GENETIC ANALYSES OF FOOD CONSUMPTION IN GROWTH SELECTED LINES OF CHICKENS

by

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Finally, in the words of Goethe,

"Light -- more light."

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INTRODUCTION

Throughout history, philosophers and scientists have proposed that the behavioral responses of organisms are predisposed by hereditary components. The study of such components included phylogenetic surveys and, more recently, the quantitative techniques of selection and hybridization. The latter usually involves estimations of various types of genetic and environmental variation and covariation.

The literature on genetic and nongenetic factors influencing the body weight of chickens is voluminous. Indeed, improvement of growth and conformation through genetic selection has been the mainstay of the poultry meat industry for several decades. Lacking, however, is a body of data concerning the influence of such selection on feed intake and ingestive patterns, and their association and/or influence on body composition. Such information is cogent because recent experiments have demonstrated that selection for body weight is not independent of modifications in appetite control mechanisms (Barbato, 1979; Cherry, 1979; Burkhart et al., 1983).

The research reported in this dissertation was initiated to study interrelating patterns of consummatory behaviors of chickens known to differ in growth rate. Experiments were designed to provide insights regarding the involvement of genetic factors influencing these relationships. The populations studied had undergone over 20 generations of divergent selection for body weight at 56 days of age (Siegel, 1962; 1978). Preliminary data concerning the role of appetite in these populations have been available (e.g., Siegel and Wisman, 1966; Barbato *et al*., 1980) and provided a working model for the research reported in this dissertation.

REVIEW OF LITERATURE

Basic mechanisms associated with food consumption and subsequent growth have been the subject of numerous investigations. Although a large majority of these studies involved mammals (see reviews by Booth, 1976; Bray, 1976; Rozin, 1976), avian species are now undergoing similar scrutiny (see reviews by Savory, 1979; Smith, 1979). Rather than repeat what appeared in those reviews, this review is restricted to those factors which were the focus of this dissertation.

Body Weight. Using individual phenotypic selection, Siegel (1962; 1978) established two lines of chickens on the basis of high and low body weight at 56 days of age. Additive genetic variation accounted for approximately 30 percent of the total phenotypic variation in body weight -- a value well within the range of those reported for other populations of chickens (see review by Kinney, 1969).

Heritabilities of body weight for cockerels are generally higher than those for females (Kinney, 1969), suggesting that additive sex-linked effects may be attributed to a non-independence of the means and variances. Although adjustments for such scaling may remove these differences (Carte and Siegel, 1970), this does not preclude the effects of sex-linkage on the genetic architecture of polygenically inherited traits in poultry (Beilharz, 1960; 1962). The separation of the confounding of maternal effects and sex-linked variation, however, requires special experimental designs (Nordskog and Pevzner, 1977). An example of such a study is that by Cock and Morton (1963) who found evidence of additive sex-linked genetic variation in the shank length:body weight ratio, while noting that maternal effects accounted for three to six percent of the total variation in body weight. Other examples include those of Yao (1961) who observed significant maternal variation for juvenile but not adult body weight, and Pym and Nicholls (1979), who reported that sex-linkage was important in the weight gain of chickens.

Feed Consumption and Feed Efficiency. Guill and Washburn (1974) obtained realized heritabilities of 0.25 and 0.35 for feed efficiency. These heritabilities were in accord with those reported by Wilson (1969) and Pym and Nicholls (1979), and slightly lower than those obtained by Thomas *et al*. (1958). Guill and Washburn (1974) also noted a negative correlated response in feed consumption and a positive correlated response in body weight to divergent selection for feed efficiency. Such responses may be variable and asymmetrical since Pym and Nicholls (1979) observed a negligible correlated response in feed efficiency when selection was for increased feed consumption.

Furthermore, feed efficiency was significantly lower for chickens from lines selected for increased feed intake than for those from lines selected for either increased feed efficiency, increased weight gain or a control population (Pym and Farrell, 1977).

In mice, divergent selection for body weight results in correlated responses in feed consumption (Hayes and McCarthy, 1976). McCarthy (1980) suggested that genetical variation in absolute growth rate is not only due to increased feed intake but to differential protein deposition, the proportion of metabolizable energy available for growth, and the efficiency of conversion of metabolic energy into body weight. In reviews involving poultry, McCarthy (1977) and McCarthy and Siegel (1983) proposed that such changes may have also occurred in the development of broiler-type chickens and that they are related to correlated responses in feed intake plus activity levels, maintenance requirements, and fat deposition. The relationship of growth rate with fat deposition may be attributed primarily to the rate of lipid turnover (Hood and Pym, 1982; Calabotta et al., 1983) and adipose cellularity (Cherry et al., 1984).

Lepore (1965) hypothesized that the response in growth observed in a line of chickens selected for methionine requirement was due to a change in feed consumption. This reasoning is consistent with the data of Siegel and Wisman (1966), which indicated that selection for body weight was positively associated with improved feed efficiency. Furthermore, they postulated that the increased feed consumption could mask positive correlated responses in feed efficiency. Similar comments were made by Proudman et al. (1970) to explain their observations in terms of differences in energy and protein metabolism -- a view supported in part by that of Lepore et al. (1963) who observed differential protein utilization in Siegel's (1962) weight lines.

Traits negatively associated with divergent selection for oxygen consumption include feed consumption, growth and deposition of lean body mass (Stewart and Muir, 1982). These results are consistent with the paradigm described above. Divergent selection for fat deposition at the abdominal fat pad depot produced variable results, in that feed efficiency was negatively correlated with the direction of selection while no differences in absolute feed intake were observed between the lines (Leclercq and Saadoun, 1982; Simon and Leclercq, 1983). Touchburn et al. (1981) observed that the low feed efficiency of a high abdominal fat line was due to increased insulin secretion and the preferential use of feed energy for lipid synthesis.

Ingestive Behavior. The previous section dealt with aspects of feed intake arising from selection for growth related traits. These alterations in intake must be mediated in a temporal sense and in an alteration of the fowl's psychological and physiological responses to food-type stimuli. Research on feeding behavior in chickens has either been descriptive (e.g., Wood-Gush, 1959; Bessei, 1977) or focused on rhythmic aspects of feed intake and/or feeding activity (e.g., Siegel and Guhl, 1956; Siegel et al., 1962; Duncan, 1972). Meal structure, or the temporal sequencing of feed intake, has received less attention and may be defined several different ways. Jensen et al. (1962) considered meals to be equivalent to visits to the feeder, whereas Duncan et al. (1970) defined a meal as a period of feeding not interrupted by more than a two-minute interval. The latter definition was arrived at from an analysis of the intervals between feeding bouts. Using several rat studies as models, Barbato et al. (1980) defined a meal as any period of feeding activity associated with a consumption of food.

Variation exists among strains of chickens for both feeding rhythmicity and meal structure. Masic et al. (1974) compared the feeding behavior and feed intake of cockerels from broiler and layer strains. Broiler-type chickens exhibited highly congruent patterns of feed consumption and feeding activity, while these patterns were highly divergent among layer-type birds. These results support those obtained by Barbato _et al_. (1980) who observed similar phenomena in lines selected for high and low weight (Siegel, 1978). Savory (1974) suggested that intake and activity patterns of chickens among layer strains resulted in inefficient feeding and, hence, larger energy expenditures than that of broiler strains. This reasoning is consistent with that of Jensen _et al_. (1962) who attributed the increased feed efficiency observed among birds fed pellets, compared to those fed mash, to decreased feeding time.

Oral and Alimentary Intake Regulation. Ingestive behavior is often determined by the acceptability of food or fluids which influences the feeding habits of animals (Rozin, 1976). Chickens have greater gustatory acuity than was previously assumed (Kare and Medway, 1959; Gentle, 1972) and the range of oral stimuli detected by the fowl does not correspond to human flavor perceptions (Kare _et al_., 1957). There is considerable variation for taste receptivity among chickens (Kare, 1961). Chickens use specific taste stimuli to select calcium-rich diets (Hughes and Wood-Gush, 1971) and they learn to avoid unpalatable substances dissolved in water (Gentle, 1976).

Response to genetic selection for hedonistic preference to flavored solutions has been demonstrated in rats (Nachmann, 1959). Although evidence that such mechanisms are directly affected by selection among chickens is lacking, Gidlewski et al. (1982) observed that pullets from Siegel's low-weight line were better able to adjust their caloric intake than those from the high-weight line. Also, Huey et al. (1982) observed a preference for a protein rich diet by males from the high weight but not the low weight line. These data implicate possible modifications of gustatory regulatory mechanisms as correlated responses to selection for body weight in the fowl.

Lastly, food intake is ultimately limited by the capacity of the gastrointestinal tract and a meal is often thought to be terminated upon the filling of the stomach (Davis et al., 1976). Smith and Gibbs (1975) suggested that ingested food affects feeding behavior prior to systemic absorption in three sequential phases: (1) pregastric (palatability), (2) gastric, and (3) intestinal.

In the avian species, the crop has been the prime organ of investigation with regard to meal activation and/or termination. Fisher and Weiss (1956; 1957) found that a cropectomy had no effect on long term intake of food. Richardson (1970) postulated that following cropectomy, the esophagus takes on the function of the removed crop. This premise led to the proposal that crop distention was the primary alimentary control mechanisms involved in short-term regulation of feed intake. Richardson (1972) subsequently modified his hypothesis to include duodenal inhibition of feed evacuation in the crop, which caused distention and a subsequent cessation of feeding.

Dror et al. (1977) noted variability among broiler and layer strains of chickens in the size of certain gastrointestinal components, notably the crop and duodenum. Using the same strains as Dror et al. (1977), Nir et al. (1978) observed a differential capacity to respond to force feeding. Chickens with characteristically high body weights could be force fed only 13 percent more feed by weight than those fed ad libitum, whereas those with low body weights could be overfed up to 70 percent. This implies that heavy chickens voluntarily eat a volume of feed approaching the capacity of their gastrointestinal tract, while lighter ones appear to eat more in accordance with their metabolic needs. Following force feeding, increases were observed in the size of the upper gastrointestinal tract (i.e., crop and proventriculus) and the small intestine, thereby confirming the hypothesis of Richardson (1972).

Behavioral regulation of feed intake in chickens during the preabsorptive phase is a highly dynamic process incorporating the physical characteristics of the food consumed, as well as elements of the gastrointestinal tract. These control variables are mediated via nutritional, physiological, and genetic subsystems. These subsystems suggest a paradigm from which a working model of growth and ingestive behavior can be synthesized.

EXPERIMENT I

GENETIC ANALYSES OF GUSTATION IN THE FOWL

INTRODUCTION

Evidence for the existence of acute taste discrimination in the fowl was reviewed by Kare and Rogers (1976). Chickens have approximately 400 taste buds in the palate and floor of the oral cavity (Saito, 1966), and the morphology is similar to that of primitive mammalian types (Lindenmaier and Kare, 1959), suggesting similarity in gustatory mechanisms. There is a lack of correspondence between human and avian sensory landscapes (Kare et al., 1957; Gentle, 1972) indicating that perceptual differences may vary according to ecological and evolutionary factors. Consistent with this hypothesis is the observation that Jungle Fowl have a greater sensitivity towards sucrose solutions and subsequent caloric intake regulation than domestic chickens (Kare and Maller, 1967).

Genetic differences in taste thresholds have been investigated in several laboratories. Both Kare (1961) and Gentle (1972) observed considerable variation among chickens in response to specific chemical stimuli and inferred that a genetic component existed for gustation. In addition, Kare (1961) suggested that it may be feasible to breed for sensory discrimination. A relationship among sensation, perception and genetics was implied by Rozin and Kalat (1971) who offered an evolutionary explanation of specific hungers and taste aversions. Two generations of divergent selection for saccharin preference in rats changed the preference ratio from 0.68 in the base population to 0.85 in the high line and 0.39 in the low line (Nachmann, 1959). Heritability estimates for taste preference of 0.1 percent saccharin and 0.3 percent sucrose solutions in mice were 0.52 and 0.32, respectively, with the genetic correlation between them being 0.93 (Ramirez and Fuller, 1976).

The existence of populations inherently diverse with respect to body weight provides *in vivo* material for investigating gustatory processes and their relationships to feed intake control and growth. Accordingly, the experiments reported here were designed to investigate gustation among populations of chickens known to be widely divergent in feed intake and growth rate.

METHODS AND MATERIALS

Stocks. Chicks from purelines and their F_1 reciprocal crosses were obtained from matings involving the S_{22} generation of two lines of chickens which had undergone divergent selection for high (H) and low (L) juvenile body weight (Siegel, 1978). The sire line is denoted first and the dam line second for a particular mating, e.g., an HL individual is the product of a sire from the high-weight line mated to a dam from the low-weight line.

Eggs from all mating combinations were incubated concurrently, and upon hatching chicks were sexed and vaccinated for Marek's disease. Males from each mating were raised in unisexual flocks until maturity with feed and water provided *ad libitum*. When 24 weeks of age, 15 males were selected at random from each mating combination and transferred to individual cages for the duration of the testing procedure. All birds were maintained in an environmentally controlled room with a photoperiod of 14-hr light followed by 10-hr darkness at 22°C.

Testing Procedure. In all cases, individual males were provided with a choice situation that consisted of two waterers, each calibrated at five ml increments. None of the males had previous experience with any of the test compounds. The volume of solution consumed during a 15-minute period was recorded from each waterer. A short testing period was used to minimize the post-ingestional effect of fluid intake. Preference ratios consisting of the volume of test solution divided by the volume of test solution plus water consumed were calculated, transformed to arc sine $\sqrt{\text{preference}}$, and subjected to one-way analysis of variance for each concentration of test solution. Comparisons among mating types were by Duncan's multiple range test (Harter, 1969) and by the nonorthogonal linear contrasts shown in Table 1 (Scheffe, 1959; 1970). Pureline effects were evaluated by contrast 1, reciprocal effects by contrast 2, possible asymmetry by contrasts 3 and 4, and nonadditive genetic effects by contrast 5.

