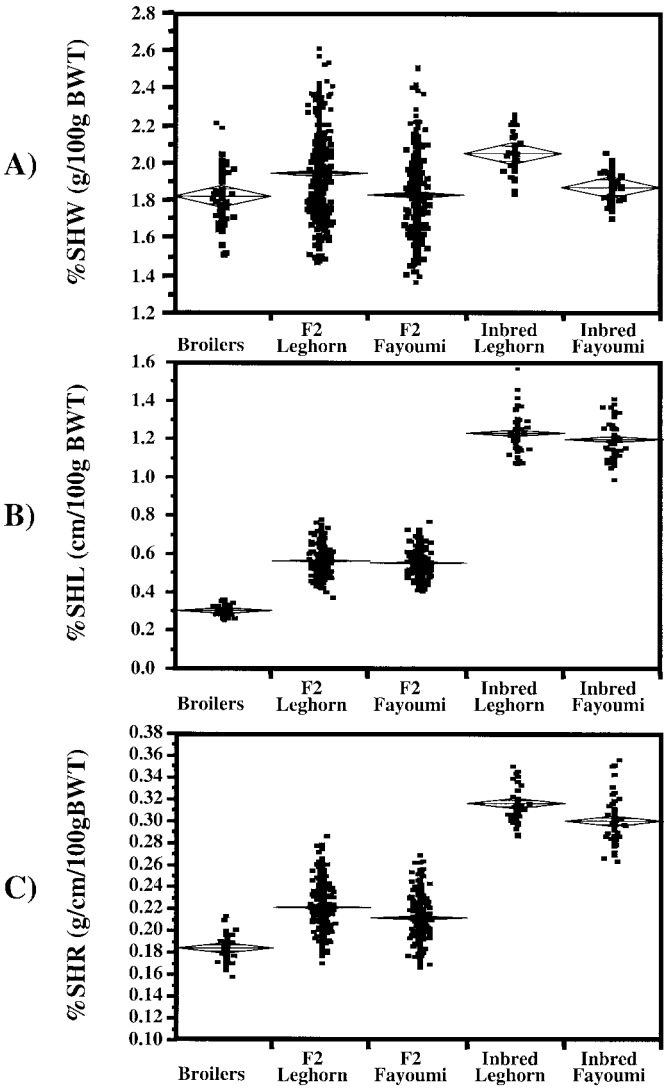

Figure 4. Means and distributions of **(A)** shank weight (%SHW), **(B)** shank length (%SHL), and **(C)** shank ratio (%SHR) of outbreds (broilers), inbreds (Leghorn and Fayoumi), and their F_2 crosses as a percentage of BWT at 8 weeks of age.

involved (Falconer and Mackay 1996). As the birds grow, heterosis values for BWT shift from positive to negative (Table 3). Similar age-dependent heterosis for BWT was also reported by Marks (1995). The changes in heterosis values with time apparently are a result of the different behaviors of the growth curves of the different crosses (Figure 1). The exponential growth curve of the pure broiler population caused an increase in the differences between them and the other populations, leading to significant negative deviation of the F_2 from their expected mid-parent value. Flock et al. (1991) reported an increase in the magnitude of heterosis with time for egg production. He explained the minimal heterosis at the peak of production as a result of the physiological limit of the F_1 to exceed one normal egg per day. BWT measurements were also made in the F_1 population (data not shown). For the F_1 crosses, however, no heterosis was found for BWT at 4, 6, or 8 weeks of age, indicating that on average over all loci, BWT has no dominance effect. This significant negative heterosis in the F_2, but not in the F_1, suggests that recombination (crossing over) negatively affected the F_2 population mean and further supports the hypothesis that selection for high body mass in modern breeds is primarily effecting changes in specific combinations of many beneficial alleles.

Except for BWT at an early age, heterosis in the F_2 crosses was undesirable for most traits (negative heterosis for BWT and internal organs, and positive heterosis for %FAT). The F_2 average performances were closer to the mean of the low parent in both instances when the low-mean parent was the inbred or the broiler line (except for %FAT). Similar results were reported in a cross between two chicken lines selected for 27 generations for high or low BWT at 56 days of age (Katanbaf et al. 1988b). At 56 days of age, the F_1 cross had negative heterosis for heart, liver, ab-

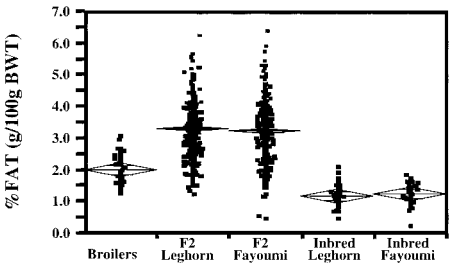

Figure 5. Means and distributions of abdominal fat (%FAT) of outbreds (broilers), inbreds (Leghorn and Fayoumi), and their F_2 crosses as a percentage of BWT at 8 weeks of age.

