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BARD

FINAL REPORT

PROJECT No. I-89-79

**Genetic Variation in Minimum Body
Weight Requirement for the Onset of
Sexual Maturity in Broiler Chickens and
its Genetic Covariation with Growth-Rate
Components**

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BARD Research Proposal No. I-89-79

Title of Proposed Research

Genetic variation in minimum body weight requirement for the onset of sexual maturity in broiler chickens and its genetic covariation with growth-rate components

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Projects Commencement date: November 1979

Type of Report: Final

Signature:

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מספרית הספרים
מסדע הקולומה
היום 1979

- 1) Broilers (Poultry) - Breeding
- 2) Poultry - Feed utilization efficiency
- 3) Poultry - Weight and measurements

$$\frac{630.72}{BAR} : 636.508.2$$

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C. ABSTRACT

Lean body development was critical for the onset of sexual maturity in White Rock broiler strain females. Body fat content or fat percentage alone was not sufficient to initiate sexual maturity (Section D.1.1). These results were confirmed by studies in quail (Section D.1.2). Level of food restriction during the rearing period did not affect minimum lean weight for onset of sexual maturity (Section D.1.1).

Food intake of broiler pullets can be restricted more intensely during the rearing period than is customary, without a deleterious effect on subsequent egg production. Any delay in onset of sexual maturity can be avoided by increasing food intake sharply toward the end of the rearing period so as to bring the birds up to the minimum weight by the desired target date for onset of lay (Section D.1.3).

A minimum age as well as a minimum body weight and/or composition is necessary for the onset of lay, and weight at sexual maturity was more closely related to mature body weight than to juvenile body weight (Section D.1.4).

Minimum weight for onset of sexual maturity showed a moderate heritability in White Rock broiler strain populations and a low phenotypic and genetic correlation with early growth-rate (Section D.1.5). Three generations of two-way selection for high and low minimum weight for onset of sexual maturity gave a strong separation between lines for this trait (350 g) with only a minor and nonsignificant effect on early growth-rate (Section D.1.6).

A theoretical model was developed relating selection for early growth-rate to fat deposition, and suggesting that selection for weight gains under conditions of uniform restricted food intake (Kielenowski, 1969) might avoid correlated effects on fat deposition (Section D.2.1). Theoretical analysis of this proposition defined a wide range of circumstances under which this sort of selection could be superior to the usual selection for early growth-rate under ad libitum feeding conditions, as a means of improving overall feed efficiency of meat producing livestock and poultry (Section D.2.2). Initial experimental studies showed moderate heritability and considerable phenotypic variation for gains under restricted uniform food intake in White Rock broiler populations, but response to three generations of selection was disappointing (Section D.1.6), probably because of technical problems (Section D.2.3).

Analysis of growth differences between light and heavy breed chicks in an advanced segregating generation of a White Rock x Leghorn cross, showed changing patterns of fat deposition over age, and evidence of segregation in weight, food intake, relative food intake and fat deposition, but not in efficiency (Section D.2.4).

Food restriction and meal feeding in light-breed chicks improved energy utilization and affected bacterial contents of the intestinal chyme, lipogenesis and digestive enzyme activity (Section D.2.5). Intermittent feeding in heavy breed chicks had marked effects on plasma hormone levels (Section D.2.6).

D.1.1 Effect of diet and early quantitative food restriction on the minimum weight requirement for onset of sexual maturity.

INTRODUCTION

The minimum weight for onset of sexual maturity is of importance in that it sets a lower limit to the degree of food restriction that can be implemented in broiler breeder flocks. This minimum weight in broiler stocks however, is well above the body weight at which layer strain females enter and maintain lay (Brody et al. 1980; Soller et al. 1983). The high minimum weight in broiler strains, therefore, may represent neither a physiological nor an anatomical requirement per se for lay. It is of interest, therefore, to determine to what extent this minimum weight for onset of sexual maturity can be manipulated by experimental procedures. This study was carried out to investigate the effect of diet and early food restriction on minimum weight for onset of sexual maturity in broiler strain females.

MATERIALS AND METHODS

The experiments were carried out at the East Talpiot (Jerusalem) experimental farm of the Hebrew University, using White Rock broiler strain female chicks obtained from Kibbutz Yavne Poultry Breeding Farm and hatched on December 5, 1978. From hatch until 5 weeks of age, chicks were kept in brooder batteries. They were then transferred to individual laying type cages, with individual feeding troughs. Birds were fed in the morning once daily. Food restriction was based on limiting the quantity of food provided. All birds were fed as follows: From 0 to 4 weeks of age, a proprietary starter mash (2950 cal ME/g, 21.2% protein); from 5 to 20 weeks, a replacement pullet mash (2950 cal ME/g, 14.0% protein). From 20 weeks diet differed according to treatment group as described in the next section. From 13 weeks of age the birds received 16 h of continuous light daily and 8 h of darkness.

Experiment 1 (early quantitative food restriction), included three experimental groups of 20 birds each, subjected respectively, to moderate,

severe and very severe quantitative food restriction during the rearing period. Food intake of severely restricted birds (designated, SR) and of very severely restricted birds (designated, SRR) was limited from day of hatch throughout the rearing period. These birds were weighed weekly or bi-weekly, and food quantities adjusted so as to allow body weight to increase gradually to the 20 week target weights (~1300 g for SR birds and ~700 g for SRR birds). Food intake of moderately restricted birds (designated, MR) followed a normal commercial feeding schedule during the rearing period. These birds were fed ad libitum (i.e., allowed unlimited access to food) from hatch to 5 weeks of age. Thereafter, and until the end of the rearing period, food intake was adjusted as necessary so as to allow body weight to increase gradually to the 20 week target weight (~1900 g). From 20 to 24 weeks the three groups were fed different quantities of a proprietary broiler breeder layer mash (2800 cal ME/g, 15.3% protein) so as to bring all groups to a uniform mean body weight of ~2200 g at 24 weeks of age. From 24 weeks they were fed increasing amounts of the above layer mash, allowing them to gain ~150 g/week. The birds were continued on this regime until first egg.

Experiment 2 (diet) included two treatment groups of 20 birds each. From hatch to 20 weeks of age, both groups were raised under the SR food restriction program as described above. From 20 weeks the birds were fed increasing amounts of food adjusted so as to allow them to gain about 150 g/week. Group 1 (low ME/P ratio) was fed a proprietary turkey starter mash (2850 cal ME/g, 25.4% protein, ME/P ratio = 116). Group 2 (high ME/P ratio) was fed a proprietary turkey finishing mash (3100 cal ME/kg, 15.0% protein) to which 2% corn oil by weight was added to give a final composition of 3215 cal ME/kg, 14.7% protein (ME/P ratio = 219). The birds continued on this regime until

first egg.

An ad libitum control group (20 birds) was fed a proprietary broiler breeder mash as above, from 20 weeks.

Data collection and analysis

Minimum weight for onset of sexual maturity in these birds was determined as follows. Body weight of the birds was kept below the minimum weight for onset of sexual maturity in this strain (about 2400-2700 g, Brody et al., 1980) until the ad libitum control group entered lay. Food intake of the birds was then increased, allowing them to increase gradually in body weight by about 150 g/week. This ensured that any age requirement for onset of lay (Brody et al., 1980; Dunnington et al., 1983) had been met, before the minimum body weight requirement for onset of sexual maturity was reached. On this basis it is assumed that as the birds gradually increased in body weight, each bird eventually reached its own minimum weight for sexual maturity, with first egg following shortly thereafter. Thus, the weight of the bird at first egg under these conditions, can be expected to stand in close relation to its minimum weight for onset of sexual maturity.

All birds were killed at first egg by chloroform anesthetization. Ovary and oviduct were examined to confirm that the birds were in lay. The birds were plucked and weighed. Gizzard and proventricular contents ("fill") were weighed and subtracted from plucked body weight to give carcass weight. Breast weight (including sternum, but with external fat removed) shank length and abdominal fat pad weight were obtained. Breast weight in this strain is highly correlated with lean body weight (Plotkin, 1982). Shank length is a commonly accepted measure of linear growth (see, e.g., Nir et al., 1978). Abdominal fat pad is highly correlated with body fat content (Becker et al., 1979).

Body composition analyses were carried out on about half of the birds in each experimental group. The featherless carcass (less fill) was ground, mixed thoroughly and a representative sample taken for duplicate determinations of dry matter, ash and fat. Protein content was obtained by subtraction ($\% \text{ protein} = \% \text{ dry matter} - \% \text{ fat} - \% \text{ ash}$). Dry matter and fat were determined as in Nir et al. (1974). Lean body weight was calculated as carcass weight $\times (1.0 - \% \text{ fat})$.

Statistical analyses were carried out using the SPSS package (Nie et al., 1975).

RESULTS

The ad libitum control birds weighed 3317 g at 138 days of age (20 weeks), at which time some of the birds had already (just) entered lay. Mean age at first egg for these ad libitum fed birds was 143.5 days.

Age and body character measures at first egg for both experiments are given in Table 1. Body composition data are given in Table 2. All birds in the treatment groups showed fully developed ovaries and oviduct at the time of sacrifice.

Effect of early quantitative food restriction on body characters and composition at onset of lay (Experiment 1).

Moderately restricted (MR) and severely restricted (SR) birds entered lay at almost the same age and were virtually identical in all body measures except for greater abdominal fat pad weight in the SR group. The severely restricted birds (SRR) entered lay significantly later than the MR or SR birds, and at a greater carcass weight, abdominal fat pad weight, and shank length. Dry matter content (i.e. both % dry matter and total dry matter) and total fat were also greater in this group. Breast weight was similar in all three groups, as were ash content, % protein and lean body weight. The greater shank length of the SRR birds may possibly represent a longer exposure to low level estrogen-dependent skeletal growth stimulation (Short, 1982). Thus, birds of the three treatment groups entered lay at the same lean body weight, ash and protein content, but at different carcass weight, shank length, dry matter and fat content.

Effect of diet on body characters and body composition at onset of lay (Experiment 2).

The birds in the two diet groups entered sexual maturity at similar ages, and were also similar in breast weight, shank length, ash content and % protein.

Table 1. Age and body characters at first egg by experiment and treatment group.¹

Experiment	Treatment group	Number of birds	Carcass weight (g)	Breast weight (g)	Abdominal fat pad (g)	Shank length (cm)	Age (d)
1	Moderate restriction (MR)	21	2755a	525.6	101.5 ^a	10.40ab	192.6 ^a
	Severe restriction (SR)	13	2810ab	498.5	121.8ab	10.35a	193.7 ^a
	Very severe restriction (SRR)	13	3060bc	534.4	145.8 ^b	10.96c	212.3 ^b
2	Low ME/P ratio	14	2879ab	512.2	119.6ab	10.66bc	189.2 ^a
	High ME/P ratio	11	3229c	507.3	229.3c	10.71bc	196.4 ^a
F-ratio ²			4.83**	0.58NS	18.59***	5.30***	4.00**

¹Values in the same column having different superscripts, differ significantly by Duncan's multiple range test ($P < 0.05$).

²F-ratios for one-way analysis of variance over all treatment groups: **, $P < 0.01$; ***, $P < 0.001$.

Table 2. Body composition at first egg by treatment group and experiment.¹

Experiment	Treatment group	Number of birds	Carcass weight (g)		Dry matter		Ash		Fat		Protein		Lean body weight ²
			(g)	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)	(g)	
1	Moderate restriction (MR)	9	2808 ^a	1079.0 ^a	38.5 ^a	1079.0 ^a	3.32	93.2	16.6 ^a	473.3 ^{ab}	18.6	527.1 ^a	2344
	Severe restriction (SR)	7	2761 ^a	1076.0 ^a	39.0 ^a	1076.0 ^a	3.26	89.6	17.3 ^a	478.8 ^{ab}	18.4	508.3 ^a	2282
	Very severe restriction (SRR)	9	2992 ^{ab}	1246.2 ^b	41.6 ^b	1246.2 ^b	3.16	94.4	19.2 ^a	574.3 ^b	19.3	577.5 ^{ab}	2418
2	Low ME/P ratio	9	2744 ^a	1088.3 ^a	39.7 ^{ab}	1088.3 ^a	3.24	88.7	17.1 ^a	466.6 ^a	19.4	533.0 ^a	2277
	High ME/P ratio	6	3279 ^b	1470.5 ^c	44.7 ^c	1470.5 ^c	2.83	93.8	22.9 ^b	756.6 ^c	19.0	619.8 ^b	2522
F-ratio ³			4.31**	10.35***	10.64***	2.26NS	0.34NS	7.04***	10.43***	0.58NS	2.91*	1.34NS	

¹Values in the same column having different letter superscripts differ significantly by Duncan's multiple range test (P<0.05).

²Calculated as Carcass weight x (1 - % fat).

³F-ratios for one-way analysis of variance over all treatment groups: *, P<0.05; **, P<0.01; ***, P<0.001.

The birds fed the higher ME/P ratio had a significantly greater carcass weight and abdominal fat pad weight. Total protein and body fat content were also greater in this group as was lean body weight. The difference in lean body weight, however, was not statistically significant by t-test ($0.10 < P < 0.05$), or by Duncan's multiple range test. Thus, the birds of the two experimental groups entered lay at the same lean body weight, shank length and ash content, but at different carcass weight, dry matter content and fat content.

Effect of experimental treatments on body characters and body composition at onset of lay (Experiments 1 and 2 considered together).

When both experiments are considered together, birds of the different treatment groups entered lay at different age, carcass weight, shank length, total protein, dry matter and fat content, but at similar breast weight, lean body weight, % protein and ash content. The implications of these observations, particularly with respect to fat content and lean body weight will be considered in the DISCUSSION.

DISCUSSION

Effect of early food restriction on WTSXM

Very severe food restriction (SRR) throughout the rearing period resulted in a significant increase in carcass weight at first egg when the birds were gradually released from restriction. Thus, this treatment appears to have increased minimum weight for onset of sexual maturity (WTSXM) as defined in METHODS. The increase in carcass weight, however, was primarily due to an increase in body fat content. When breast weight or lean body weight are considered, differences between the restriction treatment groups were small and statistically nonsignificant. Thus, restriction level during the rearing period did not appear to affect minimum lean weight at onset of sexual maturity. The increase in body fat in the SR and SRR groups may be a secondary consequence of the more or less prolonged period of compensatory growth on a mash with relatively high ME/P ratio. That the SR and SRR treatments had a true stunting effect is shown by comparable groups of birds raised simultaneously and subjected to similar restriction treatments: when changed to ad libitum feeding at the end of the rearing period, these chicks showed clear stunting as compared to ad libitum controls, even at 60 weeks of age (Eitan et al., 1983).

Effect of diet on WTSXM

A high ME/P ratio during the period of compensatory growth, also resulted in a significant increase in carcass weight at first egg on gradual release from restriction, as compared to a low ME/P ratio. Here, too, the increase in body weight can be attributed primarily to an increase in body fat content, while breast weight was virtually identical in the two groups. There was, however, an appreciable difference in lean body weight, albeit not statistically significant. Consistent with this, the SRR treatment group, which received a relatively high ME/P ratio during compensatory growth also showed an increase in lean body weight at onset of sexual maturity, while the low ME/P group had the lowest carcass weight and lean body weight of all treatment groups, although

only marginally so. Thus, the results of these experiments do not rule out an effect of diet on lean weight at the onset of sexual maturity.

Body fat content and WTSXM

Frisch and MacArthur (1974) have suggested that a minimum body fat composition may be the critical factor determining the onset of sexual maturity. In its strong form the body fat hypothesis states that attainment of a given body fat composition alone, is sufficient to trigger the onset of sexual maturity. To the extent that some minimum fat content or fat percentage is sufficient to initiate the onset of sexual maturity, however, this level would have been reached earlier by the SRR birds or by the high ME/P group, and they would have been expected to enter sexual maturity and lay earlier than the SR, MR or low ME/P groups. This did not occur. If anything, the high fat content birds entered sexual maturity at a later age and higher body weight than the other experimental groups. Similarly, 12 week old broiler female chicks (Brody et al., 1980) do not enter sexual maturity although their body composition is well within the range compatible with onset of menarche and lay. In this case, however, it is possible that the onset of sexual maturity was prevented by an age requirement, as indicated, for poultry at least, by Brody et al. (1980) and Dunnington et al. (1983). This possibility is eliminated in the present experiment, since the birds were well past any minimum age for sexual maturity as indicated by the ad libitum control group. Thus the results of this study indicate unequivocally that body fat content or fat percentage alone, is not sufficient to initiate sexual maturity in these birds.

Lean body weight and WTSXM

A provocative aspect of our results is the finding that lean body weight at first egg was relatively unaffected by a variety of experimental treatments, although these treatments did affect total carcass weight, dry matter and

fat content and age at first egg. This suggests that it was lean body development that was critical for the onset of sexual maturity in these birds, i.e., that there is a minimum lean body mass requirement for the onset of sexual maturity. These results do not exclude the possibility that a minimum body fat composition is also required for sexual maturity, but if so, the birds in this experiment and that of Zelenka et al. (1982) must have reached this minimum fat percentage before they attained the minimum required lean body weight.

D.1.2. Effect of diet and early food restriction on the onset of lay in Japanese quail.

In order to examine the relationship of body fat content to onset of sexual maturity, female Japanese quail were reared on isocaloric diets containing 26, 24, 20, 16 and 14% crude protein. For each protein level, quail were also fed ad libitum, 80% of ad libitum and 60% of ad libitum. Each quail was sacrificed on the day of first egg and abdominal fat weight, as a measurement of body fat, and breast weight, as a measurement of lean body mass, were obtained. Dietary protein did not significantly ($P \geq .05$) affect the amount of abdominal fat at the onset of lay under ad libitum feeding. Under restricted feeding, however, the females fed the higher levels of dietary protein entered lay with significantly less abdominal fat, expressed as either a percentage of body weight or on a total weight basis, than did the ad libitum fed quail. When fed diets containing lower protein (14 and 16%), the restricted fed females entered lay with more abdominal fat in comparison to the ad libitum fed birds. Breast weights, on the other hand, were relatively constant at sexual maturity. The results do not support the hypothesis that a lipostat is involved in the initiation of sexual maturity.

D.1.3 Effect of severe quantitative food restriction from day of hatch through the rearing period on egg production in broiler breeders.

INTRODUCTION

Brody et al. (1980) have proposed that the minimal body size requirement for the onset of sexual maturity and lay in pullets may be the primary explanation for the observed direct relationship in pullets between the degree of food restriction (and consequent reduction in body weight) during the rearing period, and the length of the subsequent interval between the removal of restriction and the onset of lay (Lee et al., 1971; Pym and Dillon, 1974). Aside from a shift in the entire production curve to higher ages, however, the degree of restriction does not appear to have any untoward effect on egg production (Lee et al., 1971, Pym and Dillon, 1974). This suggests that it might be possible to intensify the degree of restriction of broiler pullets during the rearing period beyond customary practice without untoward effects on egg production, while avoiding an excessive delay in the onset of sexual maturity, by allowing the birds sufficient additional food toward the end of the restriction period to bring them to the minimal weight for sexual maturity shortly before the desired target date for the onset of lay. Combined with continued food restriction during the laying period, such a feeding regime might lead to an appreciable reduction in overall food consumption (Brody et al., 1980). This study was carried out to investigate these possibilities.

MATERIALS AND METHODS

Three series of experiments were carried out, using White Rock broiler strain female chick . Experiments 1 and 3 were carried out at the Hebrew University, Jerusalem. These experiments were intended to explore the effects of severe food restriction from day of hatch throughout the rearing period, on subsequent reproductive performance. Experiment 2 was carried out at the research farm of the Israel Poultry Breeders Union, Acre. This experiment was intended to test the possibility of bringing severely restricted birds to sexual maturity at a given target date, by sharply increasing their food intake (and hence their body weight) at the end of the rearing period.