Preliminary Experiments. To determine if there were preferences to the position of the waterer, each bird was tested daily for five days using tap water and expressing the cumulative water consumption as a preference ratio for laterality to the bird's right. An 18-hr deprivation period was used prior to testing to insure a drinking response. Although no significant laterality was observed, the positions of the waterers were randomized in each subsequent trial.

The effects of the length of water deprivation on the taste response of these chickens were also examined by measuring the preference ratio of a 0.10 weight percent quinine sulfate solution to tap water after deprivation of

0, 4, 8, 18 and 24 hr. No drinking response was observed when the birds were not deprived of water prior to testing. Also, there were no significant differences in preference ratios among deprivation periods; showing that, under the testing conditions, preference ratios were not influenced by length of deprivation. Although these results were not consistent with those obtained with rats (Booth, 1972) and chickens (Gentle, 1976), the experimental situations employed were quite different. Gentle (1976) did not use a choice situation, and the two-hour test period used by Booth (1976) may have caused a confounding of preference ratios with postingestional effects.

Taste Preferences. Previous studies on the taste reactivity of chickens to dextrose (Kare and Medway, 1959) and quinine (Gentle, 1972; Kare *et al*., 1957) formed the basis for selecting these compounds as test materials in studying the mode of inheritance of taste preferences. Each preference test was preceded by a water deprivation period of 18 hours, with the choice being either dextrose (DEX) or quinine sulfate (QS) solutions and tap water. Concentrations of DEX were 1.25, 2.5, 5.0, 10.0 and 15.0 weight percent, and those for QS were 0.025, 0.05, 0.10, 0.20 and 0.30 weight percent. Preference ratios were calculated for each concentration on the basis of cumulative volume of solution consumed during five 15-minute test periods, with each test occurring on five consecutive days. An intermediate concentration of each chemical stimulus was presented first and then the concentration was alternately increased and decreased until population differences were no longer observed. Although the same birds were used in the various trials, assignments were made randomly among individuals prior to each preference determination.

RESULTS

Response to QS. Mean preference ratios of the parental lines and the F_1 crosses to varying concentrations of QS are presented in Table 2 with the sensory landscape of these genetic combinations illustrated as a function of the preference index (Klein and Defries, 1970), which extends the scale of the preference ratio from (0, 1) to (-1, 1) in Figure 1. No significant differences were found among genetic combinations at the highest and lowest concentrations of QS. Within these limits, however, a threshold pattern emerged with the response of crosses at lower concentrations being similar to that of the LL parental line. Then, as the concentration of QS increased, the birds from the F_1 crosses exhibited a preference index intermediate to the parental lines. The linear contrasts (Table 2) support the thesis that the HH birds had significantly higher preference ratios than did the LL chickens at concentrations of 0.05, 0.10 and 0.20 percent QS (Contrast 1). Reciprocal crosses responded similarly at each concentration tested (Contrast 2), suggesting that sex-linked and/or maternal effects were not important. Contrasts three and five were significant at 0.05 percent QS, suggesting that the preference ratio of the F_1 crosses was dominant for an aversion response to QS which was similar to that noted for the LL males. At 0.10 percent QS, the preference ratios for the HL and LH mating combinations were intermediate to those for the LL and HH matings (Contrasts 3 and 4). While a similar trend was observed at 0.20 percent QS, Contrast 3 was not significant.

Response to DEX. Means and standard deviations of the preference ratios for each mating combination towards graded concentrations of dextrose are presented in Table 3 with the sensory landscape shown in Figure 1. No differences were observed at concentrations of either 1.25 or 15.0 percent DEX. Within these brackets, the threshold for the LL line was reached at 2.5 percent DEX, while the threshold for the other mating combinations were noted at higher concentrations. At the 5.0 percent concentration, the preference ratio for the HL and LH crosses was not significantly different from that of the LL chickens, while the mild preference for the solution (0.69 ± 0.07) by HH males was still significantly lower than that of the other populations. This pattern among populations was also evident at the 10.0 percent concentration of DEX.

The nonorthogonal linear contrasts (Table 3) once again supported the sensory landscape illustrated in Figure 1. At concentrations of 2.5, 5.0 and 10.0 percent DEX, the LL birds had greater preference ratios than those of the HH chickens (Contrast 1) while there was no evidence of reciprocal effects at any DEX concentration (Contrast 2).

The responses of crosses were intermediate to those of the parental lines (Contrasts 3, 4 and 5). Contrasts 3 and 4 indicate that the preference ratios of the crosses were greater than those of the HH males at DEX concentrations of 5.0 and 10.0 percent and less than that for the LL birds when the concentration of DEX was 2.5 percent.

DISCUSSION

While preference behavior is not in direct correspondence with sensory thresholds, behavioral responses may be regarded as an upper limit of perceptual thresholds. Neural sensitivity may be considered as a subset of behavioral gustation and, as such, hedonic thresholds directly depend upon such sensitivities. The results presented in this paper suggest heritable components that are involved with gustation of the fowl. Hedonic thresholds to both quinine sulfate (QS; Table 2) and dextrose (DEX; Table 3) were lower in the LL than in the HH line, with the thresholds for the F_1 reciprocal crosses of these lines being dependent upon the type of solute. Parental line-F_1 comparisons provide evidence for nonadditive genetic variation for hedonic sensitivity towards QS and DEX, although they are in opposite directions. The significance of Contrast 5 (Tables 2 and 3) at intermediate concentrations of QS and DEX suggests that the behavioral threshold for QS sensitivity is in the direction of the LL parental line, while that for DEX is in the direction of the HH parental line. That genetic systems for gustatory responses towards bitter and sweet solutions are not one and the same is consistent with observations made with the mouse by Frank (1975). She observed that nerve fibers in the rat's chorda tympani sensitive to glucose were also sensitive to a variety of sweet substances. Similarly, those which were sensitive to quinine had a greater sensitivity to bitter substances. Furthermore, a slightly negative correlation was obtained between the two gustatory abilities, indicating that the underlying sensory mechanisms were different or only partially related.

In addition, additive genetic effects appeared to be responsible for the intermediate preferences ratios of the F_1 crosses at superthreshold concentrations of both QS and DEX (Figure 1). This is supported by the lack of significance for Contrast 5 at 0.10 percent QS and 5.0 and 10.0 percent DEX, as the means of the F_1 reciprocal crosses were not significantly different from their midparent averages. Additive genetic variation for gustation has been suggested or observed by several authors (reviewed by Fuller and Thompson, 1978).

An ability to behaviorally discriminate among flavors is important in determining the effectiveness of organisms to distinguish among nutritive, non-nutritive and toxic food sources (Rozin, 1976). This has obvious adaptive value during the development of an organism (Rozin and Kalat, 1971), and is probably an integral part of the evolutionary history of the fowl. If we assume that there is a continuous distribution of genetic variation underlying the gustatory response, then the expression of a preference on a phenotypic level would depend upon surpassing a threshold on the genetic level. Natural selection would be directional only after the threshold is reached and prior to saturation on a physiological level. This would tend to increase the nonadditive genetic variance for threshold sensitivity while maintaining additive variation for superthreshold stimuli.

While the relationship between genetic effects on gustation and obesity in the fowl is not clear, that between feed consumption and obesity is well documented. Feed intake is a correlated response of selection for body weight (Lepore, 1965; Siegel and Wisman, 1966; Pym and Nicholls, 1979). The feed-intake behavior of the parental populations used here differs markedly in their cumulative intake, feeding activity and frequency of meal eating (Barbato *et al*., 1980). In this case, selection for high body weight also appears to be accompanied by a relative lack of response towards certain flavors, while selection in the opposite direction has been associated with hyperresponsiveness to the same flavors. This is comparable to the situation observed in obese humans, who express an indifference or distaste for sweet solutions (Grinker *et al*., 1976).

The sense of taste is associated with the systemic control of feed intake and modifications of the sensation of perception of taste may be associated with quantitative changes in feed intake and subsequent growth. The specific mechanisms by which selection for body weight has affected feed intake are not known; however, it appears that genetic changes in gustation have occurred, which may be related to the adaptive-evolutionary history of the fowl.

SUMMARY

Preferences towards quinine sulfate (QS) and dextrose (DEX) were tested in purelines and reciprocal crosses of two lines of chickens that had undergone 22 generations of selection for high and low juvenile body weight. Parental line-F_1 comparisons provided evidence for non-additive genetic variation for hedonic sensitivity towards QS and DEX, though in opposite directions. Additive genetic variation appeared to influence the preference ratios for both stimuli at super-threshold concentrations. These results are discussed with regard to their evolutionary implications.

Table 1. Nonorthogonal linear contrasts used in analyzing preference ratios

Code	Contrast	Genetical Context
1	HH - LL	Pureline differences
2	HL - LH	Reciprocity
3	2HH - (HL ± LH)	Asymmetry
4	2LL - (HL ± LH)	Asymmetry
5	(HH ± LL) - (LH ± LH)	Nonadditive gene action

Table 2. Means and standard deviations of preference ratios by mating combination towards quinine sulfate (QS) solutions and a summary of contrasts using Scheffe's analyses

	Quinine sulfate solution (wt %)				
	.025	.05	.10	.20	.30
Mating*					
HH	.47±.09a	.46±.01b	.42±.02c	.28±.09b	.25±.08a
HL	.45±.11a	.28±.04a	.33±.14bc	.39±.13b	.22±.04a
LH	.39±.12a	.38±.03ab	.26±.07ab	.25±.19ab	.20±.06a
LL	.43±.08a	.34±.03a	.20±.02a	.16±.18a	.18±.05a
Contrasts†					
1 (pureline)	--	HH	HH	HH	--
2 (reciprocity)	--	--	--	--	--
3 (asymmetry)	--	HH	HH	--	--
4 (asymmetry)	--	--	HL±LH	HL±LH	--
5 (non-additivity)	--	HH±LL	--	HH±LL	--

Although analyses were performed on transformed values, for ease of the reader means and standard deviations are presented as nontransformed data.

*Means within a column having the same letter are not significantly different (P ≥ .05) by Duncan's multiple range test.

†If, for a specific contrast, the contrast was significant, the group with the greatest average is listed (P ≤ .05).
-- Means the contrast was not significant.

Table 3. Means and standard deviations of preference ratios by mating combination towards dextrose (DEX) solutions and a summary of contrasts using Scheffe's analyses

	Dextrose solution (wt %)				
	1.25	2.5	5	10	15
Mating*					
HH	.52±.12a	.50±.08a	.69±.07a	.74±.05a	.85±.13a
HL	.57±.09a	.53±.06a	.82±.10b	.82±.08b	.86±.09a
LH	.49±.07a	.48±.10a	.79±.08b	.86±.07b	.89±.11a
LL	.51±.11a	.73±.05b	.85±.12b	.89±.12b	.87±.08a
Contrasts†					
1 (pureline)	--	LL	LL	LL	--
2 (reciprocity)	--	--	--	--	--
3 (asymmetry)	--	--	HL±LH	HL±LH	--
4 (asymmetry)	--	LL	--	--	--
5 (non-additivity)	--	HH±LL	--	--	--

Although analyses were performed on transformed values, for ease of the reader means and standard deviations are presented as nontransformed data.

*Means within a column having the same letter are not significantly different ($P \geq .05$) by Duncan's multiple range test.

†If, for a specific contrast, the contrast was significant, the group with the greatest average is listed ($P \leq .05$).

-- Means the contrast was not significant.

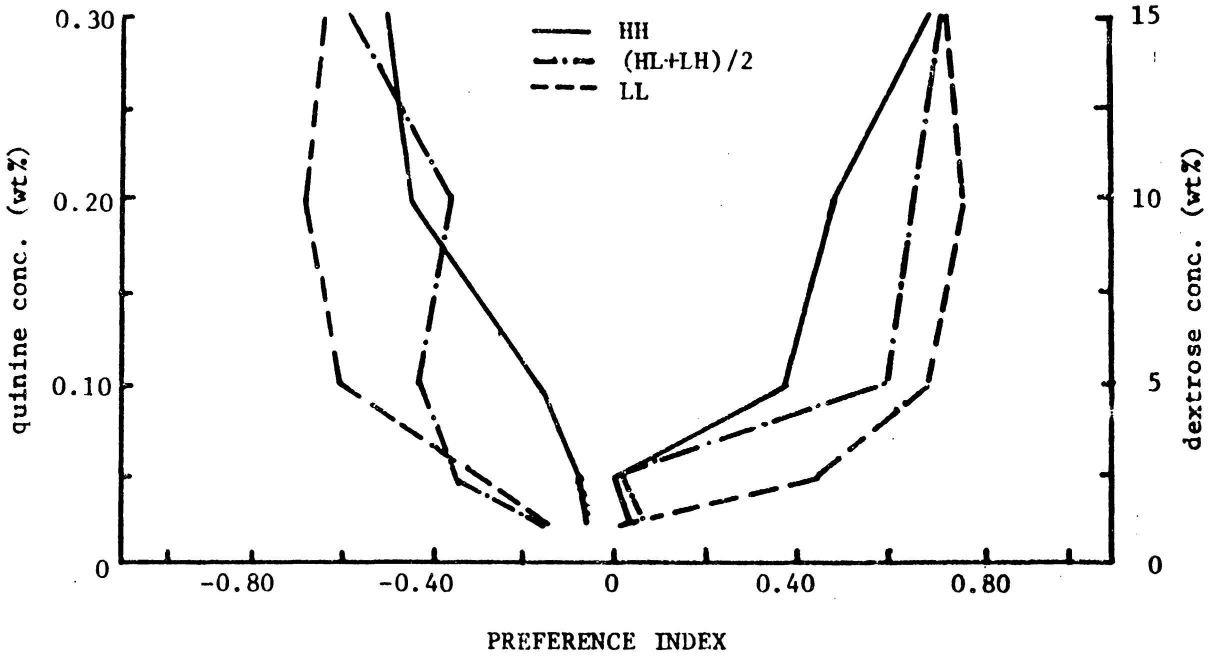

Figure 1. Sensory landscapes of the pureline mating types and the average of the reciprocally crossed mating types presented as a function of the preference index

EXPERIMENT II

INHERITANCE OF BODY WEIGHT AND ASSOCIATED TRAITS IN YOUNG CHICKENS

INTRODUCTION

Correlated responses in gross feed consumption, feed efficiency, activity levels and maintenance requirements occur concomitant to selection for body weight (McCarthy, 1977). A negative correlated response in feed consumption to selection for increased feed efficiency was noted by Guill and Washburn (1974), while selection for feed consumption resulted in a negligible correlated response in feed efficiency (Pym and Nicholls, 1979). Furthermore, feed efficiency was significantly lower for chickens from the increased consumption line than from lines selected for either increased feed efficiency, increased weight gain or a control population (Pym and Farrell, 1977). Among lines of chickens divergently selected for high and for low juvenile body weight (Siegel, 1978), feed efficiency and appetite were positively associated with directional selection (Siegel and Wisman, 1966), as were differences in meal size and length, while feeding activity was negatively associated with selection (Barbato *et al.*, 1980).