Table 6. Phenotypic variance in the five populations and the estimated number of genes controlling each trait

	Phenotypic variance					Gene number	
Trait[a]	Broiler	F_2 Leghorn	F_2 Fayoumi	Leghorn	Fayoumi	N(L)[b]	N(F)[b]
BWT0	7.031×10^{-3}	4.124×10^{-3}	4.865×10^{-3}	5.759×10^{-3}	2.741×10^{-3}	ND[c]	6.4
BWT2	9.176×10^{-3}	1.571×10^{-2}	1.403×10^{-2}	9.666×10^{-3}	1.045×10^{-2}	38.0	64.7
BWT4	1.286×10^{-2}	1.582×10^{-2}	1.560×10^{-2}	8.142×10^{-3}	9.963×10^{-3}	44.5	61.8
BWT6	6.931×10^{-3}	1.665×10^{-2}	1.510×10^{-2}	5.065×10^{-3}	1.011×10^{-2}	35.1	80.6
BWT8	4.347×10^{-3}	1.815×10^{-2}	1.552×10^{-2}	4.308×10^{-3}	8.136×10^{-3}	29.1	55.5
%BRT	2.922×10^{-3}	4.254×10^{-3}	5.182×10^{-3}	1.093×10^{-3}	1.926×10^{-3}	9.4	12.4
%DRM	1.690×10^{-3}	3.796×10^{-3}	4.384×10^{-3}	9.040×10^{-4}	1.331×10^{-3}	1.2	1.1
%FAT	3.341×10^{-2}	6.847×10^{-2}	7.784×10^{-2}	6.002×10^{-2}	4.267×10^{-2}	21.3	4.3
%HRT	9.220×10^{-3}	9.615×10^{-3}	1.349×10^{-2}	6.967×10^{-3}	6.032×10^{-3}	4.4	4.6
%LVR	2.081×10^{-2}	2.078×10^{-2}	2.328×10^{-2}	7.181×10^{-3}	5.829×10^{-3}	0.1	1.2
%SPL	2.897×10^{-2}	3.085×10^{-2}	4.022×10^{-2}	5.853×10^{-3}	1.060×10^{-2}	3.3	4.4
%SHW	2.532×10^{-3}	7.579×10^{-3}	7.752×10^{-3}	1.029×10^{-3}	9.710×10^{-4}	0.3	0.0
%SHL	2.768×10^{-3}	1.132×10^{-2}	9.986×10^{-3}	1.323×10^{-3}	4.579×10^{-3}	23.9	42.6
%SHR	2.595×10^{-3}	5.714×10^{-3}	6.708×10^{-3}	2.337×10^{-3}	4.057×10^{-3}	11.1	12.3

[a] See Table 1 for trait abbreviations and measurement units.

[b] N(L) and N(F) are the effective gene number calculated for the Leghorn and Fayoumi backgrounds, respectively.

[c] Gene number cannot be estimated because of a lower variance value within the F_2 population than within the inbred line.

dominal fat, and shank length and positive heterosis for breast muscle, as expressed as a percentage of body weight.

The two F_1 crosses differed in the age at which they reached sexual maturity, and therefore egg size and egg number (data not shown), leading to the maternal effects of differences in BWT at hatch and the early stages of growth of their F_2 offspring. Therefore differences in heterosis between the two genetic crosses at 0 and 2 weeks of age are because of differences in maternal effects (egg size) of the two genetic backgrounds. However, for all other traits, heterosis was similar for the two genetic crosses.

Conclusion

Meat-type chickens have been selected for growth and body weight for several decades. If they behave as expected in closed populations, they might now be at their selection limit and no longer responding to selection. However, broilers do not seem to be at their selection limit, and improvements in growth and meat yield are continuing. The dramatic distance between inbred and broiler BWT means indicates that commercial selection has evolved broiler performances far beyond the range of variation in the original base population. This dramatic improvement in BWT, traditionally the most important trait and thus the one for which selection was applied the longest, is possible because of the high number of genes determining the phenotype. The advantage of broiler birds over inbred birds in growth and muscling is reversed for internal organs. As a percentage of their body mass, broilers had the lowest weights of internal organs, indicating that selection for high BWT did not achieve equivalent improvement in supporting organs, possibly leading to the increase in physiological disorders among modern broiler breeds. Because of its complexity, simultaneous selection for growth and fitness must be mediated through DNA markers. The described F_2 populations represent powerful resource populations for QTL searches, with a variety of economically important traits. Because of the availability of diverse inbred and commercial lines, among all agriculture animals, chickens provide an opportunity to generate excellent families (high number of half- or full-sib progeny and high genetic variation) for genetic analysis.

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