Stocks and management

Table 1 shows source of stocks, hatching dates, duration of the experiments, rearing conditions, restriction treatments and number of birds per treatment in each experiment. Birds were fed in the morning, once daily, except for Saturdays, with a double ration on Fridays. Food restriction was based on limiting the amount of food provided. When restricted birds were in batteries or pens, a large feeding area (10 cm per bird) was provided to minimize competition for food between the birds. When in cages, birds were fed individually in separate troughs (in experiments 1 and 3, but not in experiment 2). The birds were fed as follows. In experiments 1 and 3: from 0 to 4 weeks of age, a proprietary replacement pullet mash (210 g protein and 10.7 MJ ME/kg), from 5 to 22 weeks, a proprietary grower mash (140 g protein and 11.0 MJ ME/kg) and from 23 weeks, a proprietary layer mash (150 g protein and 10.6 MJ ME/kg); in experiment 2: from 0 to 2 weeks, a proprietary broiler starter mash (220 g protein and 11.5 MJ ME/kg), from 3 to 6 weeks, a proprietary broiler mash (200 g protein

Table 1. Experimental treatments and experimental conditions

Experiment No.	Restriction level	No. of birds	Target weight for age	Experimental conditions			
1	Ad libitum (AL)	40	-	<u>Source of stock</u>			
	Moderate (MR)	20	2200 g/22 w	Exp. 1 and 3, Yavne Poultry Breeding Farm			
	Severe (SR)	20	1200 g/22 w	Exp. 2, Israel Poultry Breeders Union			
2	Moderate (MR)	162	2100 g/22 w	<u>Hatching date and duration of experiment</u>			
	Severe (SR)	150	1100 g/22 w	Exp. 1, July 29, 1978, 45 w			
				Exp. 2, July 25, 1978, 38 w			
3	Ad libitum (AL)	20	-	<u>Rearing Conditions</u>			
				<u>Batteries</u>	<u>Floor</u>	<u>Cages</u>	
	Moderate (MR)	20	2200 g/22 w	Exp. 1	0-5 w	6-22 w	23 w+
				Exp. 2	-	0-22 w	23 w+
	Severe (SR)	20	1200 g/22 w	Exp. 3	0-5 w	-	6 w+
	Very Severe (SRR)	20	700 g/22 w				

and 11.6 MJ ME/kg), from 7 to 22 weeks and from 23 weeks a proprietary grower mash and a proprietary layer mash as in experiments 1 and 3. Artificial light was not supplied during the rearing period. From 22 to 30 weeks the birds received 16 h of light daily (04:00 to 20:00 h). From 31 weeks of age this was increased to 17 h daily (0 :00 to 21:00 h).

Experimental treatments

In all experiments, food intake of severely restricted birds (designated, SR) and of very severeley restricted birds (designated, SRR) was limited from day of hatch throughout the rearing period. These birds were weighed weekly or bi-weekly, and food quantities adjusted so as to allow body weight to increase gradually toward the 22 week target weights (~1200 g for SR birds and ~700 g for SRR birds). Food intake of moderately restricted birds (designated MR) during the rearing period, was intended to follow a normal commercial feeding schedule. These birds were fed ad libitum (i.e., allowed unlimited access to food) from hatch to 4 weeks of age (experiments 1 and 3) or from hatch to 7 weeks of age (experiment 2). Thereafter, and until the end of the rearing period, food intake was adjusted as necessary so as to allow body weight to increase gradually to the 22 week target weight (~2200 g).

From 22 to 26 weeks, food intake of the MR birds was increased sharply each week, reaching 150 g/day in experiments 1 and 3 and 145 g/day in experiment 2, remaining constant thereafter, throughout lay. From 22 weeks to the end of the experiment, SR and SRR birds of experiments 1 and 3 were allowed unlimited access to food. In experiment 2, however, food intake of the SR birds was increased sharply from 19 weeks, and exceeded that of the MR birds from 21 to 28 weeks. This was done in order to bring them to the same weight as the MR birds at the target date for onset of

lay (26 weeks). From 28 weeks of age, food intake of these birds was kept constant and equal to that of the corresponding MR birds (145 g/day).

Data collection and analysis

Birds were weighed individually every one or two weeks and at first egg. Age at first egg was also recorded. Egg weight was obtained individually for each bird at a minimum of two points during the reproductive period. Egg numbers were recorded individually for each bird from first egg. Food intake of restricted birds was calculated by multiplying food allotments during a particular feeding period by the duration of the period. Food intake of ad libitum fed birds was calculated by taking the total amount of food allotted to a particular experimental group during a particular feeding period, and dividing by the average number of birds in the treatment group during the feeding period. Food intake of the ad libitum (AL) group of experiment 1 was not measured at all, and that of the AL group of experiment 3 was measured during lay only. Differences between group means were tested for significance by standard methods (Snedecor and Cochran, 1967).

RESULTS

Mortality

Table 2 shows percent mortality from hatch to 22 weeks by treatment and experiment. In experiment 1 there was little if any difference in viability between treatment groups. In experiments 2 and 3, however, there was a significant excess mortality in the severely restricted groups. In experiment 2, part of this excess mortality could be attributed to an outbreak of coccidiosis, apparently due to lack of sufficient coccidiostat in the limited ration. The reason for the increased mortality in experiment 3 is not clear.

Food intake

Table 3 gives food intakes for the various treatment groups by experiment and feeding period. In each case food intake of the SR birds until 22 weeks was about 4 kg less than that of the MR birds, while food intake of the SRR birds of experiment 3 was 6 kg less than that of the MR

Table 2. Mortality (%) from hatch to 22 weeks of age, by experiment and restriction level.

Experiment No.	Restriction level			
	<u>Ad libitum</u> (AL)	Moderate (MR)	Severe (SR)	Very severe (SRR)
1	15 ^b	17 ^b	15 ^b	-
2	-	7 ^a	28 ^{c,1}	-
3	30 ^c	17 ^b	29 ^c	62 ^d

Values with different superscripts, differ significantly from each other (P<0.05).

¹Of the total mortality, 15% was general mortality and 13% was due to an outbreak of coccidiosis at 7 weeks of age.

Table 3. Food intake (kg) by feeding period, experiment and restriction level.

Feeding period and Experiment No.	Restriction level			
	<u>Ad libitum</u> (AL)	Moderate (MR)	Severe (SR)	Very Severe (SRR)
<u>Rearing period (0-22 w)</u>				
Exp. 1	-	8.7	4.5	-
Exp. 2	-	8.9	5.1	-
Exp. 3	-	9.0	4.9	3.1
<u>Compensatory growth (23-35 w)</u>				
Exp. 1	-	12.4	17.4	-
Exp. 2	-	13.2	14.1	-
Exp. 3	-	15.7	18.2	17.6
<u>Remainder (36 to -)</u>				
Exp. 1 (40 w)	-	5.5	6.3	-
Exp. 2 (38 w)	-	3.0	3.0	-
Exp. 3 (50 w)	21.4	15.8	21.2	20.8

birds. In experiments 1 and 3 the SR and SRR birds were allowed unlimited access to food from 22 weeks of age. During the ensuing period of compensatory growth (22-35 weeks) they consumed considerably more food than the MR birds, the excess more or less equalling savings during the rearing period. In experiment 3, food intake of the SR and SRR birds following the period of compensatory growth more or less approximated that of the AL birds. In experiment 2, where food intake was controlled throughout, overall food intake of the SR birds was some 2 kg less than that of the MR birds. Thus in this case a net savings in food intake was achieved.

Onset of lay and egg production

The onset of lay by treatment groups and experiments, as indicated by the week at which 20% egg production was first achieved, was estimated from the unadjusted egg production curves (not shown, but see later) and is given in Table 4. In experiments 1 and 3 the birds in the various treatment groups were released from restriction at the same time, but at very different body weights. In these experiments, the onset of lay in the restricted groups was delayed in proportion to the degree of restriction. This effect is attributed to the additional time required for the birds in the more severely restricted groups to reach the minimal weight for the onset of lay (Brody et al., 1980). For this reason, egg production curves for the various treatment groups in these experiments were superimposed, starting from the week in which 20% production was first reached. When this is done (Figures 3 and 5) it becomes evident that the various restricted groups had similar egg production curves, counting from the onset of lay, while egg production of the AL groups was either less

Table 4. Age (weeks) at sexual maturity (20% egg production) by experiment and restriction level.

Experiment No.	Restriction level			
	<u>Ad libitum</u> (AL)	Moderate (MR)	Severe (SR)	Very severe (SRR)
1	25	27	30	-
2	-	25	26	-
3	20	23.5	27	29

persistent (experiment 1) or reached a lower peak (experiment 3) than that of the restricted groups. Experiment 1 also includes an ad libitum fed Leghorn control group. In experiment 2, as described above, a deliberate effort was made to bring SR and MR birds into lay at the same time, by allotting additional food to the SR birds (over and above that given to the MR birds) during the weeks immediately prior to lay. This was successful, and the SR birds lagged only a few days behind the MR birds on entry into lay. Thereafter, egg production of the two groups was virtually identical (Figure 4).

Egg weight and abnormal eggs

Table 5 gives egg weight by treatment group, experiment and age of birds. In experiments 1 and 3 egg weight at any given age generally decreased according to the severity of prior food restriction during the rearing period. Egg weight in all groups, however, was similar when compared at equivalent intervals from the onset of lay. In experiment 2, where SR and MR birds entered lay at almost the same time, egg weight was virtually identical in both groups. In experiment 2 a record was also kept of abnormal eggs (double yolks and soft shell). In this case the incidence of abnormal eggs was significantly less for the SR birds (2.1%) than for the MR birds (3.3%).

Table 5. Egg weight (g) by age of bird, experiment and restriction level

Experiment and age	Restriction level			
	Ad libitum (AL)	Moderate (MR)	Severe (SR)	Very severe (SRR)
<u>Exp. 1</u>				
34 w	59.6	58.1	56.8	-
37 w	60.6	60.4	58.8	-
<u>Exp. 2</u>				
30 w	-	54.8	54.2	-
31 w	-	56.5	56.3	-
<u>Exp. 3</u>				
35-39 w	59.2	60.1	58.7	57.8
40-42 w	62.2	62.1	61.2	60.2
43-48 w	63.5	63.1	62.4	61.1
49-55 w	65.5	65.2	65.9	62.7

Least Significant Difference ~1.0 g ($P < 0.05$).

DISCUSSION

Mortality

In these experiments, severe restriction during the rearing period was generally, but not always, accompanied by increased mortality. In part this was due to the difficulty in delivering sufficient coccidiostat to the restricted chicks in the limited food quantities allotted. Similar observations are common in the literature (Lee, 1971). Lee (1971) and Pym and Dillon (1974) report that administering coccidiostat in the water provided good coccidiosis control, even when rather severe restriction was practiced during the rearing period. Some or all of the remaining mortality excess in these experiments may have been due to the nutritionally naive restriction procedure utilized (all treatment groups received greater or lesser quantities of the same standard feeds). It is possible that more sophisticated rations, designed to ensure adequate nutrition to the SR or SRR chicks during the rearing period might have reduced or eliminated the increased mortality.

Onset of lay

In experiments 1 and 3 birds at different degrees of restriction were kept on restriction until a given date and then released to ad libitum (SR

and SRR birds) or to a controlled increase in food quantity (MR birds). In these experiments the onset of lay was delayed in rough proportion to the degree of food restriction during the rearing period, as reported in the literature (Lee et al., 1971; Pym and Dillon, 1974). In experiment 2 SR birds were fed increased quantities of food two weeks before food quantities were increased for the MR birds. In this experiment the onset of lay was at essentially the same age in the two groups of birds although they were subject to very different degrees of restriction during the rearing period. These results are consistent with the hypothesis that food restriction during the rearing period delays the onset of lay by increasing the time required for the bird to reach the minimal body weight required for the onset of sexual maturity and lay (Brody et al., 1980). Experiment 2 shows that even very severe restriction during the rearing period need not result in an untoward delay in the onset of lay in broilers, provided that the birds are allowed additional food toward the end of the rearing period, enabling them to reach minimal body weight for sexual maturity at the desired target date. Data which can be interpreted similarly have also been reported for cattle (Crichton et al., 1959), pig (Dickerson et al., 1964), rat (Kennedy and Mitra, 1963) and human (Frisch and Revelle, 1970; Frisch, 1972).

Egg production and egg weight

All restricted groups showed better egg production than the corresponding AL birds, either by virtue of high peak production (experiment 3) or greater persistency (experiment 1). When restriction groups are compared, however, peak production and persistency were more or less similar within the limits of sampling error. Thus a restriction schedule in broiler strain pullets, more extreme in degree and duration than those commonly reported in the literature (Blair et al., 1976; Fuller et al., 1973; Luther et al., 1976;

Powell and Gehle, 1976; Pym and Dillon, 1974; Watson, 1975) did not appear to have any major effect on the shape of the egg production curve. This is in accord with published in the literature with respect to layers (Lee, 1971), and was found whether severely restricted birds were changed to ad libitum feeding during reproduction (experiments 1 and 3) or maintained on restricted feeding (experiment 2). In these experiments the degree of restriction also did not appear to have any effect on the egg weight curve, relative to the onset of lay. Egg weights were similar at any given stage of the egg production curve, although distinctly different at any given chronological age, depending on the delay in the onset of lay induced by restriction. In experiment 2, where SR and MR groups came into lay at about the same age, egg weight was virtually identical in the two groups.

Food consumption

In all three experiments, severe or very severe restriction during the rearing period resulted in significant savings in food intake of SR and SRR birds relative to the MR birds. In experiments 1 and 3, in which the SR and SRR birds were changed to ad libitum feeding at the end of the rearing period, these savings were totally exhausted during the period of compensatory growth. In experiment 2, however, in which food consumption during the period of compensatory growth was controlled, a net savings of about 2 kg food per bird was achieved, apparently without any reduction in egg production and with a delay of only a few days in onset of lay. Even this delay could probably have been avoided by increasing the food intake of the SR birds somewhat earlier. Taken together, these experiments suggest: that broiler pullets can be restricted more intensely during the rearing period than is customary, without a deleterious effect on reproduction; that the delay in onset of sexual maturity can be avoided by increasing food intake sharply toward the

end of the rearing period, so as to bring the birds up to the minimum weight for onset of sexual maturity prior to the desired target date for the onset of lay; and that a combination of the two procedures might result in a net reduction in overall food consumption by broiler breeders. It is clear, however, that implementation in practice of restriction programs of this sort will require close attention to identification and control of potential sources of increased mortality.

D.1.4 Relationship of age and body weight at sexual maturity in selected lines of chickens.

Although an extensive literature exists concerning the relation of age at first egg with subsequent production traits, information on the association between age and weight at first egg on an ad libitum diet is limited. One early study (Hays, 1933) did examine this association in a flock of Rhode Island Red pullets where the age at first egg ranged from 150 to 319 days. The relation between age and weight at sexual maturity was linear and a correlation between them of $.47 \pm .02$ was reported.

The present study examines the relationship between age and body weight at sexual maturity in four selected populations of chickens fed ad libitum. The objectives were to evaluate the association between the two traits and to ascertain differences among the four populations.

1. Materials and Methods

1.1 Stocks

Female chickens from four genetic stocks were used in this experiment. Bidirectional selection for high and low eight-week body weight in a previously unselected group of White Plymouth Rocks produced lines HN and LN, respectively (Siegel, 1978). In the thirteenth generation of selection for divergent eight-week body weight, the recessive, sex-linked dwarf allele (dw) was introduced into samples of the two lines by crossing selected line females with males of a meat-type stock which carried the dwarf allele. In subsequent generations, repeated backcrossing of selected line normal females with heterozygous males resulted in two populations, HD and LD, which were of the same genetic origin as the HN and LN lines (Reddy and Seigel, 1977). After 23 generations of selection in the normal lines and nine generations

of backcrosses plus selection in the dwarf lines, progeny were obtained for this experiment.

1.2 Husbandry

Chicks were hatched in March 1980, wingbanded, vaccinated for Marek's disease and raised in heterosexual flocks under natural photoperiod. Chick starter and grower rations (Siegel, 1962) and water were available ad libitum. At 118 days of age, 65 females per population were placed in individual cages in a windowless house with a 14 h photoperiod from 0700 through 1100 hr. At 125 days of age the photoperiod was increased to 0600 through 2000 hr. Feed formulated with three slightly different levels of methionine (all of which were within NRC (1977) requirements for levels of methionine and total sulfur-containing amino acids) were randomly assigned to equal numbers of females from each stock and supplied ad libitum throughout the experiment. Subsequent analyses showed that diets containing different methionine levels did not affect any of the traits discussed in this experiment. Birds offered the low methionine diet did consume significantly more feed, but body weights and production traits were not changed (Cherry and Siegel, 1981).

Body weights were obtained at 4, 8, 24 and 38 weeks of age as well as on the first day of lay. A pullet was considered sexually mature when she laid at least two eggs within a 10-day period and egg production data were obtained until pullets were 10 months of age.

1.3 Calculations of specific variables

Conversion of chronological age to metabolic (physiological) age

(Taylor, 1982)

$$= t / A^{(0.27)}$$

where t = chronological age and

A = mature (38-week) body weight.

Proportion of onset of weight at x weeks

$$= \frac{\text{body weight at x weeks of age}}{\text{body weight at first egg}} \times 100$$

Percentage of hen-day (Bray et al., 1960) normal egg production

$$= \frac{\text{number of normal eggs laid}}{\text{number of trapdays}} \times 100$$

Percentage of hen-day (Bray et al., 1960) ovulations

$$= \frac{\text{number of ovulations}}{\text{number of trapdays}} \times 100.$$

2. RESULTS AND DISCUSSION

2.1 Means

Mean body weights of chickens from the four populations are indicated by the respective growth curves presented in Figure 1. At four and eight weeks of age, the two low populations (AL and LD) did not differ significantly in body weight, although they were lower in weight than HN and HD. All four stocks differed significantly in body weights at 24 and 38 weeks of age as a result of selection and presence of the dwarf allele.

Mean percentage of hen-day normal egg production and mean percentage of hen-day ovulations for the period of sexual maturity up to 10 months of age are given in Table 1 for the four populations. On a percentage of hen-day basis, LD hens produced fewer normal eggs than hens from the other stocks. The difference in normal egg production and ovulations of HN hens was due to the high incidence of erratic ovulations in that group (Reddy and Siegel, 1977).

Means of age at first egg for the four stocks (Table 1) show that, on a chronological age basis, sexual maturity was earliest in HN pullets, with those from the HD, LD and LN populations following in ascending order. Thus, the dwarf allele apparently delayed age of sexual maturity in the high line females in contrast to an earlier report on these populations by Reddy and Siegel (1977) concerning the third and fourth backcross generations. The converse occurred in the low line females - that is, the low line dwarfs became sexually mature at a significantly

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Table 1. Means and standard deviations of egg production and sexual maturity traits in four populations of chickens

	HN		HD		LN		LD	
	<u>n</u>	<u>$\bar{X} \pm sd$</u>	<u>n</u>	<u>$\bar{X} \pm sd$</u>	<u>n</u>	<u>$\bar{X} \pm sd$</u>	<u>n</u>	<u>$\bar{X} \pm sd$</u>
<u>Percent Hen-day Production</u>								
Normal Eggs	61	50 $\pm$ 15 b	62	54 $\pm$ 16 ab	53	59 $\pm$ 15 a	64	36 $\pm$ 11 c
Ovulations	61	57 $\pm$ 13 a	62	57 $\pm$ 14 a	53	59 $\pm$ 15 a	64	36 $\pm$ 10 b
<u>Traits at First Egg</u>								
Age (d)	61	169 $\pm$ 11 d	62	179 $\pm$ 14 c	53	213 $\pm$ 23 a	64	196 $\pm$ 22 b
Metabolic Age	55	19 $\pm$ 3 d	53	22 $\pm$ 2 c	53	30 $\pm$ 4 b	63	32 $\pm$ 4 a
Body Weight (g)	61	2824 $\pm$ 272 a	62	2065 $\pm$ 271 b	53	1304 $\pm$ 187 c	64	787 $\pm$ 111 d
<u>Proportion of Onset Weight</u>								
8 Wks (%)	61	41 $\pm$ 7 a	61	37 $\pm$ 4 b	53	25 $\pm$ 5 c	64	42 $\pm$ 7 a
24 Wks (%)	61	92 $\pm$ 6 a	62	88 $\pm$ 8 b	53	69 $\pm$ 13 c	64	86 $\pm$ 15 b
38 Wks (%)	55	114 $\pm$ 13 a	53	106 $\pm$ 13 b	53	108 $\pm$ 11 b	63	115 $\pm$ 23 a

Means within a row with different superscripts are significantly different ($P < .05$).

n = number of observations per mean.

earlier age than their normal counterparts. When expressed on a metabolic age basis, however, the order of mean age at sexual maturity was HN, HD, LN and LD. Thus, the normal pullets were physiologically younger than their respective line dwarfs at sexual maturity.