The relationships among intake, utilization, growth and body composition are neither clear nor typical for the chicken. Washburn *et al.* (1975) observed changes in carcass moisture and lipids associated with concurrent genetic alterations in feed efficiency, but the degree to which carcass protein was altered was population dependent. In the Japanese quail, Wyatt et al. (1982) observed that the degree of fat deposition was also population dependent. It appears that there are several developmental landscapes (sensu Waddington, 1957) involved in the overall characterization of body weight. The experiment reported in this paper was designed as a paradigm to examine these interrelationships in a genetic context using populations of chickens divergently selected for juvenile body weight.

METHODS AND MATERIALS

Stocks. Parental populations used in this experiment were the 22nd generation of two lines which had undergone divergent selection for high and low body weight at 56 days of age (Siegel, 1978). Parental lines and reciprocal F_1 crosses were produced via mass matings. Symbols denoting the mating combinations are HH, HL, LH and LL (where HL refers to the hybrid progeny derived from a cross between a high-weight sire and a low-weight dam and LH refers to progeny of the reciprocal cross). Upon maturity, these progeny served as the parental generation for the F_2 (HL x LH, LH x HL) and backcross matings (H x HL, H x LH, L x HL and L x LH). Since there were no H x LH progeny due to low fertility and zero hatchability from this mating combination, a weighting factor replaced the actual population in subsequent analyses. Repeated matings were used to produce chicks from the parental lines and the F_1 matings which were reared concurrently with the F_2 and backcross generations. Thus, all comparisons reported here were among age contemporaries.

Husbandry and Measurements. On the 22nd day of incubation chicks were sexed, wing-banded and vaccinated for Marek's Disease. Fifteen females from each mating combination were then randomly selected, weighed to the nearest g, and assigned to three flocks of five chicks.

Each flock was randomly assigned to a pen in a battery brooder where the temperature under the brooder was maintained at 28 to 30°C. Body weights were obtained to the nearest g for each individual at 0, 7, 14 and 21 days posthatching. Feed and water consumption was measured daily for each flock. At 21 days of age shank length was measured to the nearest 0.1 cm. The birds were then killed by cervical dislocation, the breast and abdominal fat pad excised and weighed to the nearest g and 0.1 g, respectively. All parts of the carcass were placed in plastic bags, tagged, and frozen for compositional analyses. Subsequently, each carcass was dried at 100°C and ground in a Salton grinder. Replicate samples were placed in crucibles and heated to 600°C in a flash furnace to determine ash content. Lipid content was determined from duplicate samples via chloroform-methanol extraction (2:1).

Statistical Analyses. Percentages were transformed to arc sin square root prior to analysis by one-way analysis of variance. Genetical inferences were based upon Scheffe's nonorthogonal linear contrasts (see Table 4; Scheffe, 1970). Comparisons were made among the P_1 (HH), P_2 (LL), F_1, F_2, B_1, and B_2 mating types using the techniques of Mather and Jinks (1971) to determine the adequacy of an additive-dominance model of inheritance. Heterosis was estimated as the percentage deviation of the F_1 generation means from the means of the parental populations (Contrast 3). Percentage recombination was estimated as the mean percentage deviations of Contrasts 7 and 8.

RESULTS

Body Weight. Means and standard deviations of body weights at all ages are presented in Table 5. Hatching weight was influenced by maternal factors expressed through the well-known high dependency of chick weight on egg weight. Chicks from the high-weight dams were significantly heavier than those from the low-weight dams. This was consistent with the weight of eggs from these lines (Reddy and Siegel, 1977). By seven days, and at subsequent ages, HH birds were more than twice as large as LL ones. The rate of gain from hatching to seven days of age was vastly different in the selected lines, being 236% for the high line and 152% for the low line. Thereafter the rate of gain was similar for both lines being 279% and 269% for the high and low lines, respectively, for the 7 to 21 day period. Heterosis for rate of gain was the same, being 1% for the 0 to 7 and 7 to 21 day period.

The degree of reciprocity for body weight between F_1 reciprocal crosses (Contrast 2) decreased from a significant high of 32% at hatching to nonsignificant values at 7, 14 and 21 days of age (Tables 5 and 6). Contrasts 4, 5, 9 and 10 were highly significant for body weight at hatching and seven days of age (Table 6), and were indicative of additive variation and asymmetry in response to selection for body weight. While Contrasts 4, 5 and 10 remained significant at

14 and 21 days of age, Contrast 9 was not significant. Heterosis was not observed at any age, and recombination effects were significant only at 14 and 21 days for the comparison between the F_1 and F_2 generations.

Feed and Water Intake. At one-day of age the feed intake of the P_2 population (LL line) was significantly less than that of the other mating combinations which did not differ from each other (Table 7). While reciprocal effects were not observed, recombinant components were large, as were the positive heterotic effects for cumulative feed intake for the first week posthatching (Figure 2). These data suggest that there is potence (sensu Mather and Jinks, 1971) in the direction of the high-weight line for feed intake at early ages. The feed intake of the various mating types diverged with age, and comparisons among them took on characteristics indicative of additive genetic variation (Table 7). This observation was confirmed by subsequent scaling tests of Mather and Jinks (1971) and the absence of recombination and heterosis by 7 and 14 days of age, respectively (Figure 2).

There were no significant differences among mating types for water intake at one day of age (Table 8). Reciprocal effects were not significant and heterosis was essentially zero, while recombination was approximately 15% at this age (Figure 2). The divergence of the mean cumulative water intake occurred in tandem with mean cumulative feed intake so that at seven days and at subsequent ages, the mean cumulative water intake appeared to be influenced by additive genetic variation and conformed to the additive-dominance mode of inheritance (Table 8). Furthermore, the percentage recombination approached zero with age.

Feed:water ratios of all mating types increased with age and converged between 30 and 34 percent by 31 days of age (Figure 3). Heterosis and recombination at this age were -2 and -1 percent, respectively. Yet, during the first week post-hatching there were considerable differences among mating combinations in feed:water ratios. The low weight parental line, in particular, had a significantly lower feed:water ratio than that of the other mating combinations until seven days of age. This was due to the very low feed intake of these birds during the first few days posthatching.

Means and standard deviations of the cumulative feed efficiency of chicks from the high weight line were superior to those of the low weight line at all ages (Table 9). Although all other means were intermediate to those of the parental lines, the percentage heterosis rose from 7 to 32 percent over the course of the experiment but recombination effects were negligible.

Compositional Analyses and Related Morphology. The mean percentage moisture for the HH parental (P_1) line was significantly greater than that of the LL parental line (P_2); while all other comparisons among population means were not significant (Figure 4). Percentage heterosis and recombination were minimal (-1 and 1 percent, respectively), reciprocal effects were not observed, and the additive-dominance model of inheritance was adequate to explain the mode of inheritance of percentage carcass moisture.

No significant differences were observed among populations for percentage ash (Figure 4). Percentage heterosis was zero, while percentage recombination was 17 percent. Shank length, a measure of absolute skeletal growth, was significantly longer for the HH parental line (P_1) than for the LL parental line (P_2). The F_1 was not different from the mid-parent value with the percentage heterosis being zero. Recombination loss was small (-5%) and no reciprocal effects were observed. The additive-dominance model of inheritance was confirmed for both percentage ash and for shank length, according to the A, B and C scaling tests.

Percentage carcass fat of chicks from the HH line (P_1) was significantly higher than that of the LL chicks (P_2) as seen in Figure 4. F_1 chicks exhibited a -33% heterosis and there was a 43% recombination increase in percentage fat.

Reciprocal effects were not evident. Although no significant differences were observed among mating types for abdominal fat pad weight (Figure 5), the 81% recombination precluded the additive-dominance model from being an adequate description of the mode of inheritance for this trait. The C scaling test was marginally significant at $P = 0.70$.

Breast weight (Figure 5) was measured as a rough estimation of carcass protein (Soller and Plotkin, personal communication). The LL chicks had a significantly lower breast weight than all P_1, B_1 and B_2 mating types, but the P_1, B_1, F_1, F_2 and B_2 mating types were not significantly different from one another. Reciprocal effects were not significant, while 15% heterosis and 22% recombination was observed. The additive-dominance model of inheritance was adequate to explain these variations (Mather and Jinks, 1971). These differences became non-significant when breast weight was analyzed relative to body weight.

DISCUSSION

The data obtained in this experiment showing that the principal mode of inheritance for juvenile body weight is additive genetic variation is consistent with reports by Siegel (1962), Cock and Morton (1963), Maloney et al. (1967) and Pym and Nicholls (1979). Reciprocal effects, due to egg size, were not observed after seven days posthatching, nor were other maternal or sex-linked components important. This is not to suggest, however, that these effects did not exist, as large, specially constructed experiments are necessary to evaluate small, confounding effects (Nordskog and Pevzner, 1977).

Skeletal growth, as measured by shank length, paralleled body weight in that the mode of inheritance appears to be principally additive genetic variation. Indeed, breast weight also exhibited characteristics indicative of additive genetic variation, although there were moderate heterotic and recombination influences on the absolute weight. Heterosis did not appear to influence the weight of the abdominal fat depot, while recombination accounted for a large degree of the variation for this trait. This would indicate that factors other than the additive-dominance action of the genes influencing fat depot weight are affecting this trait. This is consistent with the data of March and Hansen (1977), in that abdominal fat pad growth did not differ among populations until 29 days of age.

Potence for feed intake, in the direction of the high-weight line, was apparent during the first several days posthatching. Also, heterosis for feed intake at hatching dissipated during this same period. In contrast, no concomitant differences in water intake were observed. When considered in the context of feed to water ratios, values for the low-weight line were significantly lower than those for all other mating types for the first six days posthatching. Furthermore, the rapid increase in the feed:water ratio of these birds indicate that the birds were drinking relatively less water and may be related to their low carcass moisture at this age. These data support Mark's (1980) hypothesis that selection for body weight considerably alters feed and water intakes during the first few days posthatching and ultimately affects body composition.

Although low feed:water ratios are generally associated with high feed efficiencies (Lepkovsky _et_ _al_., 1960, Marks, 1981a), in this case the feed efficiency of the HH chicks was superior to that of the LL chicks, a result consistent with these lines (Siegel and Wisman, 1966; Owens _et_ _al_., 1971). This suggests that the high metabolic rate of LL chickens (Owens _et_ _al_., 1971) overrides any beneficial effects of a low feed:water ratio. These data are consistent with those of Stewart and Muir (1982), who indicated that birds selected for high oxygen consumption were slower growing and had inferior energy utilization due to decreased deposition of lean body mass. The decrease in overall energy utilization of the LL chicks may also be influenced by their higher activity levels while feeding (Barbato et al., 1980).

The large heterotic effect observed for feed efficiency (32 percent) was not associated with a similar effect for feed:water ratio (-2 percent). Indeed, body weight and cumulative feed and water intakes at 21 days of age were mainly influenced by additive genetic variation. Percentage carcass fat, however, was negatively heterotic (-33 percent), suggesting that the main factor influencing the heterotic increase in feed efficiency was the lower energetic cost of decreased fat deposition. These observations confirm inferences made by Wyatt et al. (1982) concerning negative heterosis for fat deposition in Japanese quail. White Rock by Cornish crosses (Moran et al., 1970) also show negative heterosis for fat traits.

Heterosis for the 11 traits measured in this experiment shows considerable clustering at 21 days of age (Figure 6). Heterotic effects were generally lacking for overall nutrient intake and gross morphological measures of growth, such as body weight and shank length in addition to percentages of moisture and ash content, suggesting that additive genetic variation largely influenced these traits. In contrast, traits involved with the efficiency of the organism to allocate nutrient intake into specific growth components exhibited moderate to high degrees of heterosis.