Mean proportions of onset weight at 8, 24 and 38 weeks of age afford an insight concerning the association of body weights at these ages with body weight at first egg (Table 1). The proportions of onset weight at 8 and 24 weeks of age were significantly lower in LN females than other females, indicating that, before onset of lay, these pullets were relatively smaller in body weight. The proportion of onset of weight at 38 weeks of age was essentially the same for populations HN and LD, whereas HD and LN females were significantly lower in this proportion at the same age. Since the range of proportion of onset weight at 38 weeks for the four populations (106 to 115%) was narrower than that at either 8 weeks (69 to 92%) or 24 weeks (70 to 92%), it can be inferred that mature body weight had a more intimate association than prepubertal body weights with weight at first egg. It is noteworthy that both polygenes and the dwarf gene had an effect on weight on first egg, comparable to their effect on mature body weight.

2.2 Phenotypic Correlations and Regressions

Phenotypic (product-moment) correlations of body weights at 4, 8, 24 and 38 weeks with age at first egg (Table 2) were negative in all stocks and significantly different from zero in most cases, particularly in the HD and LD populations and at 24 weeks of age for all stocks. Correlations between body weights at various ages and body weight at first egg (Table 2) were generally positive and significantly different from zero. In HN and LN correlations of early growth rate and weight at first egg were low, as

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Table 2. Phenotypic correlations of age and weight at first egg with body weights, egg production and sexual maturity traits (53 < n < 64)

	Age at First Egg				Weight at First Egg			
	HN	HD	LN	LD	HN	HD	LN	LD
<u>Body Weight</u>								
4 Weeks	-.40**	-.16	-.06	-.22	.28*	.34**	.17	.31*
8 Weeks	-.11	-.25	-.41**	-.27*	.14	.53**	.22	.35**
24 Week	-.30*	-.35**	-.64**	-.51**	.77**	.68**	.24	.47**
38 Weeks	-.12	-.27*	-.35**	-.13	.60**	.58**	.59**	.49**
<u>Percent Hen-day Production</u>								
Normal Eggs	.14	-.13	-.17	-.28**	.03	.15	.18	.39**
Ovulations	.08	-.16	-.19	-.28**	.01	.21	.19	.38**
<u>Traits at First Egg</u>								
Age					.10	-.14	-.17	.04
Weight	.10	-.14	-.17	.04				

P<.05, **P<.01.

found in the White Rock and Leghorn populations described in section ().

The only significant correlation of production traits with age and weight at first egg occurred in LD pullets (Table 2). Higher percentages of hen-day production were associated with a younger age at first egg and with a higher body weight at sexual maturity in this population.

No statistically significant associations between age and body weight at first egg were found in any stock studied (Tables 2 and 3), disagreeing with the results of Hays (1933, 1951) in Rhode Island Red pullets. An explanation for the low correlations and non-significant regressions obtained in our experiment is supplied by data in Figures 2 and 3. Minimum age at first egg is quite similar in the four populations (Figure 2), although the distribution of each stock for age at sexual maturity differs markedly, causing significantly different mean ages at first egg in the four stocks (Table 1). Figure 3 demonstrates clearly that the four populations differ greatly in the minimum weight at first egg (in addition to their significantly different mean weights at first egg - Table 1), and that each has an almost unique range of weights for the onset of sexual maturity.

2.3 General Comments

The data obtained in this study provide several insights into the

Figure 1. Growth curves from 4 to 38 weeks of age in four populations of chickens.

Figure 2. Distribution of age at first egg in four populations of chickens (calculated in 10-day increments).

Figure 3. Distribution of weight at first egg in four populations of chickens (calculated in 200 g increments).

relationship between age and body weight at first egg in these selected stocks, which are of the same genetic origin yet divergent in body weight and body form. There appears to be a clear minimum age (at approximately 155 days) below which sexual maturity rarely occurs. Distributions of weight at sexual maturity observed in the four stocks were virtually discrete, suggesting that body weight and/or some aspect of body composition (fat, percentage of fat, protein or percentage of protein) may be governing factors in the onset of ovulation.

It can be speculated from our data that, at 155 days of age, HN females had already achieved the minimum body weight or body composition for sexual maturity and all came into lay shortly after reaching the minimum age. HD females, which were somewhat smaller than their normal counterparts, took slightly more time to mature sexually but also came into lay quickly after the minimum age was reached. Conversely, the low line females had a more skewed, more spread distribution for age at first egg. It appears that, in these stocks, the required age was achieved first. Then, as Figure 3 indicates, the whole group of LD females came into lay as soon as a body weight of 600 to 1000 g was reached. Similarly, the attainment of 1000 to 1500 g body weight allowed LN females to begin egg production. Thus, within a proper neuroendocrine environment, a balance must be achieved among the physiological factors discussed here for the pullet to commence egg production.

Summary

The relationship between age and body weight at sexual maturity was studied in dwarf and nondwarf females from populations at White Rock chickens divergently selected for juvenile body weight. The data show that a minimum age as well as a minimum body weight and/or composition are necessary for the onset of egg production. Dwarf and normal females from the high lines reached the minimum weight and/or body composition first and age was the limiting factor. In contrast, pullets from the low lines achieved minimum age first and body weight and/or composition was the limiting factor. In all populations weight at first egg was more closely related to mature body weight than to juvenile body weight.

D.1.5 Heritability of Minimum Weight for Onset of Sexual Maturity in
Female Chickens and Its Phenotypic and Genetic Correlations
with Early Growth-Rate

INTRODUCTION

In this study we present data on the heritability of minimum weight for onset of sexual maturity in hens, and on its phenotypic and genetic correlations with early growth-rate. This information is of interest in clarifying the physiological basis for minimum weight for onset of sexual maturity, and the feasibility of lowering the minimum weight for sexual maturity in broiler strain females by selection, including possible correlated effects on growth-rate.

MATERIAL AND METHODS

Trait definition

Early growth-rate was estimated by body weight at 42 days of age under conditions of unlimited access to feed (ad libitum feeding). This measure of early growth-rate will henceforth be denoted WT1.

Minimum weight for onset of sexual maturity was estimated by body weight at first egg on gradual release from food restriction. That is, following an initial post-hatch period of ad libitum feeding, the birds were subjected to quantitative food restriction for a more or less extended period of time. During the period of food restriction, food quantities were adjusted so as to keep the weight of the birds below the anticipated minimum body weight for onset of sexual maturity until any possible age requirements for onset of lay (Brody et al., 1980; Dunnington et al., 1983) had been fulfilled. Entry into lay under these conditions is attributed to the attainment by each bird of its own minimum weight for onset of sexual maturity, and the weight of the bird at first egg was taken to represent a measure that stands in close relation to the minimum body weight required for onset of sexual maturity. This measure of minimum weight for onset of sexual maturity will henceforth be denoted WTSxM.

Experiments

Four separate experiments were conducted. Experiment 1, was intended to examine phenotypic relations between WTSxM and WT1 in three poultry populations differing widely in early growth-rate, namely: a White Rock broiler strain (WR) population, a Leghorn layer strain (LN) population, and the F4 segregating generation of a WR x LN cross. Experiment 2, based on WR sire families

(half-sibs) and carried out on a larger scale, was intended to provide information on the heritability of WTSXM and its genetic correlation with WT1. Daughters of the sires were characterized for WTSXM and sons for WT1. An unexpected result of Experiments 1 and 2 was a low phenotypic and a low genetic correlation between WTSXM and WT1 in the WR populations. Experiment 3, based on WR dam families (full-sibs) was therefore carried out to confirm these results in a different WR strain. In addition, Experiment 4, was carried out on the F5 and F6 segregating generations of the WR x LN cross, as a positive control, intended to examine the heritability of WTSXM and its phenotypic and genetic correlations with WT1 in a population expected to show a large amount of genetic variation in both traits. In Experiments 3 and 4, males were characterized for WT1 and females for both WTSXM and WT1. In Experiments 3 and 4 the experimental protocol was changed somewhat to include a second brief period of ad libitum feeding in order to provide information on feed efficiency of the birds under food restriction and under ad libitum feeding. This will be published elsewhere.

Stocks

Table 1 shows source of chicks, date of hatch, family structure and number of birds for the various experiments. The WR populations studied had been maintained for many generations under stringent mass selection for rapid early growth-rate. The LN population was under mass selection for egg number, egg weight and low body weight. The WR x LN cross had been maintained without selection since its inception.

Table 1. Breed and source of genetic stocks, date of hatch, family structure and number of birds for the various experiments

Experiment number	Genetic type	Date of hatch	Family structure	Number of families	Number of birds	Source of chicks
1	White Rock	1.6.79	None	-	21	Yavne Poultry Breeding Farm
	Leghorn	1.6.79	None	-	29	Yavne Poultry Breeding Farm
	White Rock x Leghorn cross F4	1.6.79	None	-	24	Hebrew University ¹
2	White Rock	9.17.79	Sire families (half sibs)	48	302 sons 297 daughters	Yavne Poultry Breeding Farm
3	White Rock	9.2.80	Dam families ² (full sibs)	34	70 sons 73 daughters	Israel Poultry Breeders Union (Masuot Yitzchak hatchery)
4	White Rock x Leghorn cross F5	11.25.79	None	-	16 males 46 females	Hebrew University ¹
	F6	12.31.80	Dam families ³ (full sibs)	46	85 daughters	Hebrew University ¹

¹This population derives from a reciprocal cross between the Yavne Poultry Breeding Farm White Rock broiler strain, and its Leghorn layer strain. The initial cross involved 20 males and 50 females of each line, and the cross has been continued at the Hebrew University by mass mating or artificial insemination using pooled semen, and retaining a minimum of 20 males and 50 females each generation.

²The families were produced by artificial insemination of each hen to an individual male. Four males in all were used, but information is not available on the male parentage. There were 25 families with male offspring, and 29 families with female offspring. Families were small and only 20 included both male and female offspring (56 sons, 52 daughters).

³Families were produced by artificial insemination of each hen to an individual male. Fourteen males in all were used.

Rearing

The experiments were carried out at the East Talpilot (Jerusalem) experimental farm of the Hebrew University. All chicks were produced by artificial insemination. From hatch until 4-6 weeks of age (depending on size) chicks were kept in brooder batteries and fed ad libitum. They were then transferred to individual laying-type cages with individual feeding troughs. In the cages the birds had unlimited access to water. Food was added separately to each trough in measured portions (by volume). During periods of food restriction, all the birds in an experimental group received the same quantity of food, added daily, except Saturday (a double portion was given on Friday). During periods of ad libitum feeding, the food trough were observed daily and food was added in 100 gram portions, as necessary.

Three different mashes were used, depending on the age of the birds and the experimental period. These were, a proprietary starter mash (2795 cal ME/g, 21% protein), a proprietary grower mash (2850 cal ME/g, 14% protein), and a proprietary layer mash (2780 cal ME/g, 15% protein). The birds were grown under natural light until 13-18 weeks of age. Starting at this time the lighting regime was 16 hrs continuous light and 8 hrs darkness.

Treatments

On a number of occasions, when these White Rock strains were raised in our facilities under ad libitum feeding or moderate restriction, mean age at first egg ranged from 21-26 weeks (Brody et al., 1980; Soller et al., 1983; Eitan et al., 1983). Similar results are routinely obtained in our facilities with the WR x LN cross birds, when raised under ad libitum feeding (unpublished data). It was therefore considered that by 26 weeks of age both the WR and

the WR x LN birds of this study would have met any minimum age requirement for the onset of lay. Feed restriction programs were therefore adjusted so as to keep the body weight of the birds below the anticipated minimum body weight for onset of sexual maturity until this age.

Female chicks of Experiments 1 and 2 were fed ad libitum until 12 weeks of age. This brought them to a relatively high body weight, and they were consequently subjected to relatively severe quantitative food restriction until 26 weeks of age. From 26 weeks of age food quantities were increased gradually, at a rate of 5 g per week, until a level of 100 g per day. Food quantities were maintained at this level for each bird until first egg.

In Experiments 3 and 4 the experimental protocol was changed somewhat in order to provide information on the feed efficiency of the birds under restricted and ad libitum feeding. The initial period of ad libitum feeding was shortened (to 6 weeks for Experiment 3 and the F5 birds of Experiment 4, and to 10 weeks for the F6 birds of Experiment 4). The females of Experiment 3 and F5 females of Experiment 4 however were allowed a further brief period of ad libitum in the midst of the period of quantitative food restriction. Except for this the birds were subjected to severe quantitative food restriction until 20 weeks of age. At this time the birds were a lower body weight than in Experiments 1 and 2. For this reason food quantities were gradually increased from 20 weeks, but again, food quantities during the period of restricted feeding were adjusted so as to keep the weight of the birds well below the anticipated minimum body weight for onset of sexual maturity.

Other studies in our laboratory (Soller et al., 1983) show that WTSXM is unaffected by the degree of food restriction during the rearing period, or by dietary composition during the period following the end of food

Table 2. Duration of ad libitum and restricted feeding periods (above) and food quantities during restricted period (below) by experiment and genetic type^{1,2}

Feeding period	<u>Experiment 1</u>		<u>Experiment 2</u>		<u>Experiment 3</u>		<u>Experiment 4</u>	
	WR	F4	LN	WR	WR	F5	F6	
First <u>ad libitum</u> feeding period	84 d	84 d	84 d	84 d	42 d	42 d	72 d	
Second <u>ad libitum</u> feeding period	-			-	59-66 d	78-94 d	-	
Restriction periods	85-182 (60-70 g/d)	(40-50 g/d)	(30-40 g/d)	85-182 d (70 g/d)	42-58 d (80 g/d)	44-77 d (40-60 g/d)	73-140 d (38 g/d)	
					66-102 d (60-70 g/d)	95-140 d (60 g/d)		
					103-142 d (70-100 g/d)			

¹Genetic types: Wr, White Rock; LN, Leghorn; F4, F5, F6, are advanced segregating generations of a WR x LN cross.

²Feed types as follows: Starter mash 0-21 d; grower mash 21 d until 26 weeks of age (Experiments 1 and 2) or 20 weeks of age (Experiments 3 and 4); laying mash thereafter.

restriction. For this reason the differences in feeding programs between experiments would not be expected to introduce genotype x environment interactions of a magnitude sufficient to change the nature of WTSXM in the various experiments. That is, the genetic correlation between WTSXM as measured in the different experiments should be sufficiently close to unity to enable the experiments to be discussed as a group.

Data collection and analysis

Live body weight was obtained by weighing the birds in the morning, before feeding, using a spring scale graduated at 25 g intervals. The birds were weighed weekly or bi-weekly in order to monitor body weight status, and at first egg. Age at first egg was also recorded for each female.

Statistical analyses were conducted with the aid of the SPSS (Nie, 1975) and BMDP (Dixon, 1981) statistical packages. Means, standard deviations and coefficients of correlation were calculated using BMP1D program (Simple Data Description). Pearson correlation coefficients were calculated using the BMDP1R program (Multiple Linear Regression). Analysis of variance was carried out using the SPSS ONEWAY program.

Heritability estimates based on between family variance components were calculated according to the following models:

For half-sib (sire) families

$$y_{ij} = u + a_i + e_{ij}$$

where,

y_{ij} is the record of the j^{th} progeny of the i^{th} sire,

u is the common mean,

a_i is the effect of the i^{th} sire, and

e_{ij} is the residual environmental and genetic deviation, including dam effects.

Variance components, heritabilities and standard errors of the heritabilities were calculated as in Becker (1967).

For full sib (sire x dam) families

In Experiments 3 and 4 the hens were mated to individual males by artificial insemination. Because of the small number of sires used (four in Experiment 3, 16 in Experiment 4), and lack of information on male parentage in Experiment 3, separate sire and dam variance components were not calculated. Instead, the data were analyzed as if each hen were mated to a different sire, i.e., according to the following model

$$y_{ij} = u + b_i + e_{ij}$$

where,

y_{ij} is the record of the j^{th} progeny of the i^{th} sire x dam family,

b_i is the effect of the i^{th} sire x dam combination, and

e_{ij} is the residual environmental and genetic deviation.

The sire x dam variance component (σ_{S+D}^2) was obtained following a one-way analysis of variance (Becker, 1967). Heritability was estimated as

$$h_{S+D}^2 = \frac{2\sigma_{S+D}^2}{\sigma_{S+D}^2 + \sigma_W^2}$$

where σ_W^2 is the within family variance component. It is recognized that this will be an underestimate, since a number of hens were mated to each sire.

The standard error of the heritability estimate was calculated by a slight modification of the corresponding expression for half-sib families (Becker, 1967).

$$S.E. (h_{S+D}^2) = 2 \sqrt{\frac{2(N-1)(1-t)^2 [1-(k-1)t]^2}{k^2(N-F)(F-1)}}$$

where,

$t = \frac{1}{2}h_{S+D}^2$, is the intra-class correlation between full-sibs,

$$k = \frac{1}{F-1} (N - \frac{\sum n_i^2}{N})$$

N = the total number of offspring

F = the number of sire x dam families, and

n_i = the number of progeny of the i^{th} sire x dam family

For parent-offspring correlations

In Experiment 4, a heritability estimate based on the parent-offspring correlation was calculated as

$$h^2 = 2 r_{PO}$$

where r_{PO} is the correlation between parent value and mean offspring value.

This will be an overestimate, but a mild one only, since the mean number of offspring per parent was small. The standard error of this estimate was taken as twice the standard error of r_{PO} (Snedecor and Cochran, 1967).

Genetic correlations, r_A , between WTSXM and WTl were calculated from correlations r_{PO} , between trait-x measured in a parent, and trait-y measured in $\bar{n}$ offspring per parent (Experiment 4); and from correlations r_{HS} (for half-sib families) and r_{FS} (for full-sib families) between family means of brothers and family means of their sisters (in Experiments 2 and 3, respectively).

The following computational formulas were used:

For parent-offspring correlations

$$r_A = 2r_{PO} / h_x b_y$$

For full-sib family correlations

$$r_A = 2r_{FS}/b_x b_y, \text{ and}$$

For half-sib family correlations

$$r_A = 4r_{HS}/b'_x b'_y$$

where,

h_x^2 is the heritability of trait-x measured in the parent,

b_x^2 or $b_y^2 = \frac{(\bar{n}+1)h^2}{(\bar{n}-1)h^2 + 2}$, are the "heritabilities" of full-sib

family averages for trait-x or trait-y,

$b'_x{}^2$ or $b'_y{}^2 = \frac{(\bar{n}+3)h^2}{(\bar{n}-1)h^2+4}$, are the "heritabilities of half-sib family

averages for trait-x or trait-y, and

$\bar{n}$ is the mean number of brothers or sisters per half-sib or full-sib family.

RESULTS

Table 3 shows means, standard deviations and coefficients of variation for WTSXM and age at first egg for the various genetic types by experiment. The phenotypic correlations between WT1 and WTSXM are also shown. There were marked differences between experiments in age at first egg. However, these were primarily a function of the restriction program. Mean age at sexual maturity in all experiments was comfortably above 26 weeks. It seems reasonable, therefore, that for these birds it was body weight that was the limiting factor for the onset of lay.