Selection for growth rate in these populations has been positively associated with feed intake, feed efficiency, and percentage carcass fat. Negatively associated traits include feeding activity (Barbato et al., 1980), metabolic rate (Owens et al., 1971), feed passage rate (Cherry and Siegel, 1978), and jejunal glucose absorption (Walker et al., 1981). These data suggest that bidirectional selection for body weight does not cause similar developmental changes in each direction. The selected trait, juvenile body weight, appears to be primarily influenced by additive genetic variation, while non-additivity appears to account for a portion of the variation in early feed and water intakes, feed efficiency and fat deposition. In addition, it was shown in Experiment I that different genetic systems appear to influence gustatory responses to sweet and bitter solutions in these populations. If different genetic systems exist for the expression of high and low body weight, with respect to feed efficiency and carcass composition, it may further aid us in determining future genetic components involved in increasing feed efficiency and lean body mass.

SUMMARY

The heritable variation of body weight in two lines of chickens divergently selected for high and low body weight was principally additive. Early feed intake was influenced by potence in the direction of the high weight line, while early water intake was similar among all populations. Heterosis was observed for feed efficiency which was associated with an equivalent negative heterosis for percent carcass fat. It was hypothesized that different genetic systems exist for the phenotypic expression of high and low body weight, and such may be applied to the future genetic improvement of feed efficiency and carcass composition of chickens.

Table 4. Summary of Scheffe's nonorthogonal linear contrasts and genetical inferences

Contrast Code	Mating Comparison	Genetical Inference
1	HH - LL	Pureline
2	LH - HL	Reciprocity
3	(LH+HL) - (HH+LL)	Non-additivity
4	2HH - (LH+HL)	Asymmetry
5	2LL - (LH+HL)	Asymmetry
6	(LHxHL) - (HLxLH)	Reciprocity
7	[(LHxHL)+(HLxLH)] - (LH+HL)	Recombination
8	[(HxHL)+(HxLH[1])+(LxLH)+(LxHL)] - [(HH+LH)+(HL+LL)]	Recombination
9	2HH - [(HxHL)+(HxLH[1])]	Potence/Sex-linkage
10	2LL - [(LxLH)+(LxHL)]	Potence/Sex-linkage

[1] Reconstructed mean.

Table 5. Means and standard deviations of body weight (g) for all mating combinations at 0, 7, 14 and 21 days of age

Mating Combination	Age (days)			
	0	7	14	21
HH	28± 2b	66± 8c	114±13c	184±41c
LH	29± 2b	51± 7b	87±14b	149±39bc
HL	22± 2a	47± 8b	75±20b	119±43ab
LL	21± 2a	32± 4a	53±11a	86±20a
LH x HL	26± 3b	53± 7b	96±15bc	165±26c
HL x LH	25± 3ab	51± 8b	92±16b	158±25bc
H x HL	26± 2b	54± 5b	101±11bc	171±28c
L x LH	23± 2ab	40± 5ab	70±15ab	110±32ab
L x HL	26± 2b	47± 4b	90±12b	151±27bc

[1] Means within a column having the same letter are not significantly different ($P \leq .05$) by Duncan's multiple range test.

Table 6. Summary and percentage deviations of Scheffe's analyses of body weight

	Age (days)			
Contrast Code	0	7	14	21
1 (Pureline)	33**	106**	115**	114**
2 (Reciprocity)	32**	9	16	25
3 (Non-additivity)	4	0	-3	-1
4 (Asymmetry)	10**	35**	41**	37**
5 (Asymmetry)	-18**	-35**	-35**	-36**
6 (Reciprocity)	4	4	4	4
7 (Recombination)	0	6	16**	21**
8 (Recombination)	0	3	6	8
9 (Potence)	8**	24**	13	8
10 (Potence	-14**	-26**	-34**	-34*

*$P \leq 0.05$.
**$P \leq 0.01$.
[1] Estimated as the percentage deviation of the first, from the second, mean of each contrast.

Table 7. Means and standard deviations of cumulative feed consumption and A, B, C scaling tests through 21 days of age

Mating Type	Age (days)					
	1	3	5	7	14	21
P_1	4± 1	21± 6	39±10	69±14	202±25	475± 30
B_1	4± 1	17± 2	38± 3	62± 6	192±12	463± 21
F_1	3± 1	16± 7	35± 8	59±11	165±20	385± 32
F_2	3± 2	18± 9	35±13	59±14	171±19	390± 27
B_2	4± 2	17± 7	35±10	52±14	153±21	337± 29
P_2	1± 1	8± 3	19± 2	41± 5	125±13	298± 20
Scaling test						
A	1± 2	-3±10	2±14	-4±21	17±40	66± 61
B	4± 4	10±16	16±22	4±30	16±48	-9± 69
C	1± 8	11±39	12±55	8±62	27±90	17±131

Table 8. Means and standard deviations of cumulative water consumption and A, B, C scaling tests through 21 days of age

Mating Type	Age (days)					
	1	3	5	7	14	21
P_1	19± 5	68± 1	124±14	220±25	594±43	1442±111
B_1	16± 2	57± 3	115± 7	195±19	621±45	1447±123
F_1	17± 3	58± 3	114± 8	177±14	518±38	1176±110
F_2	13± 4	51± 9	104±16	181±16	520±32	1206±104
B_2	16± 1	53± 3	106± 5	159±17	473±45	1102±113
P_2	15± 3	47± 5	85± 5	143±13	400±38	928±102
Scaling test						
A	-4± 4	-12± 7	-8±21	-7±48	130 ±107	276±291
B	0± 3	1± 8	13±14	-2±39	28 ±105	100±271
C	-16±10	-27±37	-21±68	7±75	50 ±160	102±494

Table 9. Means and standard deviations of cumulative feed efficiencies (g body weight gain/g feed consumed) and A, B, C scaling tests through 21 days of age

Mating Type	Age (days)		
	7	14	21
P_1	0.55±0.05	0.42±0.03	0.32±0.04
B_1	0.45±0.03	0.39±0.02	0.31±0.05
F_1	0.44±0.06	0.41±0.04	0.35±0.07
F_2	0.39±0.05	0.32±0.06	0.27±0.09
B_2	0.37±0.04	0.36±0.04	0.30±0.04
P_2	0.27±0.02	0.26±0.03	0.21±0.05
Scaling test			
A	-0.09±0.10	-0.05±0.06	-0.05±0.13
B	0.03±0.10	0.05±0.09	0.04±0.12
C	-0.14±0.24	-0.22±0.26	-0.15±0.39

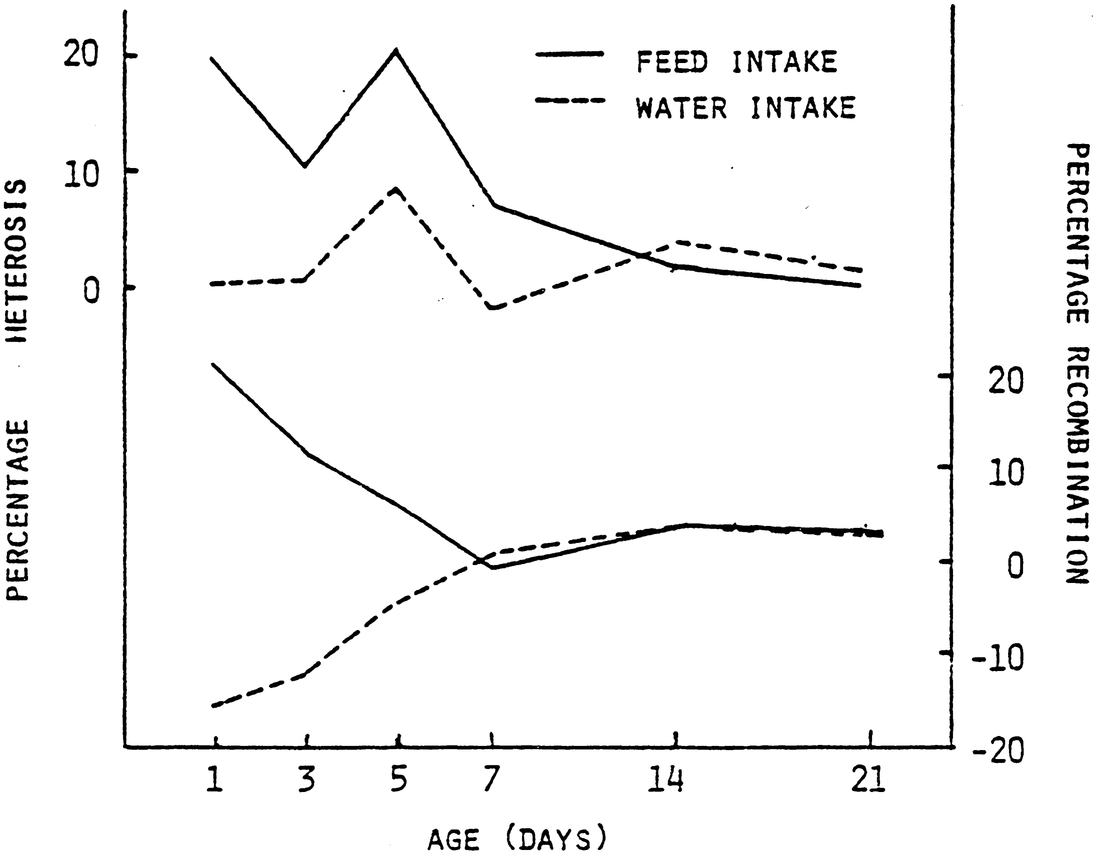

Figure 2. Percentage heterosis and recombination of feed and water intake through 21 days of age

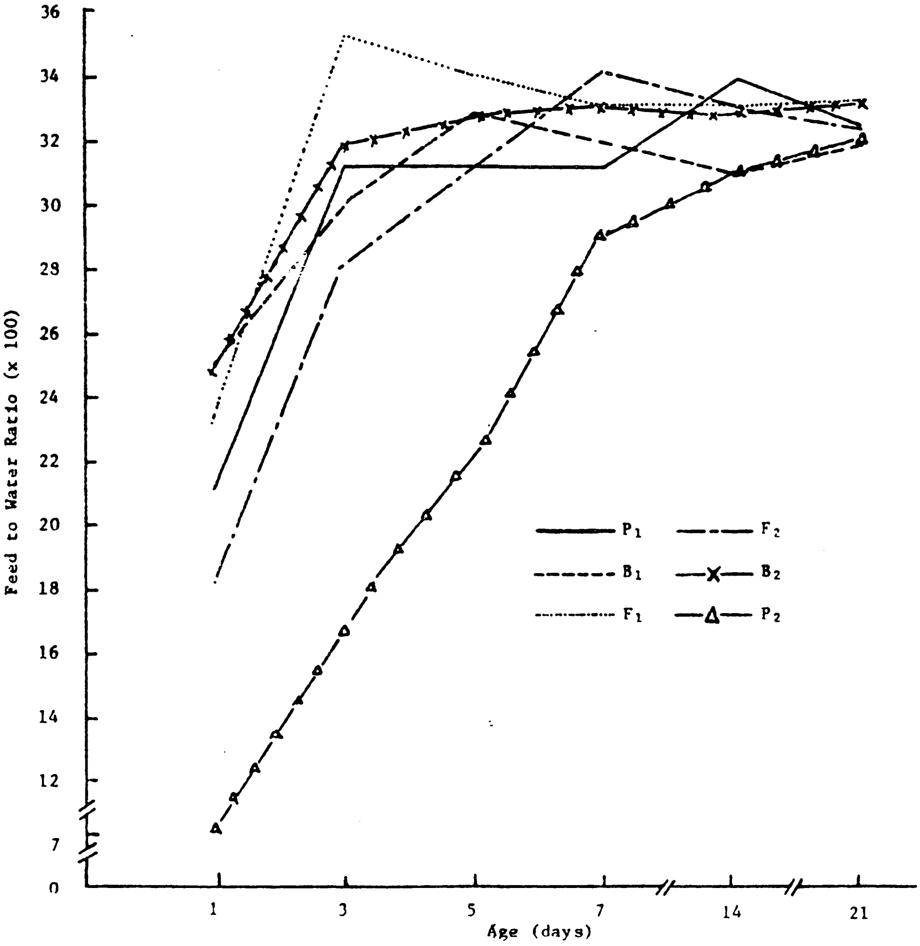

Figure 3. Ratio of feed to water by mating type and age

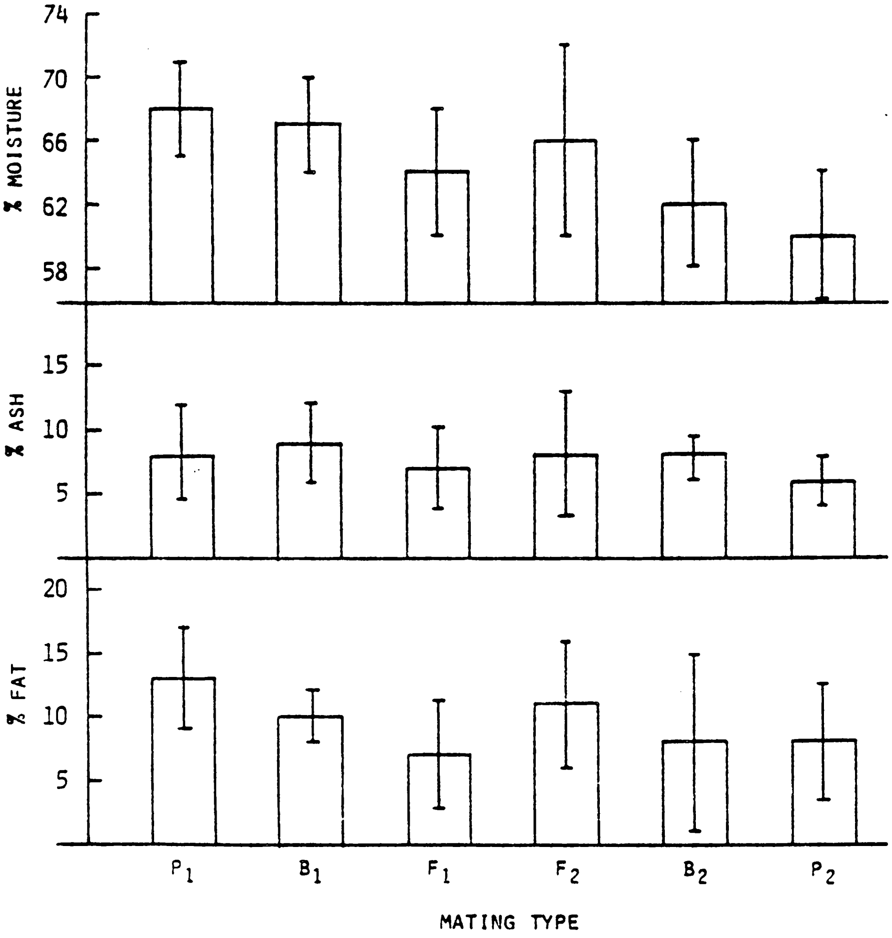

Figure 4. Means and standard deviations of percentage moisture, ash, and fat of each mating type at 21 days of age

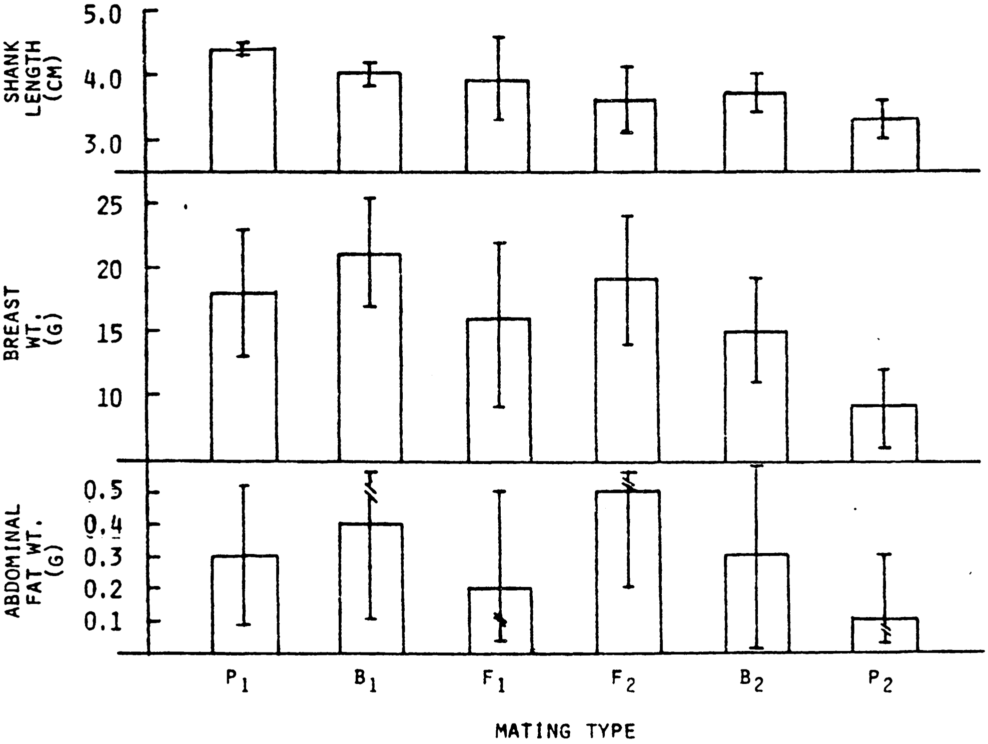

Figure 5. Means and standard deviations of shank length (cm), breast weight (g), and abdominal fat pad weight (g) of each mating type at 21 days of age

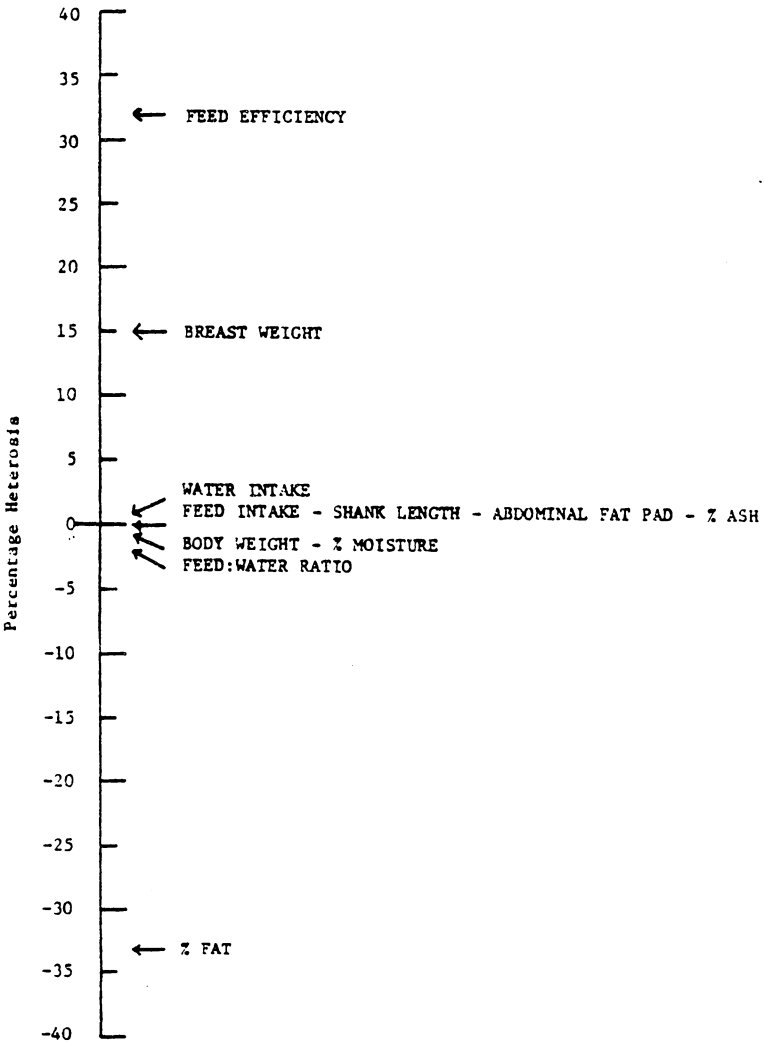

Figure 6. Percentage heterosis of various traits at 21 days of age

EXPERIMENT III

SELECTION FOR BODY WEIGHT AT EIGHT WEEKS OF AGE: RESTRICTION OF FEED AND WATER

INTRODUCTION

Growth is a dynamic process that is influenced by two discrete activities, feeding and drinking. Although most previous reports on growth have concentrated on feed consumption (e.g., Pym and Nicholls, 1979; Nir *et al.*, 1978; Siegel, 1978). The data of Marks (1980) suggest that water consumption is also a variable which can influence appetite and growth. This reasoning is consistent with gross differences in daily feed and water intake in populations of chickens known to differ in growth rate (Marks, 1979; 1980; Barbato *et al.*, 1980).

When feed and water consumption are viewed in the context of feed:water ratios, differences among populations are observable during the first week posthatching. Marks (1981b) found that quail selected for increased four-week body weight generally had lower feed:water ratios earlier in life than the nonselected control line. Similar observations were made in selected and nonselected broiler populations (Marks, 1980) and in Experiment II of this dissertation for the lines of chickens selected for high and low body weight.

The purpose of the experiment reported here was to examine the effects of restricting either feed or water on alterations of growth and feed:water ratios of young chicks.

METHODS AND MATERIALS

Chicks from parental populations and their reciprocal crosses were obtained from matings involving the 22nd generation of two lines divergently selected for high and low body weight (Siegel, 1978). The sire line is denoted first and the dam line second for a particular mating, e.g., an HL individual is the product of a sire from the high-weight line mated to a dam from the low-weight line.

At hatching, female chicks from each mating combination were randomly assigned to three treatments with each treatment-mating combination consisting of three groups of five chicks each. Groups were then assigned at random to pens in a battery brooder in a room maintained at 28 ± 2° C. The treatments consisted of (1) *ad libitum* feed and water (AL), (2) *ad libitum* feed and restricted water (RW), and (3) restricted feed and *ad libitum* water (RF). All restrictions were limited to the level of the LL line and were based on the *ad libitum* daily feed and water intake obtained from a previous experiment involving that line maintained in the same battery and room in an attempt to insure uniformity. The diet, containing 20% protein and 2684 kcal/kg, was the same for when selection was practiced (Siegel, 1962).

Feed (g) and water (g) consumption of each group were measured daily and individual body weights were obtained weekly to the nearest g. Feed efficiencies were obtained by dividing body weight gain by feed consumed. At four weeks of age, the birds were killed by cervical dislocation and the abdominal fat pad and breast excised and weighed to the nearest 0.01 g and g, respectively.

Data were analyzed by analysis of variance with the statistical model being:

$$Y_{ijk} = \mu + L_i + T_j + (LT)_{ij} + e_{ijk}$$

where $i = 1, 2 \ldots 4$ mating combinations, $j = 1, 2, 3$ feed and water treatments and $k = 1, 2 \ldots n$ individuals per mating combination subclass (three pens for intake analyses). When significant differences ($P \leq .05$) were found, Duncan's Multiple Range Test was employed as the mean separation technique.

RESULTS

Body Weight. Regardless of treatment, HH chicks were significantly heavier than the LL chicks, while the F_1 crosses were generally intermediate to the parental lines (Table 10). These results are consistent with observations for these populations in Experiment II. There were no significant interactions of mating combination by treatment for body weight. Restricting the feed intake of HH chicks to that of LL birds caused an 18% depression in body weight by seven days of age when compared to HH chicks fed *ad libitum* (Figure 7) and the depression increased to 38% by 28 days of age. In contrast, a comparable restriction of water intake depressed the body weight of HH chicks by 8 to 10% throughout the experiment.

There was a significant difference in body weights between reciprocal crosses at younger ages in favor of the maternal line (Table 10). The temporal persistence of this difference varied with treatment in that it was shortest under *ad libitum* feeding and longest under feed restriction. Although the temporal pattern of depression due to feed restriction was similar in both crosses, the effect was more pronounced for the HL than for the LH chicks (Figure 7). Water restriction depressed the body weight of the HL and LH birds to the same degree as for the HH chicks.

In the context of body weight deviations between the HH and LL lines, the difference was greater under feed restriction than under water restriction to seven days of age and then was reversed at subsequent ages (Table 11). The mean body weights of both crosses were more similar to that of the LL line under feed restriction than water restriction.

Feed and Water Consumption. Restriction of feed or water intake of HH chicks to that of LL chicks increased the relative cumulative intake of the non-restricted variable by approximately 20% at 28 days of age (Table 11). In contrast, both the HL and LH birds decreased their consumption of the *ad libitum* dietary component by -5 to -9% to the same age. While mating combination by treatment interactions were not significant for absolute feed or water intake they were significant for feed:water ratios at all ages. This interaction, as illustrated in Figure 8, was due to a higher feed:water ratio of HH chicks under water restriction, and a greater ratio of HL and LH chicks under feed restriction.

Feed Efficiency. None of the interactions between main effects was significant for feed efficiency. Under *ad libitum* feeding, means and standard deviations of feed efficiency for body weight gain to 28 days of age were .23 ± .02, .22 ± .03 and .19 ± .04 g body wt/g feed consumed, respectively, for the HH, HL and LH mating types. These means, while not significantly different from each other, were significantly larger than the .13 ± .02 for the LL line. When water was restricted, the feed efficiencies of the HH, HL and LH mating types were .25 ± .02, .23 ± .01 and .20 ± .03, respectively. While none of the means was significantly different from their ad libitum counterparts or each other, all were significantly larger than that of the LL line. When feed was restricted, HH and HL chicks were significantly more efficient than the LH and LL chicks. At 28 days of age, the means for these mating types were, respectively, .17 ± .03, .17 ± .02, .10 ± .01 and .12 ± .02.

Abdominal Fat-Pad and Breast Weight. Mean and standard deviation of weights of the abdominal fat pad of HH, HL, LH and LL chicks fed ad libitum were .67 ± .42, .08 ± .06, .04 ± .06 and .02 ± .02g, respectively, with the mean for the HH line being significantly larger than those for the other populations. Differences among populations, however, were not significant under either restriction program, thus causing a significant mating combination by treatment interaction. When abdominal fat-pad weight was expressed per 100 g body weight, there were no significant differences among either mating combinations or treatments. Also, the depression of abdominal fat-pad weight for the HH chicks due to water or feed restriction was 48 and 92%, respectively.

In an ad libitum feeding situation, the mean breast weight for the HH, HL, LH and LL progeny were 26 ± 3, 20 ± 2, 19 ± 2 and 16 ± 1 g, respectively, with the mean for the HH parental line being significantly greater than the F_1 means which were significantly greater than the mean for the LL parental line. A significant mean decrease of 22% was observed for all mating types under water restriction. Feed restriction reduced the mean breast weights to 20 ± 2, 19 ± 3, 19 ± 2 and 17 ± 4 g for the HH, HL, LH and LL progeny, respectively. These means were not significantly different from one another. In all cases, the differences among mating combinations and treatments disappeared when breast weight was expressed per 100 g body weight.