Coefficients of variation for WTSXM were similar to those of WT1, and histograms (not shown) giving the distribution of WTSXM were symmetrical, unimodal and approximately normal. Coefficients of variation for WTSXM were distinctly greater in the WR x LN cross than in the purebred WR or LN populations. This is consistent with the expected genetic heterogeneity of the WR x LN cross and suggests that genetic factors can have a major impact on minimum weight for onset of sexual maturity. Both WT1 and WTSXM varied somewhat between experiments, even for the same genetic stocks. In particular WT1 values for Experiment 1 were higher than the other experiments and WTSXM for the WR of Experiment 3 was distinctly greater than that for the WR birds of Experiments 1 and 2. Undefined environmental factors, and in the case of the WR birds genetic factors as well, may be responsible for these differences.

There was a clear proportionality between mean WT1 and mean WTSXM of the various genetic types. The ratio of WT1 to WTSXM was in the range of 0.25-0.35. The uniformity in the ratio WT1/WTSXM for the three genetic stocks in Experiment 1 is remarkable, and suggests that under a given set

Table 3. Mean (above) standard deviation (center) and coefficient of variation (below) for six week ad libitum body weight (WT1), and for age (AGSXM) and minimum body weight (WTSXM) at onset of sexual maturity, and phenotypic correlation of WT1 and WTSXM by experiment and genetic type.

Exp.	Genetic type	Number of birds	WT1 ¹ (g)	AGSXM (d)	WTSXM (g)	$\frac{WT1}{WTSXM}$	Correlation WT1, WTSXM
	White Rock	27	1111.9 122.4 0.11	294.4 19.8 0.07	3159.8 281.4 0.09	0.33	0.04
	White Rock x Leghorn F4	24	711.4 99.1 0.14	252.8 13.5 0.05	1958.1 294.4 0.13	0.34	0.56**
	Leghorn	29	402.7 80.3 0.20	240.3 5.4 0.02	1250.5 140.7 0.11	0.34	0.11
	White Rock	297	not measured	213.6 19.2 0.09	3059.6 317.6 0.10		
	White Rock	61	874.2 68.4 0.08	204.4 9.7 0.05	3445.0 277.9 0.08	0.25	0.10
	White Rock x Leghorn F5	86	489.3 56.5 0.11	189.1 13.1 0.07	1706.7 243.8 0.14	0.28	0.38**
	F6	81	554.6 104.2 0.19	206.2 29.2 0.14	1647.6 277.8 0.17	0.32	0.46**

chicks of experiments 1, 2 and 3 weighed at 42 days; chicks of experiment 4 weighed at 44 days (F5) and 45 days (F6).

of rearing conditions, the relation of early growth-rate to minimum weight for onset of sexual maturity may be similar for widely different genetic types. The ratio is subject to environmental and/or genetic effects, however, as evidenced by the differences between the F4, F5 and F6 groups of Experiments 1 and 4, and between the WR groups of Experiments 1 and 3. Nevertheless the overall correlation ($r=0.85$) between mean WT1 and mean WTSXM of the various genetic types across all experiments was highly significant. Considering that WT1 comprises only about one-third of WTSXM, this correlation is much greater than might be expected on the basis of the part:whole relationship of WT1 and WTSXM alone. This implies that for the genetic stocks studied in these experiments, a major portion of between-stock variation in minimum weight at onset of sexual maturity was associated with differences in early growth-rate. This is consistent with the relatively high phenotypic correlation between WT1 and WTSXM found in the WR x LN cross population as compared to the low correlation in the purebred WR or LN populations. It seems reasonable that any environmental correlation between WT1 and WTSXM will be of similar magnitude in the WR and LN populations and in the WR x LN population. On this assumption, the significantly greater phenotypic correlation between WT1 and WTSXM in the WR x LN population can be attributed to the additional genetic variation contributed to this population by the genetic differences between the parental WR and LN strain. Thus the phenotypic association of WT1 and WTSXM in the WR x LN population is consistent with a genetic association of early growth rate and minimum weight for onset of sexual maturity in the parental populations.

Heritability of WTSXM

Table 4 gives heritability estimates for WTSXM and their standard errors as obtained from dam-daughter correlations and from analysis of variance of between family differences. Heritability estimates for WTSXM in WR were moderate (0.40 and 0.35 in Experiments 2 and 3, respectively). Standard errors of the estimates were large, as is expected from the relatively small numbers of families and individuals involved. Nevertheless, the estimates are based on highly significant between-family differences, so that genetic differences in this trait were apparently present in these populations. The similarity of the estimates in the two experiments lends some confidence to the actual values obtained. Heritability estimates for WTSXM in the F5-F6 generations of the WR x LN cross were double the WR values (0.74 for the dam-daughter estimate, and 0.87 for the F6-family estimate). These high values may be attributed, in part at least, to the greater genetic variation in growth-rate related traits expected in a population derived from a cross between heavy-breed broiler and light-breed layer strains. Here too, although standard errors were large, the two estimates are similar in magnitude and one estimate was based on a statistically significant parent-offspring correlation, the other on highly significant between-family differences.

Genetic correlation of WTl and WTSXM

Table 5 shows the familial and genetic correlations between WTl and WTSXM for the various experiments and genetic types. In the WR x LN cross, genetic correlations were consistent, positive and high, and are based on

Table 4. Heritability estimates for minimum body weight at sexual maturity based on analysis of variance of between family differences and on dam-daughter correlations.

Exp.	Genetic type	<u>Analysis of variance</u>				Heritability estimate $\pm$ S.E.
		Source	d.f.	M.S.	F	
2	White Rock (half sib families)	Between families	48	141588	1.64**	0.40 $\pm$ 0.20
		Within families	243	86184		
3	White Rock (full sib families)	Between families	29	79123	2.22**	0.35 $\pm$ 0.29
		Within families	43	35659		
4	White Rock x Leghorn, F6 (full sib families)	Between families	45	107653	2.47**	0.87 $\pm$ 0.26
		Within families	39	43601		
<u>Dam-daughter correlations</u>						
		<u>No. of pairs</u>	<u>Correlation</u>			
4	White Rock x Leghorn F5-F6	39	0.37*			0.74 $\pm$.32

*P<0.05; **P<0.01

Table 5. Familial correlations between early growth rate (WT1) and minimum body weight for onset of sexual maturity (WTSXM), and genetic correlations calculated from them.

Experiment	Genetic type	Familial correlation	Genetic correlation
1	White Rock (half-sib families) ^{1,4}	-0.05	-0.30
2	White Rock (full-sib families) ^{1,4}	0.16	0.51
4	F5 mothers ^{2,3}	0.29	0.67
	F6 daughters	0.31*	0.72
4	F5 sires ²		
	F6 daughters	0.38	0.85

*P<0.05

¹Based on correlations between WT1 family means for sons and family means of their sisters for WTSXM.

²Based on parent-offspring correlations. See Table 1 for number of mothers, sires and daughters.

³Upper correlation: daughter WT1, mother WTSXM; lower correlation; daughter WTSXM, mother WT1.

⁴See Table 1 for number of families and total number of sons and daughters by experiment.

parent-offspring correlations that are significant or close to significance. These results suggest that there is a relatively high genetic correlation between early growth-rate and minimum weight for onset of sexual maturity in the WR x LN population. These results are consistent with the implications of the between population differences in WT1 and WTSXM, and the within-population phenotypic correlation of WT1 and WTSXM as discussed above.

In the WR populations the genetic correlations between WT1 and WTSXM were smaller in magnitude, were based on brother-sister family correlations that were far from significant, and were different in sign in the two experiments. These results suggest that the genetic correlation between early growth-rate and minimum weight for onset of sexual maturity in the WR population may be low, possibly approaching zero. This result would also be consistent with the low within-population phenotypic correlation between WT1 and WTSXM found in the WR populations, although in a formal way, such correlations could also be the result of a negative environmental correlation and a positive genetic correlation between the two traits. WT1 showed a moderately high heritability in the WR populations (data not shown) so that the apparently low genetic correlation is not a consequence of a lack of genetic variation in this trait.

DISCUSSION

Minimum weight for onset of sexual maturity

In this study, restricting food intake for extended periods and then allowing a slow increase in body weight by way of gradual increments in food intake delayed the onset of sexual maturity in female chickens well beyond the age at which females of these strains generally enter lay. Since diet and lighting regime were otherwise of a nature generally found to allow the onset of lay in hens of these strains, this delay (following Brody et al., 1980) is attributed to the low body weight resulting from the extended food restriction. The eventual entry into lay on release from restriction is attributed to the increase in body weight when food intake was increased, bringing each individual to its own minimum weight for onset of sexual maturity and lay. It is realized that the results of this study, taken alone, can also be interpreted in terms of increasing food intake per se serving to initiate sexual maturity. However, other results given in Brody et al. (1980) and the extensive literature in other vertebrates (Crichton et al., 1959; Dickerson et al., 1964; Frisch and Revelle, 1970; Frisch 1972; Glass et al., 1976; Kennedy and Mitra, 1963a,b; Sohn and Crewe, 1977; Widdowson et al., 1964; Wilen and Naftolin, 1977 and 1978) favor the interpretation in terms of a minimum body weight requirement.

In WR populations, WTSXM showed highly significant between-family differences and a moderate heritability. Heritability of WTSXM in the F5 and F6 generations of a WR x LN cross was almost double that in the WR population and the coefficient of variation for WTSXM in the WR x LN population was greater than in the WR and LN purebred populations. Thus genetic variation in minimum weight for onset of sexual maturity appears to be

present both within and between the poultry populations examined in this study.

Early growth-rate and minimum weight for onset of sexual maturity

Mean WTSXM of the various genetic stocks used in this study showed a close relationship to their mean WTl. Thus genetic factors determining rapid early growth-rate also appear to be determining a high minimum body weight requirement for onset of sexual maturity. This correlation appears to reflect more than a simple part-to-whole relationship: The measure of early growth-rate used in this study, WTl, forms only a minor part of WTSXM; and, appetite differences, a major factor determining differences in early growth-rate (Masic et al., 1974; Siegel and Wisman, 1966), are not involved in determining differences in WTSXM which is measured under conditions of controlled food intake. The very low phenotypic correlation of WTl and WTSXM within the purebred WR and LN populations also suggests that part-to-whole relationships alone are not sufficient to produce a significant correlation between WTl and WTSXM. Thus, the genetic relationship between early growth-rate and minimum weight for onset of sexual maturity may reflect a certain degree of common biological control at some non-trivial physiological level. Kennedy and Mitra (1963a) have provided evidence showing a tight relationship between hypothalamic areas regulating food intake and activity in mice (which they term an "energy balance" center), and a separation of these areas and those regulating the gonadotrophin releasing system. They point out, however, that the energy-balance center must be "aware" of the state of the somatic development of the individual, and that on the "minimum weight for onset of sexual maturity hypothesis" this must also be true of the hypothalamic center regulating gonadotrophin release (Kennedy and Mitra

1963b). Thus, early growth-rate (closely related to energy balance) and minimum weight for onset of sexual maturity may be jointly controlled by being referenced to a common somatic-development set-point. This would also be consistent with the hypothesis that many life events in vertebrates are determined by reference to mature body weight (Taylor, 1982).

Within the WR x LN population there was a high genetic correlation between early WT1 and WTSXM. This was not found in the WR population. This may reflect a real difference in the nature of the genetic relationship between early growth-rate and minimum weight for onset of sexual maturity in the two populations. That is, genetic factors segregating in the WR x LN population that affect growth-rate apparently have a greater effect on minimum weight for onset of sexual maturity than those segregating in the WR populations. It may be that loci with major effects on growth-rate, that responded first to selection, and that are close to fixation in the present broiler lines, were loci with powerful effects on minimum weight for onset of sexual maturity; while the growth-rate loci with smaller effects, that are still segregating in the broiler lines, have relatively minor effects on this trait.

Minimum weight for onset of sexual maturity as a breeding objective

The possibly low genetic correlation between minimum weight for onset of sexual maturity and early growth-rate in the WR populations suggest that continued selection for rapid growth-rate in these stocks, should produce relatively minor further increases in minimum weight for onset of sexual maturity. That is, it presents the hopeful prediction that further selection for growth-rate will not require an appreciable increase in

present minimum broiler mother feed requirements for onset of sexual maturity and optimum reproductive performance. Conversely, the high standard deviation and moderate heritability of WTSXM in the WR population, suggest that this trait could rather readily be changed by selection in commercial broiler stocks, and that such selection, initially at least, might have little correlated effect on growth-rate. To the extent that lowering the minimum weight for onset of sexual maturity also means that the birds will lay well at a lower body weight under feed restriction, such selection might provide an attractive breeding objective. Since maintenance requirements in broiler populations increase as the 0.75 power of body weight (Hurwitz et al., 1978), a reduction of 10%, say, in mature body weight under restriction, would be equivalent to a reduction of 7-8% in the food requirements for growth and maintenance of broiler mother flocks. For purposes of comparison, an increase of 7-8% in egg production (enabling a corresponding decrease in broiler mother flock numbers) would be required in order to provide equivalent savings in food requirements. From a breeding standpoint the former objective seems much more readily attainable than the latter.

D.1.6 Response to selection for high and low minimum weight for onset of sexual maturity in White Rock broiler breeders and for weight gain under restricted uniform food intake

Four selection lines were initiated that underwent join two-way selection for minimum weight requirements for the onset of sexual maturity (WTSXM) and for weight gain under restricted uniform food intake (WTGNR). The basic approach was to select for WTSXM in females and for WTGNR in males of the same line. Since both selection programs were intended for eventual commercial application, selection for both traits was carried out in the same lines simultaneously to determine possible interactions between the two selection programs. This design was also economical in that it enabled two traits to be selected in duplicate in each of two directions in a total of four selection lines. The following table shows the selection traits and direction of selection by sex in the various lines. for the unselected offspring for WTGNR, WTSXM and early growth-rate (42 day body weight) after three generations of selection are also shown in each line.

Line designation	Trait under selection				Early growth-rate (42 d body weight)
	WTGNR (males)		WTSXM (females)		
	Direction	Results	Direction	Results	
		(g)		(g)	(g)
HH I	High	552.97	High	2994.7	1176.1
LL I	Low	528.64	Low	2644.5	1194.5
HL II ¹	High	800.30	Low	3092.7	1159.6
LH II	Low	806.66	High	3140.3	1168.1

¹ Lines I and II were tested at different times and under slightly different conditions, hence the differences in their mean value.

The I series of lines originated from the White Rock broiler line of Kibbutz Yavne Poultry Breeding Farm. The II series of lines originated from the ANAK-80 White Rock broiler line of the Israel Poultry Breeders Union. Each line was maintained with 30 females and 20 males after selection. The proportion selected was 20-30% in males and 30-50% in females.

The results show a possible powerful interaction between selection for WTGNR and WTSXM. In series I, a separation between the two selection lines (HH and LL) was obtained for both traits: 24 g (not significant) for WTGNR, and 350 g (highly significant) for WTSXM. It is striking that this difference in WTSXM was obtained without any difference in early growth-rate, as predicted by the low genetic correlation between early growth-rate and WTSXM found in the White Rock populations studied in the previous section. In series II, separation between lines (HL and LH) was not found for WTGNR (-6.0 g, opposite to the direction of selection, but not significant), and was negligible for WTSXM (48 g, not significant).

Because of the possible interaction between selection for WTGNR and WTSXM, joint selection for the two traits in the same lines will be discontinued and separate selection lines will be initiated for each trait separately.

D.2.1 The relation between selection for rapid growth-rate and increased fat deposition

Introduction

Although deposition of a gram of fat has the same energetic cost as deposition of a gram of protein (Webster, 1980), fat tissue is 20% water as compared of 80% water for lean. Thus the energetic cost for deposition of a gram of fatty tissue is 4x that for a gram of lean (Pym and Farrell, 1977). Consequently, selection for maximum gain (liveweight for age) should discriminate against animals that deposit fat as opposed to lean, and should lead to an increase in the proportion of energy intake over maintenance that is utilized for lean tissue deposition as compared to fat (Brody, 1935). That is, it should lead to a change in the lean:fat partition coefficient favoring lean tissue deposition. In fact, however, selection for gain has almost universally been found to result in increased fat deposition (Biondini et al., 1976; Eisen et al., 1977; Fowler, 1958; McPhee and Neill, 1976; Proudman et al., 1970; Roberts, 1965; Sutherland et al., 1970; Timon et al., 1970; but see also a few exceptions: Baker and Chapman, 1975; Dawson et al., 1972; Pym and Solvyns, 1979). A number of studies have shown that the lean:fat partition coefficient can respond to selection (Hull, 1960; Hayes and McCarthy, 1978; Pym and Solvyns, 1979) so that genetic variation in this trait is present and accessible. Why then does selection for liveweight gain increase fatness? The purpose of this note is to present a model attempting to explain this anomaly. Some of these ideas are foreshadowed in Lin (1981).

Model

There is a general consensus that genetic variation in digestive efficiency, or in the biochemical efficiency of fat or protein deposition is negligible

(Blaxter, 1968; Bowman, 1974; Lepore, 1965; Masic et al., 1974; Stanier and Mount, 1972). Although there are contrary indications to this (Fowler, 1962; Proudman et al., 1970; Savory, 1975) and the contribution of diet induced thermogenesis (Rothwell and Stock, 1979) to energy homeostasis in the chicken is not known, we will assume that weight gains (both lean and fat) is directly related to a positive energy balance. On this basis, weight gain, G, after a given time period, will be function of the excess of energy intake, I, over maintenance requirements, M, and of the lean:fat partition coefficient, b, where b and (1-b) are the proportions of excess energy intake utilized for lean or fatty tissue deposition, respectively. That is,

$$G = (I - M) \cdot \{Cb + 0.25 C(1-b)\} \quad (1)$$

where, G, I, M, and b are as defined above, and C, and 0.25C are constants, equal, respectively, to the amount of lean tissue (0.4 g/kcal) or fat tissue (0.1 g/kcal) deposited per kcal of metabolic energy. This expression can readily be simplified to give

$$G = (I - M)C \{0.25 + 0.75 b\} \quad (2)$$

Examination of expression (2) shows that gains should be directly proportional to I and b, and inversely proportional to M. Thus, selection for gain should act to increase food intake (or appetite), I, to decrease maintenance requirements, M, and to increase the lean:fat partition coefficient, b.

There is a considerable body of evidence in the literature showing that selection for gain has in fact increased appetite (Eisen, 1974; Eisen et al., 1977; Fowler, 1962; Lang and Legates, 1969; Lepore, 1965; Masic et al., 1974; Savory, 1975; Siegel and Wisman, 1966; Sutherland et al., 1970, 1974; Timon and Eisen, 1970) and decreased maintenance requirements (including activity, Kennedy and Mitra, 1963a; Kuenzel and Kuenzel, 1977; Masic et al., 1974; Owens et al., 1971; Proudman et al., 1970; Savory, 1975). As documented above,

however, selection for gain, contrary to expectation, has generally acted to decrease the lean:fat partition coefficient.

The main point of this note is to suggest that the partition coefficient itself, is a decreasing physiological function of the excess of intake over maintenance, i.e., the greater (I-M), the smaller, b. That is, expression (2), should be redrawn to show a negative path from (I-M) to b. Support for

$$G = (I-M) C\{0.25 + 0.75b\}$$

this contention can be found in the increased fat deposition shown by force-fed or hyperphagic animals (see e.g., Nir et al., 1974; Kennedy and Mitra, 1963b). Other studies show that food restrictions results in a relative decrease in fat deposition (Burleigh, 1980 p.125; Marks, 1982; Plotkin, 1982). On this model the effect of selection for gain on the lean:fat partition coefficient would be twofold. A direct effect tending to increase the partition coefficient; and an indirect physiological effect, mediated by way of the excess of intake over maintenance (I-M), tending to decrease the partition coefficient. The latter effect, apparently predominates in determining the net overall effect of selection for gain on fat deposition.