DISCUSSION

Regardless of mating combinations and age, limiting the water intake of faster growing chicks to that of the low-weight parental line depressed body weight by about 10% from their *ad libitum* counterparts. In contrast, the effect of feed restriction on body weight varied with age and population. In no case was the 28-day body weight of the faster growing chicks depressed to that of the low-weight line to which their intake was restricted. These data are consistent with those of Marks (1980), who restricted the feed intake of broiler-type chicks to that of a nonselected line.

Evidence of compensatory growth in the low-weight line chicks can be seen from 14 to 21 days of age under the feed restriction treatment. It will be recalled that these birds were fed a given amount of feed, based upon the previous experiment. During the first 14 days, low-weight feed restricted chicks did not eat as much as their *ad libitum* counterparts, whether due to sampling error or treatment effect, and had lower body maintenance requirements. The accumulation of feed in the feeder, not eaten during this period, was consumed between 14 and 21 days of age, allowing the birds to grow to the size of the *ad libitum* fed chicks.

Differences in body weight among treatments appeared to be unrelated to the relative capacity of the birds to deposit muscle or fat tissue; no significant differences were observed in the relative weight of the abdominal fat pad or breast. Similar results were obtained by March and Hansen (1977) and Marks (1981), suggesting that gross feed efficiency and feed intake were primary factors influencing weight gain.

Water restriction effectively caused a mild restriction of feed consumption. The relatively improved feed efficiency associated with reduced feed consumption is well known (Titus, 1949) and is in accordance with the results of pair-feeding trials for the parental lines studied in this report (Siegel and Wisman, 1966). Similarly, the decrease in gross body weight and feed efficiency associated with more severe feed restriction was also reported by Titus (1949) and is apparently associated with a greater portion of the nutrient intake being allocated to body maintenance requirements. While the degree of feed restriction was not similar for the HH and F_1 progeny due to appetite differentials, the percentage restriction of the reciprocal crosses was similar. Significant reciprocal differences in body weight between these populations appeared to be due to feed efficiency and not to appetite. This suggests that genotype by environment interactions exist with respect to feed efficiency and growth under nutrient restricted regimens.

Differences in feed:water ratios among chicks fed and watered ad libitum were similar to those observed in Experiment II. The feed:water ratios of the HH chicks on a feed restricted regimen were similar to those reported by Marks (1980) for a feed restricted broiler line, but the F_1 progeny responded in opposite fashion. Furthermore, an inverse response was noted for all mating combinations when birds were water-restricted, indicative of genotype by environment interactions. These data suggest that the relationship between feed:water ratio and feed efficiency or growth may be population-dependent.

SUMMARY

The consumption of feed or water by chickens selected for high body weight was restricted to that of a line selected for low body weight. In addition, reciprocal crosses of the two lines underwent feed or water restriction to that of the low body weight parental line. Restriction of water depressed feed intake to a greater degree in the high line than in the crosses, but depressed body weight by approximately 10% in all groups through 28 days of age. Feed restriction caused a greater depression in body weight in the high line than in the crosses at 28 days of age. The effect of feed or water restriction on the feed:water ratio was dependent upon mating type, suggesting the absence of a simple relationship among growth, body composition and feed efficiency.

Table 10. Means and standard deviations of body weights (g) by age and treatments for each mating type[1]

		Age (days)			
Treatment	Mating combination	7	14	21	28
Feed & water ad libitum	HH	62± 9b	85±12a	111±17c	141±23c
	HL	41± 6a	61± 8b	81±11b	101±17b
	LH	51± 8b	68± 9b	87±13b	97±20b
	LL	41± 4a	52± 7a	58±11a	65±14a
Water restriction	HH	58± 6b	88±10c	103±17c	128±20c
	HL	37± 5a	45± 9a	68±13a	91±17b
	LH	48± 4b	57± 7b	78±10b	87±13b
	LL	37± 3a	47± 5a	61± 9a	67±12a
Feed restriction	HH	51± 6b	60± 7c	75±10c	84±12c
	HL	29± 2a	33± 4a	54± 7a	62± 9a
	LH	37± 4b	45± 9b	66±10b	76±12b
	LL	30± 3a	39± 6b	58± 8c	63±10a

[1] Means within a column subgroup having the same letter are not significantly different ($P \leq 0.05$).

Table 11. Percentage deviation of HH, HL and LH progeny from the LL line when feed or water intake was restricted to that of the LL line

Trait	Restriction	Mating combination	Age (days) 7	14	21	28
Body weight	Water	HH	57	87	89	91
		HL	0	-1	11	35
		LH	30	22	28	30
	Feed	HH	70	40	29	33
		HL	-3	0	-7	14
		LH	2	5	14	21
Cumulative feed intake	Water	HH	15	20	24	18
		HL	-15	-7	-1	-5
		LH	-30	-23	-9	-9
Cumulative water intake	Feed	HH	-2	8	17	19
		HL	-14	-20	-15	-9
		LH	-16	-14	-14	-5

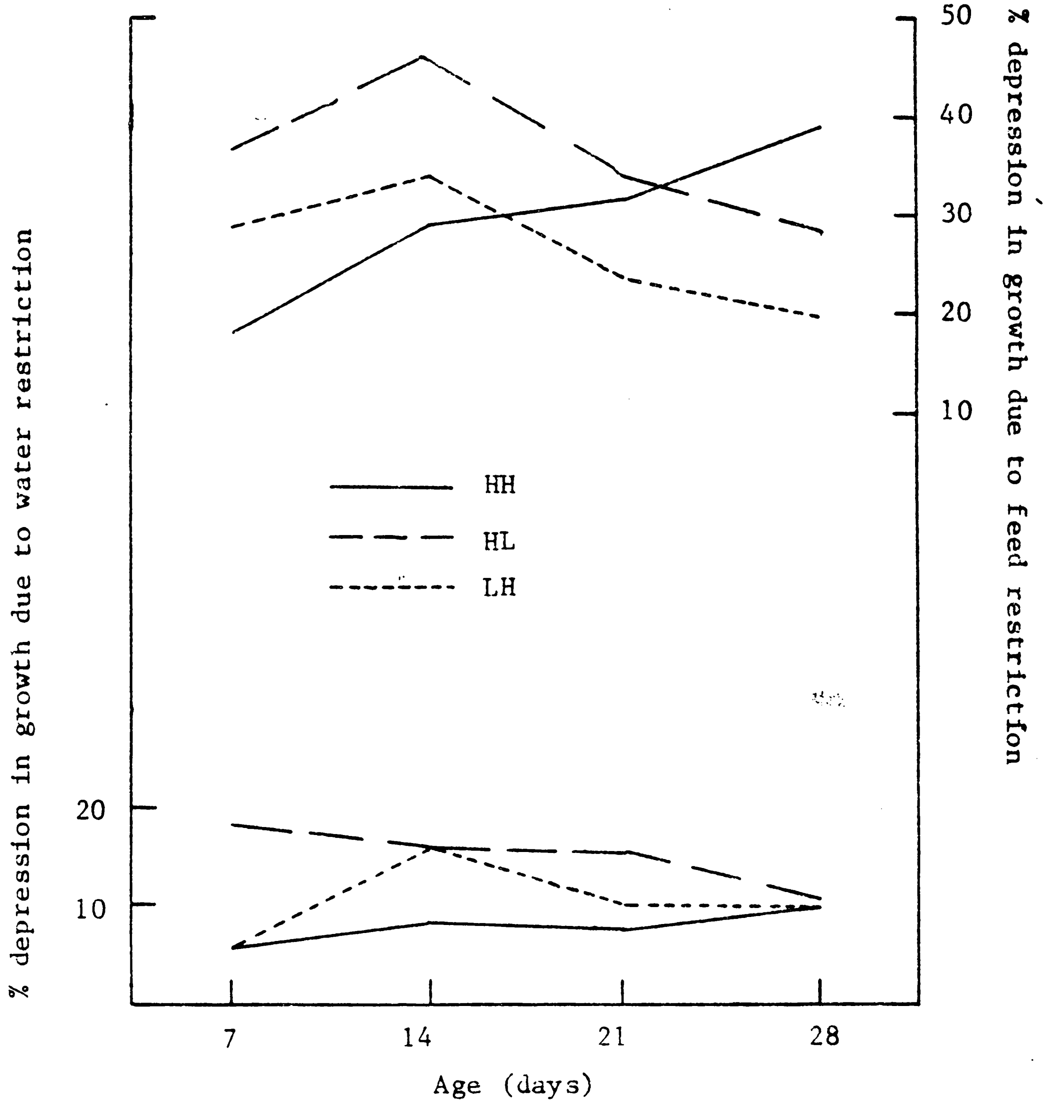

Figure 7. Percentage depression in body weight from ad libitum counterparts due to feed or water restriction in the HH, HL and LH progeny through 28 days of age

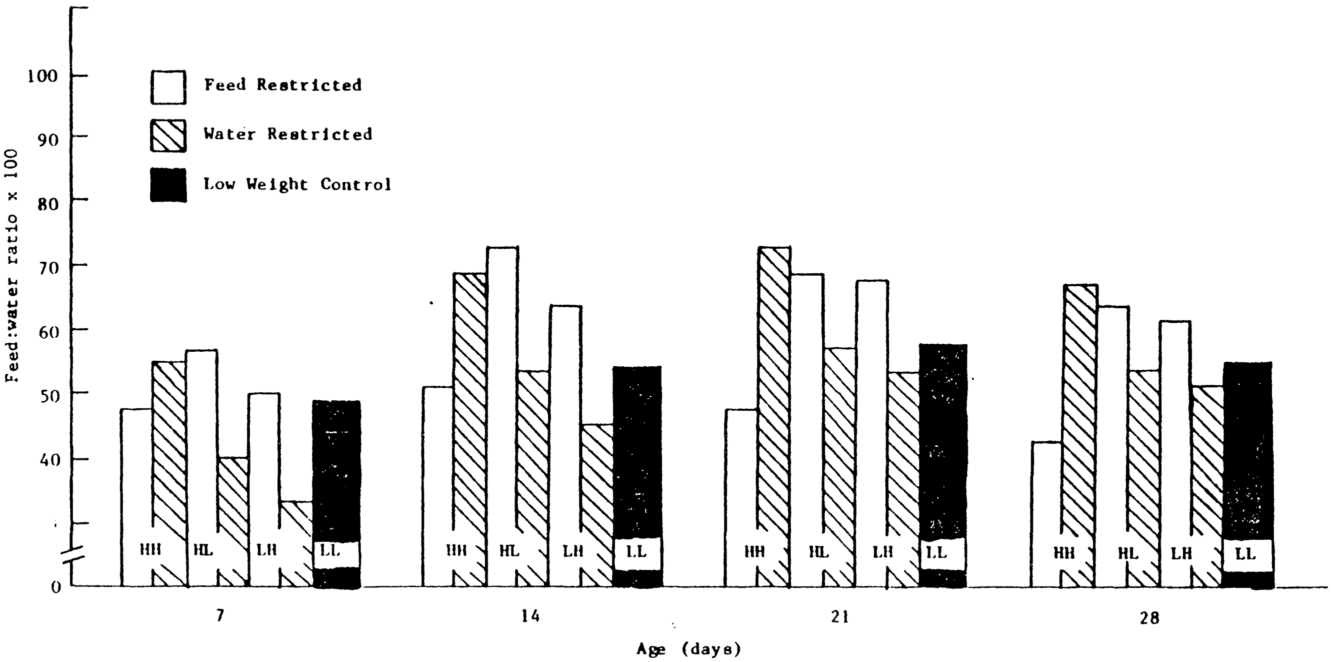

Figure 8. Feed:water ratios of progeny from each mating type undergoing feed or water restriction at seven-day intervals through 28 days of age

EXPERIMENT IV

SELECTION FOR BODY WEIGHT AT EIGHT WEEKS OF AGE: OVERFEEDING

INTRODUCTION

There is considerable interest in the relationship between genetic variation in the growth potential of chickens and responses to various feeding regimes (eg., Siegel and Wisman, 1966; Nir _et_ _al_., 1978; Marks, 1979; 1980; 1981a). Although feed utilization, metabolic efficiency, and body weight are associated with the differential growth rates of populations (Proudman _et_ _al_., 1970; Owens _et_ _al_., 1971; Washburn _et_ _al_., 1975; Stewart and Muir, 1982; McCarthy and Siegel, 1983), another major element of the paradigm is appetite (Lepore, 1965; Siegel and Wisman, 1966; Marks, 1980; Barbato _et_ _al_., 1980).

Nir _et_ _al_. (1978) observed differences among lines of chickens in their capacity for overfeeding. Lines with characteristically low body weights could be overfed up to 70% more than their _ad_ _libitum_ intake while those with characteristically high body weights could be overfed only 13% more than _ad_ _libitum_ consumption. This implies that the latter voluntarily eat a volume of feed approaching their gastrointestinal tract capacity while the former eat in accordance with their metabolic requirements.

Overconsumption of foodstuffs at an early age may influence growth, feed efficiency and carcass composition. The experiment reported here was designed to determine the effects of overconsumption of feed in parental lines known to differ for these traits and in F_1 crosses between these parental lines.

METHODS AND MATERIALS

Chicks used in this experiment were produced from the 22nd generation of two lines of chickens which had undergone bidirectional selection for high (HH) and low (LL) body weight at eight weeks of age (Siegel, 1978). All parental line and reciprocal F_1 progeny were produced simultaneously via mass matings. Upon hatching, chicks were sexed, vaccinated for Marek's Disease and wingbanded. Female chicks from each mating type were randomized into three groups, two for *ad libitum* feeding and the other for force feeding. The *ad libitum* fed chicks were assigned at random into two groups of 10 each and placed in battery brooders. Force-fed chicks were placed as a single group in the same battery brooder. Each of these chicks was overfed to gut capacity twice a day during the first seven days posthatching and thrice each day thereafter, using the force feeding technique described by Nir *et al*. (1978). Some mortality resulted from the procedure and 10 overfed individuals per mating combination were selected at random for subsequent analyses.