Discussion

The model predicts that selection for appetite alone should result in a greater degree of fat deposition than selection for gain, since the latter would include a "hidden" component increasing the partition coefficient in favor of lean deposition. This has indeed been found (Pym and Solvyns, 1979; Sutherland et al., 1970). Another implication of the model is that (I-M) can be increased by an increase in appetite (I), or by a decrease in maintenance requirements (M), either of which could lead to increased body fat.

The model also predicts that if a high gain selection line is restricted

to the same food intake as its unselected control line, the high line, having undergone "hidden" selection for a greater lean:fat partition function, should deposit less fat at any given weight than the control line. In accord with this prediction, Plotkin (1982) found that heavy breed chicks severely restricted in food intake to the point where their rate of gain is similar to that of ad libitum light breed chicks, show a lower fat percentage than the light breed chicks at any given body weight. The opposite was true when heavy breed chicks were fed ad libitum. This prediction is not supported however, by results with mice. Timon et al. (1970) compared mice from a line selected for high postweaning weight gain, to unselected controls, under both ad libitum and restricted feeding. Under restriction the high line mice had a higher fat content than the ad libitum controls, although both were at the same body weight. Similarly, McPhee et al. (1980) compared mice from two lines selected for high post-weaning weight gain under uniform restricted food intake, to unselected controls, under ad libitum and restricted feeding. Again high line restricted and ad libitum control line mice had similar body weights, but fat content of the high line mice was greater. In both of these experiments, however, both high line mice and controls showed a greater fat percentage under restriction than under ad libitum feeding! These unexpected results may be due to the fact that mild food restriction also involves a change from "nibbling" to "meal feeding" which has been found to result in increased fat (Thonney et al., 1982). Along these lines Nir (1974) found that body fat percentage is maintained constant in mildly restricted chicks as compared to ad libitum controls. Thus the reaction of fat deposition to mild restriction may involve special homeostatic mechanisms acting on the lean:fat partition coefficient.

From a practical viewpoint, the model suggests that direct selection against fat deposition under ad libitum feeding, would act to decrease appetite, gain and overall feed efficiency. The model also suggests, however, that additional selection pressure directed at the partition coefficient might increase it sufficiently to counteract the physiological effect of increased appetite on fat deposition. This might be achieved by selecting for feed efficiency ad libitum or by selecting for gain under restricted uniform food intake as suggested by Kielenowski (1969). Under both systems genetic variation in maintenance and in the partition function would make relatively greater contributions to variation in the traits under selection than to variation in ad libitum gain. As a result, selection for feed efficiency, or gains under restricted uniform food intake should have a greater effect on maintenance requirements and the lean:fat partition function than selection for ad libitum gain. In poultry, selection for food efficiency has in fact been found to decrease fat deposition as compared to unselected controls (Guill and Washburn, 1974; Pym and Solvyns, 1979). In mice, however, selection for food efficiency (Dickerson and Gowen, 1974; Palmer et al., 1946) or for gain under restricted uniform food intake (McPhee et al., 1980; Yuksel et al., 1981) apparently results in increased fat deposition. These differences between poultry and mice may be due to the relative genetic variability in maintenance requirements as compared to genetic variability in the lean:fat partition coefficient in the two species at the age of selection. As mentioned above, a decrease in maintenance requirements, by increasing the excess of intake over maintenance (I-M), would also exert a physiological effect increasing fat deposition. Thus selection for efficiency, if manifested primarily on maintenance requirements, need not necessarily result in decreased body fat, and might even induce a relative

increase. This may be the situation in mice, while in poultry, the presence of significant genetic variation in the lean:fat partition coefficient may allow selection for feed efficiency to reduce fat deposition.

Summary

Since selection for growth-rate has been found to increase appetite and decrease maintenance requirements, it will lead to an increase in the excess of intake over maintenance. It is proposed that weight gain, both lean and fat, is directly related to a positive energy balance, but that the lean:fat partition coefficient is a decreasing physiological function of the excess of intake over maintenance. On this model the effect of selection for gain on fat deposition would therefore be twofold: (1) A direct effect tending to increase lean deposition at the expense of fat, and (2) An indirect physiological effect, mediated by way of the excess of intake over maintenance, tending to increase fat deposition at the expense of lean. The latter effect apparently predominates in determining the net overall effect of selection for gain on fat deposition.

D.2.2. Selection for weight gains under conditions of uniform restricted food intake as a means of increasing feed efficiency in meat production.

In all meat producing animals, we can distinguish between a reproductive population, e.g., broiler mothers or beef cows, maintained primarily to produce a market population, e.g. broiler chicks or young calves, raised and marketed for meat. Total food costs to produce a unit of marketed product include food to raise and maintain the reproductive population, as well as food to raise the market animals until market age or weight. Selection for more rapid growth-rate is an effective means of increasing food efficiency in the market population but early growth-rate has been found to have a fairly high genetic correlation with mature body weight in meat producing animals. As a result, selection for AL-gains will generally result in an increase in mature body weight as well. Since food consumption of the reproductive population stands in proportion to their mature bodyweight, this means that a certain proportion of the saving in food consumed by the market population, due to increasing early growth-rate, are cancelled by increased food consumption of the mature reproductive population (Eitan, 1982). In some cases, e.g., purebred beef cattle, the additional food cost of increased mature body weight can completely offset any gain in feed efficiency in the market population, so that selection for more rapid growth-rate cannot be employed as a means of improving feed efficiency of the market population. Kielenowski (1969) suggested that selection for weight gains under restricted uniform food intake (henceforth: K-gains and K-selection) may provide a means of reducing maintenance requirements and fat deposition during the early growth-period, contributing in this way to increased feed efficiency of

market animals. In this design animals are individually fed restricted but equal amounts of food. Since food intake is restricted, all animals consume their entire ration so that uniform food intake is achieved. In this way appetite is eliminated as a variable affecting growth-rate, and gains during the test period are a function of maintenance requirements and degree of fat deposition only. In this study we present a theoretical analysis of some factors that may determine the relative usefulness of K-selection, as compared to selection for early growth-rate under conditions of unlimited access to feed (henceforth: selection for ad libitum gains, or AL-gains and AL-selection), as a means of improving feed efficiency of meat producing livestock, taking into account direct effects in the market population and indirect effects on the reproductive population. Preliminary experimental data are also given.

I. THEORETICAL MODEL

It will be assumed in what follows that the market population, when under commercial management, will be fed ad libitum, and that food restriction is limited to a specific test period in the breeding population under selection. In this case, the relative effectiveness of K-selection as compared to AL-selection, as a means of improving overall feed efficiency, will depend on the following agro-biological considerations:

- (i) The relative expected genetic response to K-selection as compared to AL-selection when market animals are raised under ad libitum feeding.
- (ii) The manner in which K-gains are expressed under AL-feeding.
- (iii) The marketing strategy (Eitan, 1982).
- (iv) The proportion of total food required to produce a unit of marketed product, that goes to the reproductive population.

These will now be defined more precisely and combined into general expressions, S_{ij} , for various conditions of K-gain expression ($i=1,2$) and marketing strategy ($j=1,2$).

Expected response to K-selection as compared to AL-selection when market animals are grown under AL-feeding

Following Falconer (1960) the expected response to K-selection and to AL-selection will equal the product of their respective heritabilities (h_K^2, h_{AL}^2) phenotypic standard deviations (σ_K, σ_{AL}) and selection intensities (i_K, i_{AL}). Thus the expected relative response to K-selection as compared to AL-selection, will equal

$$\frac{h_K^2 \sigma_K i_K}{h_{AL}^2 \sigma_{AL} i_{AL}} \quad (1)$$

Following Falconer (196) the genetic regression of AL-gains on K gains (b_A) will depend on the genetic correlation, r_A , between K-gains and AL-gains and on their respective genetic standard deviations, $\sigma_{A,K}, \sigma_{A,AL}$

$$b_A = r_A \frac{\sigma_{A,AL}}{\sigma_{A,K}} \quad (2)$$

Combining expressions (1) and (2), relative progress under ad libitum feeding conditions, as a result of K-selection as compared to AL-selection will equal

$$R = \frac{b_K h_K^2 \sigma_K i_K}{h_{AL}^2 \sigma_{AL} i_{AL}}$$

It will be convenient in what follows, to express genetic gains due to selection, as the proportionate increase, $g_K = R g_{AL}$ over the values in the population prior to selection.

Expression of K-gains under AL feeding conditions

A priori, when a population selected for K-gains is allowed to grow under ad libitum feeding, the effects of selection can express themselves (1) as increased gains under ad libitum feeding, but at the same food consumption as obtained prior to selection (condition 1), (2) as lower food consumption for the same gains as obtained prior to selection, or (3) as some combination of increased gains but lower food consumption than would have been required for similar gains made under AL-selection.

Marketing strategy

Two marketing strategies are found in meat producing animals (Eitan, 1982): (1) marketing at fixed body weight, as in broiler type chickens. In this case, increased growth-rate by reducing the time to market, saves maintenance costs per kg of liveweight, (2) marketing at fixed age (degree of maturity), as in beef cattle or sheep. In this case, increased growth-rate, by increasing market weight per animal, reduces reproduction costs per kg liveweight. The relative effect of K-gains compared to AL-gains on food costs per kg liveweight will differ in the two marketing strategies.

Savings in the market populations: We now consider relative savings in food consumption in the market population as a result of K-selection as compared to AL-selection for each combination of K-gain expression and marketing strategy. Relative costs in the reproductive population will be considered in a following section.

1. K-gains expressed as increased AL-gains, fixed market weight

In this case, the assumption is that increased growth-rate during AL-feeding as a consequence of K-selection will be obtained without a

corresponding increase in food consumption. Consequently, food savings in reaching a given market weight will equal growing days saved as a result of the increased growth-rate $\times$ food intake per day, I , at the end of the growing period. Growing days saved will equal $Tg_K/(1+g_K)$, where T is the original growing period in days, and $(1+g_K)$ is the proportional increase in ad libitum growth-rate as a result of K-selection. Therefore, total food savings in this case will equal $TIg_K/(1+g_K)$.

For AL-gains, gross food savings will come as a result of the decrease in the growing period due to more rapid growth rate. This, however, will require increased daily food consumption, both for the additional tissue growth, and for increased maintenance of the larger bird. Consequently, food savings will equal $TK_2Ig_{AL}/(1+g_{AL})$, where k_2 is a factor relating net food savings to gross food savings for AL-gains.

Based on these expressions, therefore, and recalling that $g_K=Rg_{AL}$, relative food savings, S_{11} , for the above conditions, in AL-raised market animals as a result of K-selection as compared to AL-selection will equal

$$S_{11} = \frac{TIRg_{AL}/(1+Rg_{AL})}{Tk_2Ig_{AL}/(1+g_{AL})} = \frac{R}{k_2} \frac{(1+g_{AL})}{1+Rg_{AL}}$$

2. K-gains expressed as decreased AL-food consumption, fixed market weight.

In this case, it is plausible that food savings will be proportional to the increase in growth-rate on restricted food intake, obtained as a result of K-selection. Consequently, food savings will equal $Tk_1Ig_K/(1+g_K)$, where k_1 is a factor relating mean food intake to final food intake, and Tk_1I is total food consumption during the growing period.

For AL-gains, net savings will be as in the previous section. Based on these expressions, therefore, and again substituting $g_K = Rg_{AL}$, relative food savings, S_{21} , under the above conditions in AL-raised market animals as a result of K-selection as compared to AL-selection, will equal

$$S_{21} = \frac{Tk_1 IRg_{AL}/(1+Rg_{AL})}{Tk_2 Ig_{AL}/(1+g_{AL})} = \frac{k_1 R (1+g_{AL})}{k_2 (1+Rg_{AL})}$$

3. K-gains expressed as increased AL-gains, fixed market age.

In this case, the assumption again is that increased growth-rate during AL feeding as a result of K-selection will be obtained without a corresponding increase in food consumption. Consequently, food savings at a given market age, will come from two sources: (1) Reduced food to the reproductive population, per unit of market product due to increased liveweight at market age. This will equal $Vg_K/(1+g_K)$, where V is the proportion of total food per unit market product going to the reproductive population, and (2) Reduced food per unit market product going to the market population, due to increased liveweight at market age at no increase in food consumption. This will equal $(1-V)g_K/(1+g_K)$. Thus, the total food savings will equal $g_K/(1+g_K)$.

For AL-gains, the larger market animal at market age, will have consumed additional food in proportion to its larger body weight, and food consumption by the market animal per unit of product will be unchanged. Thus, for this case, food savings are due to reduced food to the reproductive population, per unit of market product, only, and will equal $Vg_{AL}/(1+g_{AL})$.

Based on these expressions, and substituting $g_K = Rg_{AL}$ as before, relative food savings, S_{12} , under the above conditions in AL-raised market animals, as a result of K-selection as compared to AL-selection will equal

$$S_{22} = \frac{(1-V)Rg_{AL}/(1+g_{AL})}{Vg_{AL}/(1+g_{AL})} = \frac{(1-V)}{V} \frac{R(1+g_{AL})}{(1+Rg_{AL})}$$

Table 1 summarizes these relationships, letting B equal the terms $R(1+g_{AL})/(1+Rg_{AL})$, which appears in each of the expressions. Since k_1 and $(1-V)$ are both less than 1.0, it is clear that the relative effectiveness of K-selection in the market population will be greater when K-gains result in increased gains under AL feeding, than when K-gains result in decreased feed consumption under AL-feeding. Similarly, under a fixed market age strategy, K-selection will be most effective, when the reproductive population takes only a small portion of total food requirements per unit product.

Costs in the reproductive population

The proportional change in food costs of the reproductive population as a result of K or AL-selection will depend on:

(1) The proportional change in K or AL-gains as a result of K or AL-selection, equal to

$$\frac{g_K}{1+g_K} = \frac{Rg_{AL}}{1+Rg_{AL}}, \text{ and } \frac{g_{AL}}{1+g_{AL}} \text{ respectively, and}$$

(2) The genetic correlation between K or AL-gains and mature reproductive animal food consumption, $r_{A,K}$ and $r_{A,AL}$, respectively.

On this basis, the proportional change in mature animal food costs as a result of K or AL-selection will equal

$$r_{A,K} \frac{Rg_{AL}}{(1+Rg_{AL})} \text{ and } r_{A,AL} \frac{g_{AL}}{(1+g_{AL})}, \text{ respectively.}$$

Net savings

Net food savings, W_{ij} , for the various forms of K-gain expression and market strategy, as defined above, as a result of K-selection as compared to AL-selection can now be expressed by combining the results of the previous two sections, weighting proportional food savings in the market population by $(1-V)$ and proportion food costs in the reproductive population by (V) , to give:

$$W_{11} = \frac{(1-V)(1/k_2)Rg_{AL}/(1+Rg_{AL}) - Vr_{A,K}Rg_{AL}/(1+Rg_{AL})}{(1-V)g_{AL}/(1+g_{AL}) - Vr_{A,AL}g_{AL}/(1+g_{AL})}$$

$$= B \frac{(1/k_2) - V((1/k_2) + r_{A,K})}{1 - V(1+r_{A,AL})}$$

and similarly,

$$W_{12} = B \frac{k_1/k_2 - V((k_1/k_2) + r_{A,K})}{1-V(1+r_{A,AL})}$$

$$W_{21} = B \frac{1 - V(1+r_{A,K})}{V(1 - V - r_{A,AL})}$$

$$W_{22} = B \frac{1-V(2 - V + r_{A,K})}{V(1 - V - r_{A,AL})}$$

These expressions are complex, but show clearly that the effect of considering costs in the reproductive population depends critically on the values of $r_{A,K}$, $r_{A,AL}$ and V . In particular, when both V and $r_{A,AL}$ are large, the denominator of W_{ij} can become negative, indicating that AL-selection will yield negative net food savings. Although this can happen for K-selection as well, examination of the numerators of W_{ij} show that in each case, the critical regions of V and $r_{A,K}$ are smaller for K-selection than for AL-selection.

Numerical data

Only limited data on the genetics K-gains are available in the literature. In two studies with mice (McPhee et al., 1980; Yuksel et al., 1981) K-gains responded to selection with realized heritabilities of 0.27 and 0.16, respectively. Control populations subjected to AL-selection (Yuksel et al., 1981 only), showed similar realized heritabilities. Preliminary observations on limited family data for heavy breed chicks in our laboratory (section D.2.3) show heritability of K-gains about half that of AL-gains. Surprisingly, however, the phenotypic standard deviation for K-gains was almost as great as for AL-gains! This raises the possibility of significant genotype x restriction interactions acting on K-gains. In both mouse studies, mice selected for K-gains showed increase growth under AL-feeding. Thus, in these experiments at least part of K-gains are expressed as increased AL-gains. A priori, when feeding levels during the test period are low, differences in K-gains will depend primarily on difference in maintenance requirements. In this case, both h_K^2 and σ_K can be expected to be low. When feeding levels during the test period are relatively high, differences in K-gains may depend primarily on fat deposition. In this case, both h_K^2 and σ_K may be relatively high. Also, when feeding levels are high, just short of ad libitum, the genetic correlation between K-gains and AL-gains can be expected to be high as well. In contrast when feeding levels are low, part of the difference in K-gains may be due to differences in the mode of adaptation of the animals to feed restriction itself, i.e. to genotype x restriction interactions. Thus, Nir (19) has shown that light breed chicks adapt to intermittent feeding (a form of feed restriction) by conserving body fat composition at the expense of weight gains, while heavy breed chicks apparently respond by conserving growth-rate at the expense of body fat content. Clearly, variation along this axis could produce genetic

differences in K-gains between animals that are not expressed under AL feeding.

In most situations AL-selection and K-selection would be combined in a sequential manner, with initial selection on the basis of AL-gains, and a final selection step on the basis of K-gains. In this case, incremental selection intensity for pure AL-selection as compared to the combined AL and K-selection might be of similar magnitude as the K-selection step, so that selection intensities for the comparison of AL-selection and K-selection are similar. Thus, relative gains for K-selection as compared to incremental AL-selection will depend on relative values for the heritabilities and phenotypic standard deviations, and on the genetic correlation between AL-gains and K-gains. Both of these may depend on the level of restriction used when testing for K-gains. Thus, in the absence of experimental information, R can be expected to range from close to zero to almost 1.0.

With respect to the other parameters in Table 1: V , k_1 and k_2 , Eitan (1982) has calculated V for a number of meat producing animals, and found values of .05 for turkeys, .12 for broilers, .30 for hogs, .65 for beef cattle and .70 for sheep. Over the linear portion of the growth curve, it is easy to see that mean food intake per animal will be about half of final food intake, so that $k_1=0.5$. The factor k_2 , relating net to gross savings under AL-selection can be estimated as follows. Of the total food that would have been consumed during the growing days saved, part would have been utilized for additional tissue growth, part for body maintenance. It is reasonable that the part utilized for tissue growth will simply be redistributed over the shortened growth period of the AL-selected birds. Thus, there will not be any net savings for this part of the saved food intake. The maintenance part of the food intake will also be redistributed over the shortened growth-period, since the birds will be somewhat larger throughout. However, since the larger size is present, on the average,

only over half of the (shortened) growing period, only half of the maintenance savings are redistributed. If at the end of the growing period food intake is partitioned about 1/2 to growth and 1/2 to maintenance, then k_2 can be estimated as equal to $0.5 \text{ (net maintenance saved)} \times (0.5) \text{ (portion of maintenance of total intake)} = 0.25$.

Thus, for fixed market weight, relative effectiveness under AL-feeding of K-selection as compared to AL-selection, considering market population only, will be about 4B, when K-gains are expressed as increased AL-gains, and about 2.0B, when K-gains are expressed as decreased food consumption, with no increase in AL-gains. Thus, depending on the mode of expression of K-gains under AL feeding, and on the value of R and hence B, there are a wide range of agro-biological conditions under which K-selection could be equal or even superior to AL-selection as a means of improving feed efficiency in the market population.

For fixed market age, relative effectiveness of K-selection depends primarily on V, the proportion of total food intake per unit of product, that goes to the reproductive population. When V is low K-selection will compare favorably with AL-selection (say, in turkeys or hogs) as a means of increasing feed efficiency in the market population. When V is large, as in cattle or sheep, K-gains will be useful only if R and hence B are close to 1.0.