The diet fed was that on which selection was practiced (Siegel, 1962) and contained 20% protein and 2684 kcal of metabolizable energy/kg of feed. Feed consumption was measured daily for each force fed bird and all *ad libitum* groups, and individual body weights were obtained weekly.

All weights were taken to the nearest g. At 21 days of age, birds were sacrificed by cervical dislocation and the liver, breast, and abdominal fat pad excised and weighed to the nearest g, g, and 0.1 g, respectively. The gastrointestinal tract (GI) from the anterior end of the cervical esophagus to the cloacal orifice (McLeod et al., 1964) was removed and the contents emptied. The following components of the GI tract were dissected and weighed to the nearest 0.1 g: (1) cervical esophagus, crop and thoracic esophagus, (2) proventriculus, (3) gizzard, (4) duodenum, and (5) remainder of the intestine. Each carcass, less the gut contents, was then placed in individual plastic bags and frozen. Subsequently, individual carcasses were thawed at room temperature, oven dried at 100°C, and ground in a Salton grinder. Replicate samples were placed in crucibles and heated to 600°C in a flash furnace to determine ash content. Lipid content was determined from replicate samples via chloroform:methanol extraction (2:1). Carcasses were not analyzed for protein.

Feed consumption data were analyzed between feeding treatments within mating types via moving average processes, and their respective oscillators (Box and Jenkins, 1976). Moving average oscillators are calculated as the difference between two moving average processes and illustrate both temporal and absolute differences between the time series.

Data were also analyzed using a two-way analysis of variance with mating combination and feeding regime as main variables with fixed effects. When the interaction of mating type by feeding regime was significant, comparisons were made between feeding regimes within a mating combination. In the case of feed consumption and feed efficiency, values for *ad libitum* fed birds were obtained by dividing the pen value by the number of birds in the pen. Feed efficiencies were corrected for chick weight. Subsequently, F_1 data were pooled as no significant differences were observed between the reciprocal crosses. Scheffe's (1970) nonorthogonal linear contrasts were used to determine the significance of percentage heterosis, calculated as the percentage deviation of the F_1 means from the means of the parental populations. The first contrast,

$$[F_1 - (HH + LL)/2]$$

tested the difference between the F_1 and parent means, while the second contrast

$$[F_1 - (HH + LL)/2]_{AL} - [F_1 - (HH + LL)/2]_{OF}$$

tested the difference between the mean heterosis expressed under *ad libitum* feeding (AL) and the overfed (OF) regimes.

RESULTS AND DISCUSSION

Feed Intake and Body Weight. Mating combination by feeding regime interactions were significant at all ages due to the propensity of LL chicks to be overfed and a general inability to overfeed HH birds above their _ad libitum_ consumption. At one day of age HH chicks could not be overfed while F_1 and LL chicks could be overfed 50 and 150%, respectively (Table 12). At 21 days of age, the percentage overfeeding above _ad libitum_ was 10, 18 and 23 for HH, F_1 and LL chicks, respectively. Although overfed chicks had the opportunity to consume feed voluntarily, this did not occur as measured by weight change of their _ad libitum_ food supply.

The significant temporal pattern of overfeeding may be illustrated by expressing the intake of _ad libitum_ and overfed chicks as moving average oscillators (Figure 9). Chicks from each mating combination had a unique pattern of overfeeding. HH chicks could be minimally overfed during the first seven days posthatching, with the degree of overfeeding increasing modestly thereafter. In contrast, LL chicks could be overfed at all ages, while the pattern of overfeeding of F_1 chicks combined aspects of both parental lines in that they resembled the HH line initially and the LL line by seven to nine days of age. This temporal patterning supports the view of Marks (1980) that most alterations in feed intake among weight selected populations occur during the first week posthatching.

Mating combination by feeding regime interactions were significant for body weight at 7, 14, and 21 days of age with the pattern of proportional differences consistent over time (Table 13 and Figure 10). Overfeeding had a minor influence on growth of HH chicks ($< 10\%$) and a major effect on F_1 and LL progeny ($> 40\%$). These results are consistent with those of Nir _et_ _al_. (1978) that the response to overfeeding is considerably greater in slower than in faster growing chickens.

Feed efficiency. _Ad_ _libitum_ feed efficiencies of LL chicks were poorer than those of the other mating types at seven days of age and at subsequent ages; a result consistent with that noted in Experiment II of this dissertation. Also, mating type by feeding regime interaction was significant at all ages. This was because overfeeding, while not altering the efficiency of HH chicks, significantly increased the gross feed efficiency of F_1 and LL females (Table 14).

Gastrointestinal Tract. Overfeeding appeared to have a major influence on components of the upper GI tract (Table 15). Significant increases in the size of the esophageal passages and crop were observed among all mating combinations. This was expected, as the force feeding procedure involved intubation of the crop (Nir et al., 1978). Relative increase in esophagus and crop size in HH chicks was about threefold when expressed as either an absolute weight or per 100 g of body weight. For LL and F_1 progeny, however, the increase was considerably greater on an absolute basis than per 100 g of body weight.

Mating combination by feeding regime interactions were significant for proventriculus weight both on an absolute and a relative body weight basis because overfeeding increased proventriculus weight of HH but not F_1 and LL progeny (Table 14). With regard to absolute gizzard weight, all mating combinations responded in a similar manner, in that overfeeding increased the size of this organ. On a relative body weight basis, the mating combination by feeding regime interaction was significant, as overfeeding increased relative gizzard weight in HH, but not F_1 or LL chicks (Table 15).

Overfeeding had a uniform influence on the remainder of the GI tract (Table 15). That is, while increases due to overfeeding were observed for absolute weights of the duodenum and intestine in all mating types, they disappeared when data were expressed on a relative body weight basis. Mating combination by feeding regime interactions were not significant in any case.

Although all chicks exhibited an increase in absolute and relative crop and esophageal weights due to the force feeding procedure, only HH chicks responded with an increase in upper GI tract size without a concomitant increase in body weight. This response suggests that HH chicks were reacting to the force feeding technique rather than the degree of overfeeding, while F_1 and LL chicks had a systemic capacity to deal with a larger volume of feed than ingested ad libitum. These data support the hypothesis of Nir et al. (1978), that chickens from lines selected for large body weight are inclined to eat a volume of feed corresponding to the size of their gastrointestinal capacity.

Body Composition and Related Morphology. Percentage of carcass ash was not influenced by either mating combination or feeding regime, nor was the interaction between these variables significant. With regard to percentage carcass moisture, differences among mating combinations were significant with the LL mean less than the HH mean. The F_1 was intermediate. Neither feeding regime nor the mating combination by feeding regime interaction was significant.

Differences among mating types for percentage of carcass fat were significant with the mean for the HH line being greater than that for the LL line with the F_1 being intermediate. No significant differences were observed among mating types for relative fat pad weight. Mating combination by feeding regime interactions were significant for both traits, since overfeeding did not cause an increase in the percentages among HH chicks, but resulted in significant increases among F_1 and LL chicks (Table 5).

No significant differences in relative liver or breast weight were observed among mating types or feeding regimes, nor were there significant interactions between these two variables.

Heterotic Influences. Percentage heterosis under *ad libitum* feeding for the traits presented in Table 17 were consistent with those observed for these lines in Experiment II, in that relatively little heterosis was observed for gross morphological traits, food intake and percentage of moisture. The percentage of heterosis under *ad libitum* feeding for feed efficiency reported here, while lower than that reported earlier (15 vs 32), was consistent with the classical observations of Hess and Jull (1948) and with the negative heterosis for percentage of carcass fat obtained here and for Japanese quail (Wyatt *et al*., 1982).

Overfeeding, in contrast to *ad libitum* feeding, modifies the environment in which the traits are measured and may in turn alter genetical inferences. When the F_1 means were compared to their midparent means in overfeeding situations, there was a significant increase in heterosis for body weight, feed efficiency, and percentage of fat pad and a significant decrease in the negative heterosis for percentage of carcass fat to that observed for *ad libitum* feeding (Table 17). With regard to the parts of the GI tract, the degree of heterosis observed for the absolute and relative weights under *ad libitum* feeding were, in general, considerably larger than that noted under force feeding (Table 18).

General. Our results show that patterns of overfeeding, growth and feed efficiency of chickens are present at hatching and receive fine tuning during the first seven days posthatching. Overfeeding could be accomplished to a high degree among low-weight and F_1 chicks, suggesting that their relatively low *ad libitum* feed intake has minor influences on their biological capacity to utilize larger amounts of feed. Conversely, chicks selected for high body weight eat until they reach a limit apparently set by gastrointestinal capacity. In this regard, electrolytic lesions of the ventromedial hypothalamus produced hyperphagia in birds from the low-weight line, but not the high-weight line (Burkhart *et al*., 1983). Other studies have shown that intubation of tyrosine into the crop stimulated feed intake of White Leghorns, while having no effect on a broiler strain (Lacy *et al*., 1982). Furthermore, Jungle fowl had greater sensitivity to dietary dilution and subsequent compensation than domesticated chickens (Kare and Maller, 1967). In addition, lower hedonic sensitivity to bitter and to sweet substances was observed in the HH than in the LL line in Experiment I of this dissertation. These data suggest that domestication of the contemporary broiler chicken which has emphasized intensive selection for growth has resulted in attenuation of the feed intake control systems and, hence, a bird which consumes feed over and above its metabolic requirements. The consumptive limit set by the gastrointestinal capacity of such chickens may ultimately bring about a plateau in the response to selection for increased body weight under current dietary formulations. This reasoning is consistent with the suggestion of Dror *et al*. (1977) that intestinal capacity be considered in selection programs.

On the other hand, the degree of heterosis observed for some of these traits under *ad libitum* feeding, suggests that directional dominance is influencing their phenotypic expression -- at least with regard to these specific populations. Not only was directional dominance expressed among the hybrid progeny, but overdominance was evident for several gastrointestinal traits as well as for feed efficiency in the overfed birds. There is reason to suspect that these characteristics are important components of fitness in the fowl, as Leamy (1982) has shown for morphometric characters in mice. Whether or not results obtained using these lines can be generalized is moot, since the notion that meat-type chickens are overfeeders is well accepted. As such, standard breeding strategies for increasing body weight in the future may be disappointing, in spite of the amount of additive genetic variation that exists for this trait. Selection for a fixed weight which reduces market age, rather than for weight at a fixed age may partially circumvent such a plateau. Market age, however, has a lower limit. An alternative solution may be to alter current diets to ones with higher nutrient densities, enhancing the opportunities to capture potential combining ability for feed efficiency without the restrictive context of limited feed intake.

SUMMARY

Female chicks from lines selected for high and low body weight and their reciprocal F_1 crosses were overfed via force feeding to crop capacity from hatching to 21 days of age. Low-weight line chicks could be overfed at an earlier age to a greater extent than those from the high-weight line and F_1 progeny. The degree of overfeeding appeared to be associated with the relative size of certain gastrointestinal components. Differences among lines in their capacity to be overfed were reflected in concomitant changes in body weight and carcass fat. Relationships among feed consumption and growth are discussed within the context of selection for body weight and heterosis under various feeding regimes.

Table 12. Means and standard deviations of the cumulative feed intake (g) by mating and feeding regime at 7, 14, and 21 days of age

	Mating combination					
Age	HH		F1		LL	
(days)	ad lib	overfed	ad lib	overfed	ad lib	overfed
1	5± 2a	5± 3a	4± 1a	6± 1b	2± 1a	5± 2b
5	40± 7a	46± 6a	33± 5a	44± 6b	21± 6a	37± 9b
7	73±12a	84± 7a	58± 9a	76± 8b	45±10a	59±11b
14	196±16a	222±10b	164±11a	193±10b	129±12a	184±18b
21	465±22a	510±18b	371±16a	438±14b	274±15a	338±24b

Means within the same row subgroup having the same letter are not significantly different ($P \geq 0.05$).

Table 13. Means and standard deviations of the body weight (g) by mating and feeding regime at 7, 14, and 21 days of age

	Mating Combination					
	HH		F1		LL	
Age (days)	ad lib	overfed	ad lib	overfed	ad lib	overfed
7	61± 9a	66± 7a	51± 8a	72± 6b	31± 3a	46± 5b
14	109±14a	118±10a	82±10a	119±11b	55±12c	83± 9b
21	185±26a	199±21a	131±18a	194±20b	89±23a	137±16b

Means within the same row subgroup having the same letter are not significantly different ($P \leq 0.05$).

Table 14. Means and standard deviations of cumulative feed efficiencies by mating and feeding regime at 7, 14, and 21 days of age

	Mating Combination					
Age (days)	HH		F1		LL	
	ad lib	overfed	ad lib	overfed	ad lib	overfed
7	.44+.02a	.44+.05a	.43+.01a	.61+.04b	.27+.04a	.42+.07b
14	.41+.04a	.40+.07a	.34+.02a	.48+.06b	.26+.02a	.34+.05b
21	.33+.03a	.32+.06a	.31+.02a	.40+.03b	.21+.01a	.32+.04b

Means within the same row subgroup having the same letter are not significantly different (P ≥ 0.05).