The regression $b_{v,AL}$ of food consumption of mature animals on AL-gains will be determined primarily by the genetic regression of mature body weight on early growth-rate (market weight). This, in turn will be the product of the genetic correlation between the two traits, and the ratio of their respective genetic standard deviations. The genetic correlation between early growth-rate and mature body weight has generally been found to be in the range 0.5-0.7. The ratio of the genetic standard deviations for the

two traits will be expected to stand in proportion to the ratios of their mean values, generally greater than 1.0. Thus, the genetic regression of mature body weight on market weight can be expected to be close to 1.0. This value was found in dairy cattle (Soller and Bar-Anan, 1972). Thus, as a first approximation, the denominator of M will equal $(1-2V)$. The regression of mature food consumption on K-gains can be expected to be appreciably less than that for AL-gains. If K-gains are expressed as decreased food consumption, without an increase in AL-gains, $b_{V,K}$ can be expected to be negative. In this case, selection for K-gains will result in food savings in the reproductive population as well as in the market population. Even when K-gains are expressed as increased AL-gains on AL feeding, $b_{V,K}$ can be expected to be less than $b_{V,AL}$ since the increased mature body size should require less food to produce and maintain than an increase due to AL-selection.

When V is large, as in beef cattle or sheep, the denominator of $M = (1-2V)$ will be very small, or even negative. In this case, K-selection will generally be more useful than AL-selection, unless R is very small indeed (in which situation it might be best not to select at all!). For small values of V however (as in turkeys, broilers, hogs), M would not be as great, but even in this case, depending on R, the value of M might be sufficient to tip the scales in favor of K-selection.

DISCUSSION

These analyses have clarified the conditions under which selection for gain, under restricted uniform food intake (K-gains) can serve as a useful addition to selection for growth-rate alone. These include (i) Conditions contributing to larger R. Primarily the presence of adequate heritability and phenotypic variation in the trait and lack of strong genotype x restriction interactions between K-gains and AL-gains, and a large proportion of total food intake to the market population. When a small proportion of total

food goes to the reproductive population, K-selection will be most useful if K-gains are expressed as increased gain on AL-feeding. In contrast, when a large proportion of total food goes to the reproductive population, K-selection will be useful if K-gains are expressed as less food consumed to reach the same market weight. This is due to the negative cost of increased AL-gains in the reproductive population when these are expressed as increased mature body weight. Thus, the results of this analysis show that there are a broad spectrum of conditions in which K-selection might make a positive contribution to genetic efficiency of meat producing livestock or poultry.

These experimental data are obviously insufficient to allow even a preliminary assessment of the economic potential of K-selection, and further studies are clearly needed to characterize the genetics of K-gains: heritability, standard deviation, genetic correlation with AL-gains under AL feeding, mode of expression and genetic correlation with lifetime food consumption of mature animals in the reproductive population.

D.2.3. Genetic aspects of weight gain under restricted uniform food intake: experimental results.

The previous discussion has shown that the relative effectiveness of selection for gains under uniform restricted food intake, as suggested by Kielenowski (1969, henceforth: K-gains and K-selection), as compared to selection for gains under ad libitum food intake (henceforth: AL-gains and AL-selection) depends critically on the heritability and phenotypic standard deviation of K-gains as compared to AL-gains, and on the genetic correlation of K-gains and AL-gains. We now present initial estimates of heritabilities and phenotypic standard deviations in K-gains and AL-gains in two White Rock broiler strain female line populations.

MATERIALS AND METHODS

Two experiments were conducted, both at the East Talpiot (Jerusalem) experimental farm of the Hebrew University. Experiment 1 involved White Rock half-sib (sire) families, obtained from Yavne Poultry Breeding Farm. Experiment 2, small in scale, involved White Rock full-sib (dam) families obtained from the Israel Poultry Breeders Union Mefalsim Farm. In Experiment 1 data were obtained on male chicks only. In Experiment 2, data were obtained on both male and female chicks.

From hatch to 28 days of age the chicks were kept in brooder batteries, and in floor pens until 42 days of age. Until 42 days they were allowed unlimited access to food and water (ad libitum feeding). At the end of this period birds were transferred to individual cages with individual food troughs for determination of gains under restricted uniform food intake. During this period, which lasted 14 days in Experiment 1 and 16 days in Experiment 2, all birds in an experiment received the same, restricted, quantity of food

added daily. Food was not given on Saturdays, but a double portion was given in two feedings on Friday. Food quantities were set at 65 g/d in Experiment 1, and 80 g/d in Experiment 2. Food quantities were such that all healthy birds consumed the entire ration.

Chicks were fed a starter mash (2795 cal ME/g, 21% protein) from hatch to 21 days of age, and a grower mash (2850 cal ME/g, 14% protein) thereafter.

Weight at 42-days of age (AL-gains) and weight gain during the period of restricted uniform food intake (K-gains) were recorded for each bird. In Experiment 1, the birds were slaughtered at the end of a second 8-day period of ad libitum feeding, and abdominal fat pad weights were obtained for each bird.

Since maintenance food requirements are determined in part by body weight, weight gains during the period of food restriction are negatively correlated with body weight at the beginning of the period. For this reason, the regression of K-gains on weight at the beginning of the restriction period was calculated (separately for each experiment and sex), and used to correct K-gains for each bird according to its initial weight.

Heritability estimates were calculated separately for each experiment and sex, as described in section D.1.5. In Experiment 2, mean parameter estimates over both sexes were calculated as the simple arithmetic mean of the two estimates. Mean parameter estimates over both experiments were then taken as the simple arithmetic mean of the estimate from Experiment 1, and the mean estimate of Experiment 2.

RESULTS AND DISCUSSION

Table 1 shows means, standard deviations and coefficient of variation for total gains in the initial ad libitum feeding period (AL-gains) and in the subsequent restricted feeding period (K-gains). On an absolute basis, K-gains were small in Experiment 1, only 21% of AL-gains. This can be attributed to the relatively low feeding levels during restriction in this experiment (65 g/d). Feeding levels in Experiment 2 were greater (80 g/d) and K-gains were correspondingly larger, 66% of AL-gains. Standard deviation of K-gains and of corrected K-gains were similar in magnitude in both experiments, and surprisingly large as compared to AL-gains. On an absolute basis, the mean standard deviation of K-gains and corrected K-gains over both experiments were 0.75 and 0.63 of the corresponding AL-gain, respectively. Thus, these results demonstrate the presence of considerable phenotypic variation in gains under restricted uniform feed intake. Other experiments show similar results (unpublished data).

It is difficult to reach a conclusion from these data as to the relative biological variation in K-gains as compared to AL-gains. A priori, K-gain variation is expected to be less than that of AL-gains, since appetite differences, a major component of AL-gain variation do not influence K-gains. This effect, however, would be balanced to an unknown degree by variation in physiological response to restricted feeding. Furthermore, part of the effect of variation in appetite could be balanced by internal homeostatic mechanisms, e.g., correlated changes in fat deposition (Section D.2.1), reducing their effect on variation in AL-gains. In this study, K-gains were obtained over a shorter period of time and a smaller absolute weight gain than AL-gains, so that variation in K-gains can be expected to be less

Table 1. Mean (above) standard deviation (center) and coefficient of variation (below) for growth related traits in the various experimental groups

Trait	Experiment 1 (White Rock sire families)	Experiment 2 (White Rock dam families)	
		Males	Females
No. of birds	252	73	70
AL-gains	929.7	1042.4	874.2
	87.4	68.1	68.4
	0.094	0.065	0.078
K-gains	197.4	617.6	630.4
	61.6	52.3	54.4
	0.312	0.095	0.090
Corrected ¹	-----	-----	-----
K-gains	46.2	51.2	54.4
	-----	-----	-----

¹Standard deviation only. For corrected gains, mean values equal zero.

than in AL-gains. It is difficult, however, to obtain a quantitative estimate of this effect. The coefficient of variation does not appear to be a suitable comparative measure, i.e., even if feeding levels during restriction were very low, so that K-gains were zero, considerable variation in K-gains would still be expected. Indeed, the standard deviation of K-gains in Experiment 1 was greater than in Experiment 2, although absolute K-gains were only one-third as great. Thus, the coefficient of variation of K-gains is probably inflated by the low absolute value of K-gains, which is not necessarily related to changes in K-gain variation. Perhaps the best estimate could be obtained by comparing variation in K-gains and AL-gains over the same weight-gain range (e.g., from 1000 g to 1500 g).

Table 2 shows heritability estimates for AL-gains and K-gains by experiment and sex, and mean heritabilities calculated as described in methods. Means heritability of AL-gains was 0.68. This is high for 42-day weight, considering that both populations had been under long term selection for rapid early growth-rate. The high value is due particularly to the very large heritability obtained in Experiment 1 ($h^2=0.86$). Values in Experiment 2 are closer to those ordinarily obtained in populations of this sort. Mean heritability of K-gains and corrected K-gains were 0.36 in both cases. Thus, heritability of AL-gains in these experiments was about twice that of K-gains. This may be an overestimate, however, in view of the very large value for heritability of AL-gains found in Experiment 1. In any event, heritability estimates for K-gains were greater than zero in all three analyses, and indicate the presence of moderate family variation in this trait, although less, in all likelihood, than found in AL-gains.

Table 2. Heritability estimates (above) for growth-related traits based on analysis of variance of between-family differences. F-values of between family differences are also given (below)

Trait	Experiment 1 (White Rock sire families)	Experiment 2 White Rock dam families	
		Males	Females
Degrees of freedom			
Between families	38	25	29
Within families	257	44	43
AL-gains	0.86 3.08**	0.53 1.72*	0.46 1.89*
K-gains	0.32 1.65	0.55 1.41	0.26 2.01*
Corrected K-gains	0.22 1.47	0.57 1.67	0.42 2.00

*P 0.05; **P 0.01

In these experiments, AL-gains and K-gains were determined sequentially on the same animals. Consequently the phenotypic and genetic correlations between the two parameters are thoroughly confounded by (1) the negative correlation between initial weight at the start of the restriction period and subsequent K-gains, and (2) the negative correlation between K-gains and subsequently compensatory growth during ad libitum feeding. For this reason, in spite of their great interest, the phenotypic and genetic correlations between K-gains and AL-gains calculated from these data, are not presented in this report. In fact, because of these factors, it is difficult to conceive of any experimental design, based on family data, that would allow unbiased estimates of the genetic correlation between K-gains and AL-gains from family data, and this question will have to wait upon the results of experimental selection programs.

As described in methods, the birds in Experiment 1 were allowed a second 8-day period of ad libitum feeding, and were then slaughtered and abdominal fat-pad weights obtained. Table 3 shows heritability calculations for abdominal fat pad weight, and its phenotypic and genetic correlations with AL-gains and K-gains. The outstanding feature of Table 3, is the weak positive correlation of abdominal fat pad weight with AL-gains, and the strong negative correlation with K-gains and corrected K-gains. This is exactly the result predicted for K-gains as compared to AL-gains. A note of caution is in order, however, since this result may be an artifact due to complex relationships between K-gains, subsequent compensatory growth and fat deposition.

Table 3. Heritability of abdominal fat pad weight and its genetic and phenotypic correlations with AL-gains and K-gains and corrected K-gains.

Trait	Correlations	
	Phenotypic	Genetic (S.E.)
AL-gains	0.14*	0.22 (0.254)
K-gains	-0.31**	-1.05 (0.993)
Corrected K-gains	-0.30**	-1.81 (4.91)

<u>Heritability</u>				
Source	d.f.	M.S.	F	h^2
Between families	38	761.88	3.16**	0.56
Within families	221	241.20		

Taken as a whole, the results suggest that phenotypic standard deviation and heritability of K-gains are less than those for AL-gains, but not so much so as to rule out the possible economic utility of K-gains selection with respect to the considerations developed in section D.2.2. Based on these family analyses, selection for K-gains ought to show an appreciable direct response, along with decreased fat deposition as a correlated response. In fact, three generations of selection for K-gains gave little or no response. We attribute this, in part at least, to the following technical factors,

- (i) Possible interactions with WTSXM (in the Series II lines),
- (ii) Low selection differential, since selection was carried out in males only, and
- (iii) Low effective heritabilities due to a number of reasons, including
 - (a) The necessity to correct gains under restricted uniform feeding for initial weight at the start of the restriction period, since birds that weigh more at the start of the period of uniform food intake, will have greater maintenance requirements, and hence will tend to gain less on the less on the same food intake as lighter birds,
 - (b) Retrospective analysis of the data showed that location of the bird in the hen house had a powerful effect on K-gains: birds in the center of the house had greater gains than birds at the ends or sides. This is probably due to temperature differences within the henhouse, and consequent differences in maintenance requirements. Thus, selection in the high line was basically limited to selection among birds in the central portion of the henhouse; selection in the low lines, to birds at the ends and sides.
 - (c) Although obviously sick birds were not selected in the low lines, it may be that birds with smallest gains were those with transient, subclinical illness.
 - (d) Allocation of food by volume rather than weight may have introduced differences between birds in total food consumed.

In order to overcome these deficiencies we propose to establish two new series of selection lines with K-gains as the sole selection objective. Selection in each series will be carried out in both males and females. Birds will be weighed at the beginning of the K-gain test period, and grouped in 50 g weight classes. The birds will be placed in the henhouse in groups of four birds of the same weight class and sex within a horizontal row of cages. Food allotments will be weighed to the nearest gram. Selection will be on an intra-group basis: for males, the individual with the highest gain out of four; for females, the two individuals with the highest gains out of four. This will avoid the necessity of correcting for initial body weight and for location within the henhouse.

The amount of food allowed will be chosen so that it is entirely consumed by 95% of the birds within a given weight class. In this way food intake will be uniform but on the high side. A restricted food intake close to ad libitum is desired so as to enable considerable fat deposition to occur. This will allow K-gains to be influenced primarily by variation fat deposition as opposed to variation in maintenance requirements. An amount close to ad libitum can also be expected to minimize physiological adjustments to feed restriction and possible genotype x treatment interactions derived from this.

D.2.4. Genetic analysis of growth differences between light and heavy breed chicks by way of an advanced segregating generation of a White Rock x Leghorn cross

INTRODUCTION

Correlated responses of selection for rapid growth have been the subject of intensive investigation in farm animals such as poultry, pigs and mice. Selection for increased body weight usually leads to increased food intake, gross efficiency and fat deposition (Roberts, 1979). Forced feeding of the slow growing layer genotype results in fattiness and only partially in an increase in lean body mass (Lepkovsky and Furuta, 1971; Nir et al., 1974). These observations have led to the belief (Hull, 1960; Hayes and McCarthy, 1976) that rapidly growing genotypes have a different food direction function whereby food is preferentially directed towards increased muscle mass, as opposed to fat or heat. In addition, increased food consumption by chickens of rapidly growing lines of chickens is accompanied by differences in feeding behavior. Broilers spend about half as much time feeding and eat larger meals than Leghorns (Masic et al., 1974). The activity of layers is thus wasteful in growth efficiency terms.

The existence of several components to the growth rate trait, altered feeding behavior, a changed lean:fat partition function, and differences in energy expenditure through activity differences, leads naturally to questions of the genetic basis of these phenomena. It can be asked: (1) whether these traits are dependently or independently controlled at the genetic level, (2) whether each of the components exhibit different dominance relationships, (3) whether one or several of the traits are under monogenic or polygenic control, and (4) whether different traits have different developmental patterns with age. Answers to these questions would allow for more sophisticated

approaches to breeding for growth rate and for altering some of the uneconomic side effects of rapid growth, such as fat deposition and reduced reproduction performance.

Until now, analysis of growth characters of rapid and slow growing lines has been carried out only to the F_1 generation (Eisen et al., 1977), although Punnet and Bailey (1914) examined segregation for weight in an F_2 generation. Pym and Nicholls (1979) have shown independent genetic control of gain, food consumption and efficiency in selected lines, thus casting light on the complex genetic structure of growth related characters. Described here is an attempt to analyze the components of growth in a segregating generation (F_5 and F_6) derived from a cross between rapidly growing White Rock broiler line (WR) and a slow growing Leghorn layer line (LN).

The segregating line is compared with two other genetic stocks, the WR line used in creating the segregating line and a Leghorn-New Hampshire cross (LN x NH). These populations are genetically more uniform than the segregating line thus allowing them to serve as reference populations for comparison of their developmental pattern and level of trait variation with that of the segregating line. Analysis of body parameters was carried out at 35, 60 and 90 days post-hatching. Food intake, growth and body composition parameters in the genetic stocks are reported, as well as the level of variation of traits within and between families.

MATERIALS AND METHODS

Genetic Stocks and Experiments

Two experiments were performed, both using males. Experiment A had two replications. Replicate 1 included 35 Leghorn x New Hampshire (LN x NH) hybrid chicks from the Yarkon tinted layer strain of Israel Poultry Breeders Union 38 White Rocks (WR) broiler chicks from Kibbutz Yavneh Breeding Farm, and 71 chicks from the F_5 generation of a Leghorn x White Rock (LN x WR) segregating line maintained at the Genetics Department of the Hebrew University. Chicks were hatched on February 1, 1979. Replicate 2 included 39 LN x NH, 39 WR and 71 LN x WR F_5 segregating line hatched on January 11, 1979. Experiment B included 39 LN x NH, 33 WR and 114 F_6 LN x NH chicks hatched on January 1, 1980.

Feeding and Husbandry

All chicks were separated by genetic stock and raised to 5 weeks in battery brooders, at which time they were moved into individual cages. The groups were raised ad libitum on chick starter mash (metabolizable energy to protein ratio of 14) and then transferred to broiler mash (metabolizable energy to protein ratio of 17) each at 3000 Kcal/kg. From 5 weeks until sacrifice, birds were kept under 18 hours of artificial and natural lighting per day.

Data Collection

For Experiment A, birds were weighed by spring balance to 12.5 g.

Food was provided ad libitum in 100 g portions as needed, and unconsumed food recorded. For Experiment B, bird weight and food intake were recorded every other week from 35 days. At five weeks, 10 LN x NH, 10 WR and 20 F₅ birds of Experiment A, half from each of the two replications, were selected at random and sacrificed. At 60 days, 35 birds of Experiment B were selected at random and sacrificed. The remaining birds of Experiment A replications 1 and 2 were sacrificed at 62 and 67 days, respectively, and the remaining birds of Experiment B were sacrificed at 90 days. Weights of birds and unconsumed food were recorded at sacrifice.

Birds were sacrificed by neck dislocation. Feathers, breast, abdominal fat pad, crop, proventriculus, gizzard, duodenum, pancreas, liver, spleen, testes, and caecum were removed, body parts were rinsed, blotted and tweezer stripped when needed, and weighed to the nearest mg. Shank and tibia length were measured to the nearest mm with a caliper. Internal organs were not weighed in Experiment B.

Body Composition Determinations

Whole featherless carcasses were ground and mixed for determination of percentage fat, dry matter and ash contents. Fat content was determined after extraction by chloroform-methanol.

Efficiency Calculations

Food intake and weight gain were calculated for each bird during the individual caging period. Gross energy efficiency was calculated as weight gain/food intake. Relative intake was calculated as gram intake/body weight^{.75}.

Statistical Analysis

Significance of differences between means was tested using the Student T-test. Significance of differences between coefficients of variation were tested by an F ratio based on the square of the coefficients of variation (Ferguson, 1971).

One way analysis of variance within and between families was carried out using the SAS general linear model procedure. Dam families were nested within sire families to correct for the large sire effects. Pearson product moment correlation coefficient was calculated using the SAS correlation procedure.

RESULTS

Body Parameters at 35 Days of Age

Significant differences between body composition and body part measurements of replicates 1 and 2 of Experiment A were generally not found at 35 days of age. Therefore, 35 day data from the two experiments were pooled. Mean values are given in Table 1. The small number of animals studied did not allow for a comparison of the level of variation in the segregation line relative to the reference lines. Body weight and breast of the segregating line are 11% and 15% below the average of the two control lines. This may indicate the size difference between the LN x NH reference population and the LN line used as parent for the segregating line.

When organ size is examined as percentage of body weight, values for the segregating line generally fall very near to the average of the two control lines. The exceptions, however, are of particular interest. As percentage, pancreas, abdominal fat pad, and total carcass fat of the segregating line are well below the average of the reference population, while crop and feathers are above the average of the two reference populations.

Body Parameters at 62 and 69 Days of Age

For the most part, significant differences unrelated to the week difference in the age of slaughter of the two replicates of Experiment A were not found. Therefore, 62 and 69 days data from the replicates A1 and A2 respectively were pooled. Mean values of body composition and growth parameters are given in Table 2a and organ weights for animals are given in Table 2b. Breast and body weight of the segregating line are below the average of the reference populations as they were at 35 days. Most of the other characters follow the same pattern as seen at 35 days, in being below the average of the reference populations in absolute value and nearly equal to the average as percentages. Pancreas %, which was well below the average of the reference populations at the earlier ages, remained low at these later ages. Total carcass fat % and abdominal pad % are above the average of the reference populations. Thus, total carcass fat and abdominal fat pad appear to have changed developmental patterns from 35 to 70 days. In the segregating line, energy intake of replicate 2 was above and gross efficiency below the average of the reference population ($p < .01$), but not in replicate 1. Although replicates 1 and 2 were terminated only one week apart, this difference may reflect a real difference in developmental patterns with age (see below).

Coefficients of variation (CV) of body weight, composition, intake and efficiency parameters are given in Table 3a. All parameters except for total carcass fat and efficiency are more variable in the segregating line than in WR, but not more variable than in

Table 1. Mean values ($\pm$ standard deviation) and percent of body weight of weight, composition, and body parts at 5 weeks

	LN x NH	F ₅	WR	Midpoint of LNxNH and WR*
Body Weight	334 ^{a**} $\pm$ 69	480 ^b $\pm$ 70	740 ^c $\pm$ 140	
Breast %	35.9 ^a $\pm$ 9.5 10.7	53.6 ^b $\pm$ 9.4 11.2	87.8 ^c $\pm$ 17.9 11.9	11.3
Total Carcass Fat %	32.9 9.9	49.0 10.3	94.0 12.7	11.3
Abdominal Fat Pad %	1.85 ^a $\pm$.88 .55	3.92 ^b $\pm$ 2.1 .82	10.61 ^c $\pm$ 3.76 1.43	0.99
Shank Length	5.98 ^a $\pm$.63	6.72 ^b $\pm$.49	7.69 ^c $\pm$.56	
Tibia Length	7.29 ^a $\pm$.52	7.96 ^b $\pm$.42	8.82 ^c $\pm$.55	
Feathers %	13.24 ^a $\pm$ 5.7 3.96	19.90 ^b $\pm$.42 4.14	26.70 ^c $\pm$ 13.90 3.60	3.78
Proventriculus %	2.48 ^a $\pm$.25 .74	3.13 ^b $\pm$.46 .65	4.67 ^c $\pm$.39 .63	.68
Gizzard %	10.77 ^a $\pm$.89 3.2	14.05 ^b $\pm$ 1.69 2.9	18.89 ^c $\pm$ 1.91 2.5	2.88
Crop %	1.95 ^a $\pm$.48 .58	3.06 ^b $\pm$.72 .63	4.33 ^c $\pm$ 1.21 .58	.58
Duodenum %	2.82 ^a $\pm$.44 .84	3.29 ^a $\pm$.52 .67	3.81 ^b $\pm$.49 .51	.68
Pancreas %	1.46 ^a $\pm$.11 .44	1.45 ^a $\pm$.14 .30	2.81 ^b $\pm$.50 .38	.41
Caecum %	1.77 ^a $\pm$.24 .53	2.29 ^b $\pm$.54 .47	3.16 ^c $\pm$.43 .42	.48
Liver %	10.60 ^a $\pm$ 6.5 3.2	15.21 ^b $\pm$ 2.28 3.2	21.87 ^c $\pm$ 2.29 3.0	3.1

* Average of LN x NH and WR percents

** Means within a row with different superscripts are significantly different by a t-test ($P < 0.01$)

LN x NH. CV of organ size parameters are given in Table 3b. The gizzard, proventriculus, caecum and feathers are more variable in the segregation line than in WR, but when examined as percent of body weight, the parameters of segregating line are not significantly more variable. Thus, we cannot conclude that there is genetic segregation independent of body weight for any of the organ size parameters.

Comparison of Body Parameters at 60 and 90 Days

The finding of changing patterns of fat deposition with time in the segregating line relative to the reference populations lead to the examination of the patterns of intake, gain and fat over time, and to an extension of the examination to 90 days to see how the pattern develops as growth proceeds.

Means and standard deviations of body composition and body parts for animals slaughtered at 60 and 90 days (Experiment B) are given in Tables 4 and 5. Especially striking is the relatively low food intake in the segregating line during the 45-60 day interval in comparison to the reference lines and in comparison to later ages. Abdominal pad % in the segregating line at 60 days (Table 4) was well above the average of the reference lines. At 90 days, abdominal pad % of the segregating line is even above the WR value. Relative gain (gain %) of the segregating line over the 45-90 day growth period was well below the mean of the two reference lines and is close to that of the LN x NH cross. Efficiency of the segregating line is low during the 76 to 90 day interval. Thus, the predominant feature of the growth of the segregating line in the 60 to 90 day intervals is the tendency of the gain to

Table 2b. Mean values ($\pm$ standard deviation) and percent of body weight of body parts at 62 and 69 days (Experiment A, replicates 1 and 2)*

	LN x NH	F ₅	WR
Proventriculus %	3.8 ^{a**} $\pm$.5 .45 ^a $\pm$.06	5.6 ^b $\pm$.8 .42 ^a $\pm$.05	7.5 ^b $\pm$.8 .31 ^b $\pm$.05
Gizzard %	18.4 ^a $\pm$ 3.2 2.20 ^a $\pm$.28	28.1 ^b $\pm$ 4.2 2.09 ^b $\pm$.26	37.0 ^c $\pm$.39 1.70 ^c $\pm$.18
Crop %	2.9 ^a $\pm$.5 .35 ^a $\pm$.05	4.6 ^b $\pm$ 1.0 .34 ^a $\pm$.06	7.10 ^c $\pm$ 1.4 .33 ^a $\pm$.07
Duodenum %	3.8 ^a $\pm$.77 .46 $\pm$.10	4.4 ^b $\pm$.8 .33 $\pm$.06	6.2 ^c $\pm$ 1.0 .29 $\pm$.05
Pancreas %	2.4 ^a $\pm$.4 .28 ^a $\pm$.03	2.8 ^b $\pm$.4 .21 ^b $\pm$.02	4.1 ^c $\pm$.6 .19 ^b $\pm$.03
Caecum %	3.4 ^a $\pm$.6 .41 ^b $\pm$.07	4.0 ^b $\pm$.7 .30 ^a $\pm$.04	5.8 ^c $\pm$.7 .27 ^a $\pm$.03
Liver %	23.9 ^a $\pm$ 3.4 2.9 ^a $\pm$.3	33.2 ^b $\pm$ 4.5 2.5 ^b $\pm$.3	49.2 ^c $\pm$ 6.2 2.3 ^c $\pm$.2
Feathers %	57 ^a $\pm$ 7 6.8 $\pm$.6	79 ^b $\pm$ 6 5.8 $\pm$.09	106 ^c $\pm$ 11 4.9 $\pm$.5
Shank length	8.9 ^a $\pm$.6	10.4 ^b $\pm$.6	11.8 ^c $\pm$.6
Tibia length	10.7 ^a $\pm$.5	11.1 ^b $\pm$.5	13.0 ^c $\pm$.3

* The data from the two replicates were pooled

** Means within a row with different superscripts are significantly different by a t-test ($P < 0.01$)

Table 2a. Mean values ($\pm$ standard deviation) and percent of body weight of growth, food intake, efficiency and composition parameters at 62 and 69 days (Experiment A, Replicates 1 and 2)

	LN x NH	F ₅	WR	Midpoint of LNxNH and WR
Body wt.	838 ^{a**} $\pm$ 93	1347 ^b $\pm$ 154	2164 ^c $\pm$ 168	1501
Breast %	110 ^a $\pm$ 17 13 ^a $\pm$ 1.0	188 ^b $\pm$ 29 14.0 ^b $\pm$ 1.1	318 ^c $\pm$ 35 14.7 ^c $\pm$.95	214 13.9
Wt gain %	504 ^a $\pm$ 66 146 ^a $\pm$ 23	867 ^b $\pm$ 152 180 ^b $\pm$ 33	1424 ^c $\pm$ 127 190 ^c $\pm$ 20	168 ⁹⁶⁴
Intake %	1471 ^a $\pm$ 137 2.08 ^a $\pm$.22	2814 ^b $\pm$ 243 2.09 ^a $\pm$.16	3672 ^c $\pm$ 251 1.70 ^b $\pm$.27	2571 1.89
Gross eff.	.290 ^a $\pm$.033	.308 ^b $\pm$.059	.388 ^c $\pm$.087	.339
Carcass fat %	70 ^a $\pm$ 13 .084 ^a $\pm$.012	156 ^b $\pm$ 36 .116 ^b $\pm$.019	269 ^c $\pm$ 55 .124 ^c $\pm$.022	170 .104
Abdominal pad %	3.67 ^a $\pm$ 1.8 .44 ^a $\pm$.18	25.3 ^b $\pm$ 10.6 1.88 ^b $\pm$.68	43.3 ^c $\pm$ 13.1 2.00 ^b $\pm$.57	23.5 1.22

* The data from the two replicates were pooled

** Means within a row with different superscripts are significantly different by a t-test ($P < 0.01$)

move away from the WR rate of growth toward that of the LN x NH cross while the carcass fat % exceeds that of the WR line.

Examination of coefficients of variation (CV) at 60 and 90 days in Experiment B (Table 6) reveals generally higher variation in the segregating line than in one or two of the reference populations in body weight, food intake, and relative intake. Variation in fat percent but not in fat was significantly greater in the segregating line. For gain and gain percent, no greater CV in the segregating line was found. In most cases in the segregating line, the magnitude of CV in younger ages is greater than that at the later periods. The exception is relative intake.

Partitioning of variance within and between families.

Significant between family variances (Table 7) were found in sample 1 at 60 days in sire and dam families for weight and for abdominal fat pad and fat pad %. No significant between family variation was found in food intake, feed efficiency, body fat or weight gain.

In sample 2, sacrificed at 90 days of age, significant between family variances in sire families were found for body weight, gain, intake and abdominal fat pad (Table), but no significant between family variance was found in feed efficiency nor in any of the traits in dam families except for food intake.

Partitioning of variance in traits in terms of percent of body weight was examined. In sample 2 relative gain (gain %) had no significant family component. Pad % on the other hand, had a significant sire effect. Most of the variation in intake was due to differences in weight as is seen when the weight component is removed as it is in relative intake (intake/45 day body weight^{0.75}).

Table 3a. Coefficients of variation (x 100) of growth, food intake efficiency and composition parameters and of their percents at 62 and 69 days (Experiment A, replicates 1 and 2)*

	LN x NH	F ₅	WR
Body weight	11 ^{b**}	11 ^b	8 ^a
Breast %	15 ^b 8 ^a	15 ^b 8 ^a	11 ^a 6 ^a
Weight gain %	13 ^b 16 ^b	17 ^a 20 ^b	9 ^c 10 ^a
Food intake %	9 ^b 10 ^b	9 ^b 8 ^a	6 ^a 6 ^a
Gross efficiency	11 ^b	19 ^b	22 ^a
Carcass fat %	19 ^a 14 ^a	23 ^a 16 ^a	20 ^a 18 ^a
Abdominal fat %	49 ^b 41 ^b	41 ^b 36 ^b	30 ^a 28 ^a

* The data from replicates 1 and 2 were pooled

** Coefficients of variation within a row with different superscripts are significantly different by an f ratio based on the squares of the CVs

Table 3b. Coefficient of variation (x 100) of organ size parameters and of their percents at 62 and 69 days (Experiment A)*

	LN x NH	F ₅	WR
Proventriculus	13 ^{b**}	14 ^b	11 ^a
%	13 ^a	12 ^a	16 ^b
Gizzard	17 ^b	15 ^b	10 ^a
%	13 ^a	12 ^a	11 ^a
Crop	17 ^a	22 ^a	20 ^a
%	14 ^a	18 ^a	21 ^a
Duodenum	20 ^a	18 ^a	16 ^a
%	21 ^a	18 ^a	17 ^a
Pancreas	17 ^a	15 ^a	15 ^a
%	11 ^a	10 ^a	16 ^a
Caecum	18 ^a	18 ^b	12 ^a
%	17 ^a	14 ^a	11 ^a
Liver	14 ^a	14 ^a	13 ^a
%	10 ^a	12 ^a	9 ^a
Shank length	7 ^a	6 ^a	5 ^a
Tibia length	5 ^a	5 ^a	2 ^a
Feathers	12 ^a	8 ^b	10 ^a
%	8 ^a	16 ^b	10 ^{ab}

* The data from the two replicates were pooled

** Coefficients of variation within a row with different superscripts are significantly different by an f ratio based on the squares of the CVs

Table 4. Mean values ($\pm$ standard deviation) and percent of body weight of growth, food intake, efficiency, and composition parameters at 60 days (Experiment B)

	LN x NH	F ₅	WR	Midpoint of LNxNH and WR*
45 day wt.	564 ^{a**} $\pm$ 80	698 ^b $\pm$ 104	1027 ^c $\pm$ 127	796
60 day wt.	789 ^a $\pm$ 87	979 ^b $\pm$ 160	1532 ^c $\pm$ 191	1160
Wt. gain	225 ^a $\pm$ 47	281 ^b $\pm$ 70	506 ^c $\pm$ 101	366
%	.41 ^a $\pm$.13	.40 ^a $\pm$.07	.50 ^b $\pm$.10	.45
Food intake	896 ^a $\pm$ 189	1051 ^b $\pm$ 240	1554 ^c $\pm$ 122	1225
Gross efficiency	.251 ^a $\pm$.082	.276 ^{a,b} $\pm$.064	.328 ^b $\pm$.073	.290
Relative intake	7.71 ^a $\pm$ 1.74	7.76 ^a $\pm$ 1.65	8.57 ^b $\pm$.97	8.14
Abdominal fat pad	5.8 ^a $\pm$ 4.04	13.2 ^b $\pm$ 7.2	21.6 ^c $\pm$ 11.3	13.7
%	.67 ^a $\pm$.38	1.36 ^b $\pm$.69	1.39 ^b $\pm$.55	1.03
Total carcass fat	81.3 ^a $\pm$ 12.8	95.1 ^b $\pm$ 14.6	112.3 ^c $\pm$ 20.2	968
%	10.6 ^c $\pm$ 2.0	10.0 ^b $\pm$ 2.1	7.2 ^a $\pm$ 1.0	8.9
Feathers	64.6 ^a $\pm$ 5.0	91.0 ^c $\pm$ 9.8	77.3 ^b $\pm$ 10.3	710
%	8.6 ^c $\pm$.80	6.3 ^b $\pm$.70	5.0 ^a $\pm$.60	6.8

* Average of LN x NH and WR

** Means within a row with different superscripts are significantly different by a t-test ($P < 0.01$)

Table 5. Mean values ($\pm$ standard deviation) of growth, food intake efficiency and composition parameters for birds terminated at 90 days (Experiment B)

	LN x NH	F ₆	WR
<u>Weight</u>			
45 d	550 ^{a*} $\pm$ 68	682 ^b $\pm$ 124	981 ^c $\pm$ 132
60 d	776 ^a $\pm$ 91	985 ^b $\pm$ 174	1472 ^c $\pm$ 222
75 d	1088 ^a $\pm$ 114	1395 ^b $\pm$ 214	2374 ^c $\pm$ 310
90 d	1291 ^a $\pm$ 128	1716 ^b $\pm$ 257	3100 ^c $\pm$ 403
<u>Gain</u>			
45-60 d	226 ^a $\pm$ 43	303 ^b $\pm$ 68	491 ^c $\pm$ 128
61-75 d	312 ^a $\pm$ 58	410 ^b $\pm$ 60	902 ^c $\pm$ 149
76-90 d	202 ^a $\pm$ 62	321 ^b $\pm$ 90	726 ^c $\pm$ 201
TOTAL	740 ^a $\pm$ 103	1034 ^b $\pm$ 156	2119 ^c $\pm$ 162
<u>Gain %</u>			
45-60 d	41.1 ^a $\pm$ 8.4	44.4 ^b $\pm$ 10.1	50.0 ^c $\pm$ 11.2
61-75 d	40.2 ^a $\pm$ 8.0	41.6 ^b $\pm$ 6.5	61.2 ^c $\pm$ 10.7
76-90 d	18.6 ^a $\pm$ 6.3	23.0 ^b $\pm$ 5.4	30.5 ^c $\pm$ 7.1
<u>Intake</u>			
45-60 d	927 ^b $\pm$ 99	892 ^a $\pm$ 165	1515 ^c $\pm$ 154
61-75 d	953 ^a $\pm$ 120	991 ^b $\pm$ 187	1864 ^c $\pm$ 209
76-90 d	1070 ^a $\pm$ 67	1520 ^b $\pm$ 192	2500 ^c $\pm$ 154
TOTAL	2950 ^a $\pm$ 210	3400 ^b $\pm$ 423	5892 ^c $\pm$ 243
<u>Relative intake</u>			
45-60 d	8.09 ^a ^b $\pm$ 1.29	6.72 ^a $\pm$.92	8.65 ^b $\pm$.80
76-90 d	6.51 ^b $\pm$.89	5.70 ^a $\pm$ 1.02	8.01 ^c $\pm$ 1.04
<u>Efficiency</u>			
45-60 d	.244 ^a $\pm$.054	.339 ^b $\pm$.060	.324 ^b $\pm$.081
61-75 d	.327 ^a $\pm$.072	.413 ^b $\pm$.076	.485 ^c $\pm$.064
76-90 d	.188 ^a $\pm$.060	.211 ^b $\pm$.053	.240 ^c $\pm$.050
TOTAL	.251 ^a $\pm$.041	.304 ^c $\pm$.034	.359 ^b $\pm$.028
<u>Fat</u>			
Pad	8.3 ^a $\pm$ 5.8	32.6 ^b $\pm$ 24.8	50.5 ^c $\pm$ 32.8
Pad %	0.6 ^a $\pm$ 0.4	1.8 ^b $\pm$ 1.5	1.6 ^b $\pm$ 0.9

* Means within a row with different superscripts are significantly different by a t-test ($P < 0.01$)

Table 6. Coefficients of variation (x 100) of all measured parameters and of their percents (parentheses) for birds terminated at 60 and 90 days (Experiment B)

	60 day		90 day	
	LN x NH	F ₆	LN x NH	F ₆
Weight				
45 d	14 ^{a*}	15 ^a	12 ^a	18 ^b
60 d	11 ^a	16 ^b	12 ^a	18 ^b
75 d			11 ^a	18 ^b
90 d			10 ^a	15 ^b
			10 ^a	15 ^b
				13 ^a
				13 ^{ab}
				13 ^{ab}
Gain				
45-60 d	21 ^a (32)	25 ^a (18)	20 ^a (20)	19 ^a (20 ^a)
61-75 d				19 ^a (20 ^a)
76-90 d				31 ^a (33 ^a)
TOTAL				14 ^a
				22 ^{ab} (22 ^a)
				15 ^a (16 ^a)
				28 ^a (23 ^a)
				15 ^a
				26 ^b (22 ^a)
				17 ^a (17 ^a)
				28 ^a (23 ^a)
				73 ^a
Intake				
45-60 d	21 ^a	22 ^a	8 ^a	11 ^a
61-75 d				13 ^a
76-90 d				6 ^a
TOTAL				7 ^a
				18 ^b
				19 ^b
				13 ^b
				12
				10 ^a
				11 ^a
				6 ^a
Efficiency				
45-60 d	33 ^{ab}	23 ^b	22 ^a	22 ^{ab}
61-75 d				22 ^a
76-90 d				32 ^a
TOTAL				16 ^c
				18 ^b
				18 ^a
				25 ^b
				11
				25 ^a
				13 ^b
				17 ^a
				8 ^a
Relative intake				
45-60 d	22 ^{ab}	21 ^b	11 ^a	16 ^a
76-90 d				14 ^{ab}
				14 ^{ab}
				18 ^b
				9 ^c
				13 ^a
Fat				
Abdominal pad	70 ^a (57 ^a)	54 ^a (51 ^a)	52 ^a (40 ^a)	70 ^a (67 ^a)
Total carcass	16 ^a (19 ^{ab})	15 ^a (21 ^b)	18 ^a (14 ^a)	76 ^a (83 ^b)
				64 ^a (56 ^a)
Feathers	8 ^a (9 ^a)	11 ^a (11 ^a)	13 ^a (12 ^a)	

* Coefficients of variation within a row with different superscripts are significantly different by an f ratio based on the square of the CVs

Table 7. Relative partitioning of variance between and within families in the segregating line (F values)

	60 Days		90 Days	
	Sire families	Dam** families	Sire families	Dam families
<u>Weight</u>				
45 days	5.01*	7.26*	2.10*	1.55
61 days	4.16*	4.59*	3.09*	1.67
76 days			3.42*	2.13*
90 days			1.94*	1.12
<u>Gain</u>				
45-60 days	1.50	0.99	1.96*	1.42
61-75 days			1.82	1.65
76-90 days			0.48	0.90
Total			1.17	1.03
<u>Gain %</u>				
45-60 days	.83	0.48	0.80	1.22
61-75 days			1.20	.063
76-90 days			0.73	1.57
Total			0.86	1.24
<u>Food intake</u>				
45-60 days	1.68	0.74	3.45*	1.94*
61-75 days			1.53	1.21
76-90 days			1.74	1.24
Total			2.89*	1.77
<u>Efficiency</u>				
45-60 days	1.84	0.84	0.66	1.05
61-75 days			1.86	1.16
76-90 days			0.38	1.18
Total			0.77	1.05
<u>Relative intake***</u>				
45-60 days	1.20	0.66	1.26	1.43
61-75 days			1.35	0.58
76-90 days			1.03	1.65
Total			1.50	1.14
<u>Fat</u>				
Abdominal pad	6.65*	3.32*	2.18*	1.29
Abdominal pad %	4.27*	1.69	2.45*	1.19
Body fat	1.50	1.40	N.D.	N.D.
Body fat %	0.70	1.95	N.D.	N.D.