Table 15. Means and standard deviations of the absolute (g) and relative (g/g body weight x 100) weight of gastrointestinal (GI) components at 21 days of age by mating and feeding regime

	Mating Combination					
	HH		F_1		LL	
GI Comp.	ad lib	overfed	ad lib	overfed	ad lib	overfed
<u>Absolute</u> <u>Wt</u>.						
Esop.&crop	1.5±0.4a	4.5±0.8b	1.5±0.4a	4.6±0.6b	0.7±0.3a	3.5±0.3b
Proven.	1.0±0.5a	1.6±0.1b	1.4±0.4a	1.5±0.2a	0.8±0.3a	1.2±0.2a
Gizzard	5.7±1.3a	8.0±0.5b	6.5±0.7a	8.2±0.6b	4.3±0.4a	6.2±1.0b
Duodenum	1.4±0.4a	2.4±0.4b	1.6±0.4a	2.5±0.2b	1.0±0.3a	2.1±0.7b
Intestine	4.9±1.7a	8.9±1.2b	6.0±1.7a	8.4±1.2b	3.3±1.0a	6.0±1.2b
<u>Relative</u> <u>Wt</u>.						
Esop.&crop	0.8±0.2a	2.3±0.3b	1.1±0.5a	2.3±0.2b	0.8±0.2a	2.6±0.3b
Proven.	0.5±0.1a	0.8±0.2b	0.9±0.2a	0.8±0.3a	0.9±0.2a	0.9±0.3a
Gizzard	3.1±0.2a	5.0±0.4b	4.3±0.4a	4.2±0.2a	4.8±0.4a	4.5±0.3a
Duodenum	0.8±0.1a	1.2±0.3a	1.2±0.5a	1.3±0.2a	1.1±0.4a	1.5±0.2a
Intestine	2.6±0.5a	4.5±0.8a	4.6±1.6a	4.3±1.1a	3.5±1.4a	4.4±1.1a

Means within a row subgroup having the same letter are not significantly different (P ≥ 0.05)

Table 16. Means and standard deviations of compositional analyses and related morphology (g/g body wt x 100) at 21 days of age by mating and feeding regime

	Mating Combination					
	HH		F1		LL	
Trait	ad lib	overfed	ad lib	overfed	ad lib	overfed
Ash	8+3a	9+4a	9+4a	8+2a	9+3a	6+3a
Moisture	66+4a	68+2a	64+3a	67+2a	62+3a	65+3a
Fat	15+4a	18+2a	7+4a	13+5b	4+3a	9+2b
Fat pad x 100	3+2a	7+3a	2+2a	6+2b	1+2a	7+3b
Liver	4+2a	5+3a	3+2a	4+1a	3+1a	4+1b
Breast	13+3a	13+4a	13+3a	13+5a	11+2a	10+2a

Means within a row subgroup having the same letter are not significantly different ($P \geq 0.05$)

Table 17. Percentage of heterosis of various traits under *ad libitum* and overfed feeding regimes at 21 days of age

	Feeding regime	
Trait	ad lib	overfed
Body weight	-4a	15b*
Cumulative feed intake	0a	3a
Feed efficiency	15a*	25b*
% fat pad weight	0a	17b*
% breast weight	8a	13a
% ash	6a	7a
% moisture	0a	0a
% fat	-26b*	-4a

Means within a row having the same letter are not significantly different ($P \geq 0.05$).

*F1 is significantly different from midparent values.

Table 18. Percentage of heterosis of absolute and relative (g/g body weight x 100) gastrointesintal tract (GI) components under ad libitum and overfed feeding regimes at 21 days of age

GI Component	Feeding Regime	
	ad lib	overfed
Absolute Weight		
Esophagus and crop	36b*	15a*
Proventriculus	25b*	7a
Gizzard	30b*	15a
Duodenum	33b*	11a
Intestine	46b*	14a
Relative Weight		
Esophagus and crop	38b*	-6a
Proventriculus	10a	6a
Gizzard	9a	1a
Duodenum	26b*	7a
Intestine	80b*	27a*

Means within a row having the same letter are not significantly different ($P \geq 0.05$).
*F1 is significantly different from midparent values.

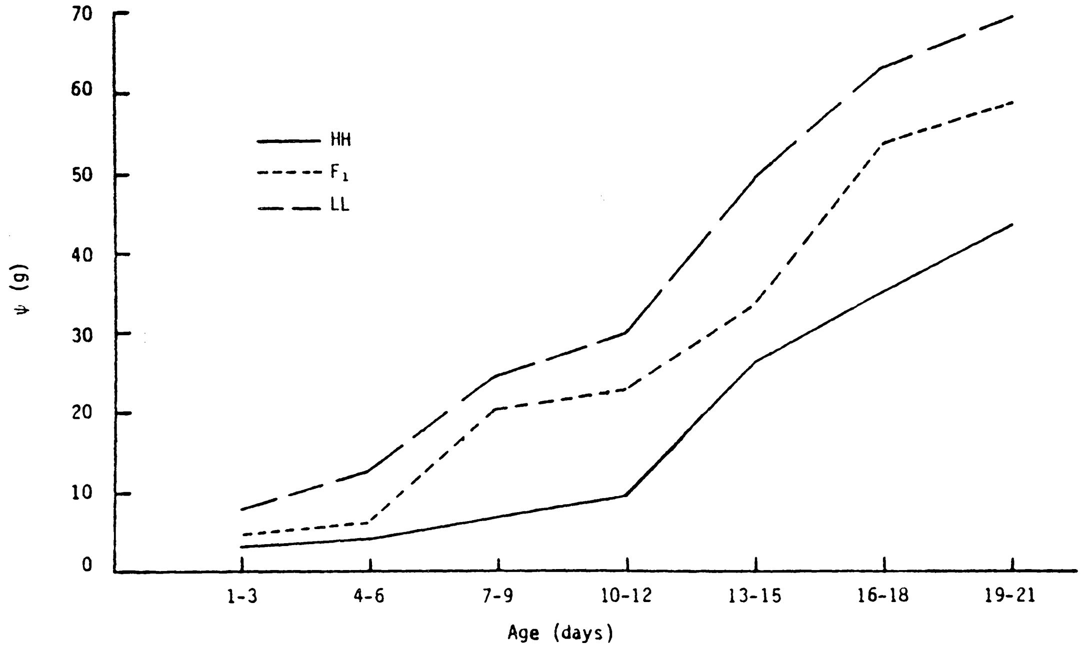

Figure 9. Oscillators of the moving average processes for the cumulative ad libitum and overfed intake (g) of each mating type

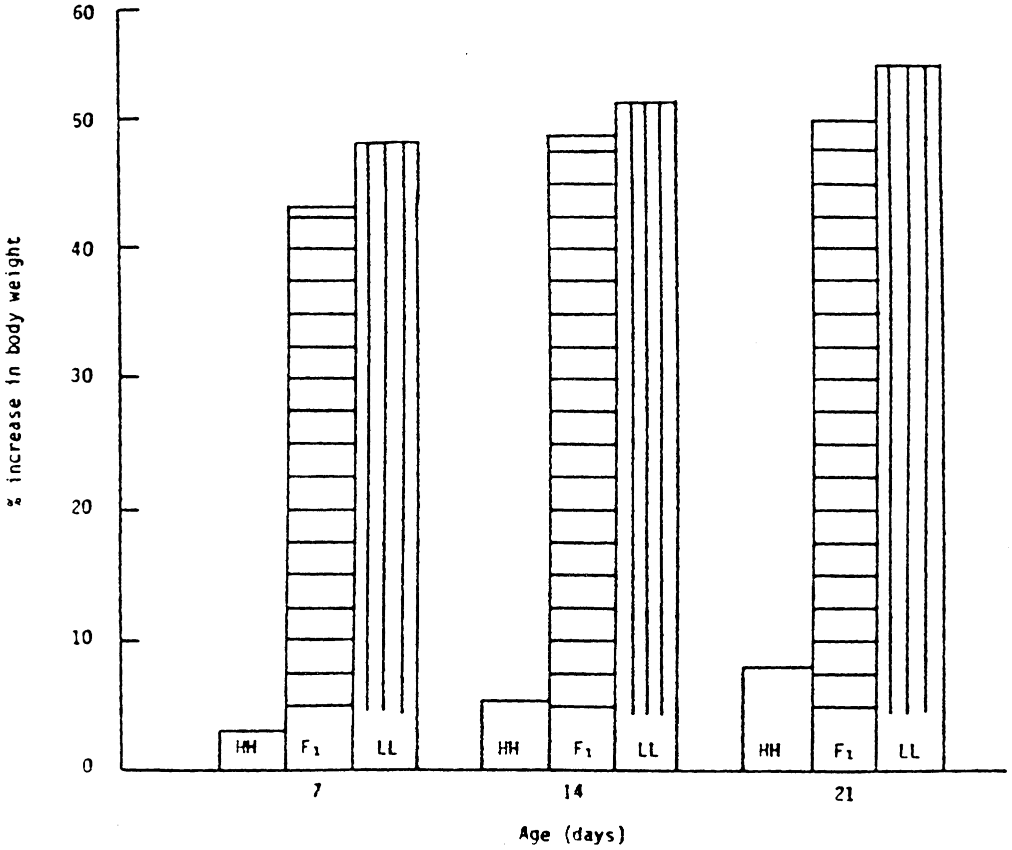

Figure 10. Percentage increase in body weight of each mating type due to overfeeding

GENERAL SYNTHESIS

Two lines of chickens, one selected for high and the other for low body weight at 56 days of age, were established through individual phenotypic selection (Siegel, 1978). Twenty-five generations of such selection has resulted in a greater than five-fold phenotypic difference between the lines for the selected trait. A major positive correlated response to selection for body weight is feed consumption (McCarthy and Siegel, 1983). When feed consumption exceeds an optimum there are, in addition to negative reproductive consequences, undesirable aspects in the context of broiler production. This undesirability is because food consumption in excess of that required for maintenance and normal growth increases fat deposition which, in turn, increases processing losses and consumer resistance to the product.

The experiments reported in this dissertation support the thesis of Marks (1979; 1980) that important alterations in growth rate and feed consumption in weight selected populations occur during the first week posthatching. Major differences in relative growth rate between the high and low weight lines were observed within this time frame. Differences between lines in feed consumption were observed during the first week posthatching, while differences in water intake appeared at older ages. These temporal disparities caused major differences in the feed:water ratios between the lines during the first week which, in turn, possibly influenced the gross feed efficiency and body composition of the lines.

Genetic analyses of feed and water consumption, using data from F_1, F_2 and backcross generations, indicate that the heritable variation was principally additive. Early feed intake appeared to be influenced by potence in the direction of the high weight line, while concurrent water intake was similar among all pureline and crossbred chicks. Positive heterosis was observed for feed efficiency and was associated with an equivalent negative heterosis for percentage of carcass fat. In addition, there was evidence for non-additive genetic variation for hedonic sensitivity towards quinine sulfate and dextrose solutions, while additive genetic variation appeared to influence the preference ratios for these solutions at super-threshold concentrations.

Manipulation of early feed and water intake via restriction and force feeding techniques, effectively eliminated ingestive behavior as a variable in growth rate and its correlates. The improved feed efficiency associated with limited feed intake of faster growing birds indicated that positive appetite differentials (i.e., overeating) influence gross feed efficiency. That appetitive factors can be overcome via force feeding, and the feed efficiency of a slow growing bird can be improved further suggested that a negative appetite differential (i.e., undereating) can also reduce gross feed efficiency. This observation would implicate the existence of an intermediate optimum genetic factor when balanced within normal physiological limits.

These data, along with those from the taste trials, further support the existence of a genetic threshold influencing food intake control mechanisms. Directional potence was observed for traits considered having fitness value (e.g., early feed intake, feed efficiency, adipose depots, responsiveness to food related stimuli), whereas additive genetic variation was observed for traits indirectly influencing overall fitness (e.g., cumulative feed and water intake, body weight, % carcass ash, % carcass moisture).

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GENETIC ANALYSES OF FOOD CONSUMPTION IN GROWTH SELECTED LINES OF CHICKENS

by

Guy F. Barbato

(ABSTRACT)

The heritable variation of body weight in two lines of chickens divergently selected for high and low juvenile body weight, as determined from parental line, F_1, F_2 and backcross generations, was principally additive. Feed intake during the first few weeks posthatching was influenced by potence in the direction of the high-weight line, while no comparable pattern was noted for early water intake. Heterosis was observed for feed efficiency which was associated with an equivalent negative heterosis for percentage carcass fat.

Feed intake of chicks from the high-weight line and reciprocal crosses were restricted to that of chicks from the low-weight line. This restriction resulted in a greater depression in body weight of the high-weight line than of cross chicks. In contrast, a comparable restriction of water consumption resulted in a similar (10%) depression of body weight among both high-weight line and cross chicks. The effect of feed and water restriction on feed:water ratios was dependent upon mating type.

The amount of feed introduced into the crop of chicks from the high-weight line via overfeeding was similar to their *ad libitum* intake. Chicks from the low-weight line could be overfed at earlier ages and to a greater degree than either high-weight or cross chicks. The degree of overfeeding was associated with the relative size of certain gastrointestinal components. Differences among populations were reflected in concomitant changes in body weight and carcass fat.

Comparisons among the parental line and F_1 progeny provided evidence for nonadditive genetic variation for hedonic sensitivity towards quinine sulfate and dextrose, though in opposite directions. Additive genetic variation appeared to influence the preference ratios for both stimuli at super-threshold concentrations.

These data suggest the absence of a simple relationship among growth, feed intake control and body composition. It is hypothesized that in addition to their commonality, different genetic systems exist for the expression of high and low body weight as well as their various correlates. The implications of these systems are discussed within the context of feed intake control and future genetic changes in growth.