*Starred values indicate significance between vs. within family variances.

**Dam families within sire families

***Food intake/body weight .75

Segregation of complexes of traits

Correlation analysis was used to characterize the segregating line. A correlation matrix of the various traits from sample 1 birds slaughtered at 60 days is shown in Table 8. Traits most closely related to body weight were intake and body fat, with correlation coefficients of 0.46 and 0.74, respectively. Neither abdominal fat pad % nor body fat % was correlated with body weight. Total body fat and abdominal fat pad were positively correlated with each other (0.72), validating the fat determination.

The correlation matrix for sample 2 is given in Table 10. As in sample 1, intake and pad are correlated with body weight. Unlike sample 1, relative intake is correlated with rate of gain and body weight is negatively correlated with rate of gain. Fat and fat % are correlated with intake in sample 2 but not in sample 1, but in neither sample is fat correlated with relative intake.

DISCUSSION

Comparative Developmental Patterns

The significant feature of the comparison of trait means over time is the changing patterns of fat deposition and efficiency. At 35 days, the segregating line was leaner than the average of the reference genotypes (Table 1) while at 60 days it was slightly above (Tables 8 and 10) and at 90 days it was above the mean of WR.

The changing pattern of fat deposition over time is reflected in a changing pattern of intake and efficiency over time. Experiment A and B, however, gave slightly different results. The relatively low intake of the segregating line in the 45 to 60 day interval in Experiment B had no counterpart in Experiment A, even in replicate 1 which was terminated at 62 days. Likewise the low efficiency of

Table 8. Correlation coefficients of traits in Sample 1 (60 days)

	60 days wt.	Gain	Gain %	Food intake	Feed effic.	Relative intake	Abd. fat pad	Abd. fat pad %	Body fat	Body fat %
45-day weight	.94**	.67**	.08	.46**	.18	-.05	.45**	.20	.74**	.15
60-day weight		.87**	.39*	.43**	.38*	-.05	.48**	.22	.74**	.10
45-60 day gain			.78**	.31	.60**	-.04	.44**	.20	.60**	.02
45-60 day gain %				.02	.67**	-.03	.21	.10	.21	-.07
Food intake					-.55**	.86**	.08	-.06	.32	.04
Feed efficiency						-.73**	.30	.23	.24	-.05
Relative intake							-.17	-.19	-.07	-.03
Abdominal fat pad								.95**	.72**	.60**
Abdominal fat pad %									.59**	.68**
Body fat										.73**

*Significant at $p < .05$

**Significant at $p < .01$

Table 9. Mean trait values and coefficient of variation x 100 (in parentheses) for truncated groups in Sample 1 (60 days)

	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Total
Trait	Weight*	Efficiency**	Abdominal pad %**	Relative intake	Weight* Relative intake**	Weight* Food**	
Limit	>800	>.33	> 2.0	>9.0	<700 <6.9	<700 >950	
# of animals	5	7	7	7	7	6	35.

<u>Weight</u> 45 day	851 (2)	739 (12)	732 (12)	726 (17)	621 (8)	591 (9)	699 (15)
60 day	1228 (5)	1075 (13)	1035 (15)	1000 (20)	856 (8)	825 (10)	981 (16)
<u>Gain</u> 45-60 day	377 (11)	336 (18)	302 (22)	274 (35)	236 (15)	234 (22)	282 (24)
<u>Gain %</u> 45-60 day	.443 (10)	.454 (13)	.408 (12)	.37 (25)	.379 (11)	.398 (24)	.40 (18)
<u>Intake</u> 45-60 day	1272 (17)	966 (17)	998 (19)	1434 (5)	765 (11)	1143 (16)	1051 (23)
<u>Efficiency</u> 45-60 day	.30 (17)	.35 (3)	.303 (10)	.19 (34)	.236 (15)	.21 (35)	.275 (23)
<u>Relative intake</u> 45-60 day	8.0 (16)	6.1 (12)	7.6 (12)	10.3 (11)	6.1 (7)	9.6 (7)	7.7 (12)
<u>Abdominal Pad</u> Total	18.2 (51)	13.2 (70)	24.6 (20)	10.5 (36)	13.1 (59)	8.1 (64)	13.5 (55)
Percent	14 (47)	11 (57)	24 (19)	10 (29)	15 (60)	10 (58)	13 (51)
<u>Body fat</u> Total	113 (16)	90 (21)	108 (17)	92 (25)	82 (18)	76.0 (20)	93 (23)
Percent	9.9 (14)	8.4 (18)	10.5 (18)	9.4 (6)	9.5 (18)	9.2 (14)	9.5 (15)

* 45 day

** 45-60 day

Table 10. Correlation coefficients of traits in Sample 2 (90 days)

	90 d wt.	45-60 d gain	61-75 d gain	45-60 d gain %	61-75 d gain %	45-60 d int.	61-75 d int
45 day wt.	.83**	.42**	-.53**	-.43**	-.53**	.67**	.43**
90 day wt.		.65**	-.27*	-.05	.11	.69**	.55**
45-60 d gain			.44**	.62**	-.37**	.67**	.43**
61-75 d gain				.40**	.40**	.50**	.44**
45-60 d gain %					.11	.10	.05
61-75 d gain %						-.27*	-.15
45-60 d intake							.44**
61-75 d intake							
45-60 d effc.							
61-75 d effc.							
45-60 d rel. int.							
61-75 d rel. int.							
Abdominal fat pad							

* Significant at $P < .05$

** Significant at $P < .01$

Coefficients of traits in Sample 2 (90 days)

[illegible]

replicate 2, terminated at 69 days, had no counterpart in Experiment B. In spite of these differences, it appears that the growth of the segregating line is more directed towards lean efficient growth early and more directed towards fat and less efficient growth late. Hayes and McCarthy (1976) suggest that lean growth takes place in selected lines up to the time of selection, after which there is a tendency to become fat.

Evidence for Genetic Segregation

Increased variation due to genetic segregation in an F_2 as compared to a parental line or an F_1 is taken as an indication that the parental lines differ in quantitative loci effecting the trait in question (Mather and Jinks, 1971). By analogy, in a cross between two widely separated lines genetic differences should also express themselves in increased variation in an F_3 and subsequent generations. We have used this to test for genetic differences between White Rock Leghorns in the traits of interest.

The predominant feature of the analysis of variation within the lines is the finding of generally higher CV relative to the reference populations in weight, and food intake, in the segregating line. In Experiment A, differences between LN x NH and the segregating line were not significant. There was no higher variation in total body fat or abdominal fat pad in the segregating lines. Nevertheless, it will be shown in the next section that there is significance between family variance for abdominal fat pad in the segregating line, both at 60 days and at 90 days. From this we conclude that there are genetic

differences in weight, intake and relative intake in the WR and LN parents of the segregating line which can be detected by enhanced variation in the F_5 and F_6 generation of the segregating line.

It is interesting to note that although CV for food intake and of the segregating line is larger than those of the reference lines during the 45 to 60 day interval, of Experiment B, the magnitude of this difference decreases during the later intervals. This means that birds that were extreme in intake during the early intervals are no longer extreme in the later intervals. We conclude that the physiological genetic causes of efficiency and intake differences act early and that later their effect is reduced. Nevertheless, higher CV for relative intake persists and is perhaps enhanced late, when greater variation in fat percent is apparent in the segregating line.

In contrast to the finding of genetic segregation in body weight and food, there is no evidence for segregation independent of body size of internal organ size. It appears that a significant proportion of the growth rate character cannot be ascribable to genetic differences in organ size per se between the two parents of the segregating line.

The finding of genetic segregation of appetite and weight in the segregating line still does not answer the question of whether one of these components, appetite for example, could be responsible for all the variation in growth rate. That there are significantly higher variation in the segregating line in fat percent argues against this since some growth component (or lack of it) must be used to explain the appearance of extra fat or lean animals. Interestingly, no higher variation was found in efficiency and therefore efficiency differences per se cannot be important in confirming the growth rate trait. Solid

evidence for independence of several of the factors comes from the work of Pym and Nicholls (1979) who showed selection response for three characters, weight gain, food consumption, and food conversion by selection in a high weight line. Siegel and Wisman (1966) showed that a recognizable component of the growth rate trait could be explained by differences in efficiency. We confirm the conclusion of Proudman et al. and Pym and Nicholls (1979) that the major component differentiating lines is appetite. An attempt to deal with the problem of the nature of segregating components in the growth rate trait by analysis of variation in the segregating line will be presented in a subsequent publication.

Family Study

Each of the traits for which genetic segregation was found in the family analysis of variance are complex in that each one is dependent on others and can be expressed as a function of one or more other traits. In evaluating whether there is independent

segregation of one or another trait, an attempt must be made to untangle traits from others upon which they are dependent. Food intake, for example, is certainly a function of weight. Use of relative intake (food intake/weight) attempts to disentangle the weight component from the food intake component. Also, food intake is a function of the rate of gain. Use of efficiency (gain/intake) attempts to disentangle the rate of gain component from the food intake component. Food intake per se has a significant between family variance component but not relative intake. In no cases were there significant differences between families in feed efficiency.

Previous studies also showed that intake is the major growth rate associated trait. Pym and Nicholls (1979), who achieved a 25% response in weight selected lines over three generations of selection, found a 20% increase in food consumption while there was only a 5% improvement in efficiency. Siegel and Wisman (1963) and Proudman et al. (1971) concur in the belief that intake is the major growth rate associated trait, but these studies also show a small efficiency component. Abdominal fat pad corrected for weight (abdominal pad %) is also significantly different between families. Segregation for fat independent of body weight, may indicate a second growth rate component segregating in the segregating line. It is concluded here that both food intake and abdominal pad are not entirely dependent on absolute body weight.

Weight is significantly different between families, but

weight at second, third, and fourth measurements, being so highly correlated with early weight (0.90 to 0.96) has no new family variance component that was not present at the earliest age (45 days). This follows since the rate of gain (gain %) was not significant between families. Thus, the variation in weight in older birds is dependent on the variation in weight at younger ages. We can conclude that the causes of between family differences in weight all act earlier than 45 days. Because of the lack of between family variance in rate of gain, we conclude that the significant between family differences in gain are all due to differences in weight, the larger animals gaining more than the smaller ones.

Correlation Analysis

It is interesting that relative intake is not correlated with body weight in either of the samples. If intake were driving growth then one would expect higher relative intake in larger birds. Such is not the case.

Body fat percent is related to body weight in the 90-day sample but not in the 60-day sample. It is reasonable to conclude that larger birds become fatter with age.

The main difference between the samples is that relative intake is correlated with rate of gain in sample 2 but not in sample 1 and body weight is negatively correlated with rate of gain in sample 2. There is a large group of birds in sample 2 (group 2) with low relative intake and low gain that is not apparent in sample 1. The existence of this group would account for the difference in correlation matrices between samples 1 and 2.

D.2.5. The effect of meal feeding and food restriction on body composition, food utilization and intestinal adaptation in light-breed chicks

Restricted feeding is associated with periods of intense feeding and periods of feed deprivation. The effects of periodic feeding or meal eating were first studied with pigeons (Von Seeland, 1887) and salamanders (Margulis, 1913). More recent studies have utilized chickens (Lepkovsky et al., 1960; Cohn et al., 1961; Feigenbaum et al., 1962; Griminger et al., 1969). A review of classical work in this area has been presented by Fabry (1967). Intubation of two meals/d, an amount of food equal to that consumed by ad libitum-fed chicks, increased metabolizable energy, body fat and energy utilization but decreased nitrogen retention without affecting body gain (Nir et al., 1979). It was postulated that the above effects could be due partly to a slower passage of the food through the gastrointestinal tract (GIT) and therefore to a longer exposure of the food to chemical, physical and microbiological alterations. The longer stay of the food in the GIT could cause a full sensation which reduced the activity of the tube-fed birds and improved energy retention.

Light-bodied chicks exposed to intermittent feeding (fed every second day) consumed about 80% the amount of ad lib-fed chicks. They were able to maintain a body composition similar to that of the ad lib-fed controls (Nir & Nitsan, 1979). In chickens of a heavy breed, a similar restriction caused a marked reduction of body fat (Simon & Blum, 1972). It seems that the strategy of the light-breed chicks is to maintain a normal body composition and to reduce growth rate, when food restriction is moderate.

Among the gastrointestinal organs, only the crop weight was significantly increased by tube, as compared with ad lib, feeding. The activity of the

digestive enzymes in the small intestine corresponded to the amounts of the intestinal contents. The purpose of the present work was to study the combined effects of food restriction and meal feeding.

Light-breed chicks were exposed to different levels of food restriction, in order to estimate up to what degree of restriction they were able to maintain their body composition. In addition, meal feeding was accentuated by pair-feeding chicks by the tube technique. The food consumed by groups fed ad libitum or restricted, was pair-fed to parallel groups in two meals/d by the tube feeding technique.

EXPERIMENTAL

Animals and diets

Two week-old New Hampshire x White Leghorn male chicks were divided into seven equal groups of similar mean body weight (ten chicks per group). They were identified with wing bands and kept in colony cages with raised wire floors. The chicks received proprietary starter crumbs (calculated 210 g/kg crude protein and 12.5 MJ ME/kg). The room was illuminated continuously. Two groups were fed ad libitum (V_{100}) and had free access to food and water. Food intake of each group was measured daily. One group of the restricted chicks was fed 75% (V_{75}), and one group 50% (V_{50}) of the average amount consumed by the ad libitum-fed chicks the previous day. Three groups of chicks were fed by intubation into the crop twice daily (at 08:00 and 19:00 h). These groups - T_{100} , T_{75} and T_{50} - were pair-fed to V_{100} , V_{75} and V_{50} , respectively. The food was mixed with warm water (4 parts food:6 parts water, w:w), and intubated as described by Nir et al. (1979). Half the average amount consumed by the V_{100} or by

the V_{75} and V_{50} chicks, respectively, was fed in each meal. This was done by weighing the tube-fed chicks before, during, and after intubation. Variations from the amounts designed were corrected at the following meal. The total amount of food intubated during the experimental period varied from the designed amount by 1g/chick.

All the chicks were killed following 14d, starting at 10:00, 2 hours after the last meal. The chicks were killed sequentially, one chick from each group. The autopsy of each chick lasted about 6 minutes. Autopsy, chemical analyses and determination of digestive enzymes activity were carried out as described earlier (Nir & Nitsan, 1979; Nitsan et al., 1974).

Statistical analysis was performed as described by Snedecor and Cochran (1967), by Newman's Q-test, the significance of main effects and of interactions being assayed by the F-test.

RESULTS

Body weight gain, body composition and food utilization (Table 1)

Body weight gain and linear growth (shank length) were decreased by feed restriction. Tube feeding increased body weight gain in the 50% restricted chicks only. Linear growth was increased by tube feeding; this increase was highest in the 50% restricted chicks.

In the voluntarily fed chicks, carcass dry matter and fat concentration were reduced in the V_{50} chicks only. The effect of tube feeding on carcass dry matter and fat concentration varied in the different feeding levels: while these parameters were increased markedly in the T_{100} , no effect was observed in the T_{75} and T_{50} chicks. Nitrogen and ash concentrations in the carcass were negatively related to dry matter and fat concentrations.

Since food intake was not measured individually in the voluntarily fed

TABLE 1. GROWTH, BODY COMPOSITION, FOOD INTAKE, ENERGY AND NITROGEN RETENTION IN CHICKS FED AD LIBITUM OR RESTRICTED AMOUNTS OF FOOD VOLUNTARILY (V) OR PAIR FED TWO MEALS DAILY BY INTUBATION (T).

Body Weight (g)	V ₁₀₀	T ₁₀₀	V ₇₅	T ₇₅	V ₅₀	T ₅₀
Initial ¹	138	140	137	139	136	137
Final ¹	365a	353a	282b	297b	209d	230c
Gain	227a	213a	145b	158b	73d	93c
Shank length (mm)	63.1a	64.5a	59.1b	60.6b	53.0d	55.5c
Carcass Composition ²						
DM (g/kg)	269b	282a	254bc	258bc	237c	254bc
Fat (g/kg DM)	208b	271a	205b	201b	157c	151c
Nitrogen (g/kg DM)	109b	101c	111b	111b	116a	116a
Ash (g/kg DM)	113b	106c	110b	118b	127a	126a
Energy (MJ/kg DM)	24.5b	25.7a	24.5b	24.4b	23.4c	23.2c
Food Intake (g)	510	510	383	383	255	255
Energy Retention ³	0.176	0.192	0.138	0.154	0.076	0.119
Nitrogen Retention ³	0.411	0.369	0.331	0.370	0.238	0.357

¹Body without gastrointestinal content.

²Body without liver, pancreas and intestinal content.

³ $\frac{x-y}{F}$, where x,y=body nitrogen or energy at end or start of experiment, respectively (means of 5 chicks. F=intake of nitrogen) or energy during the experimental period.

Gross energy and nitrogen determined in food were 17.5 MJ/kg and 33.0 g/kg, respectively.

chicks, no statistical analysis could be conducted on energy and protein retention. Energy and nitrogen retention were reduced parallel to the degree of feed restriction. Tube feeding improved energy retention, the improvement being intensified as the restriction increased. Nitrogen retention was decreased by tube feeding in the T_{100} chicks, and improved in the restricted ones.

Organ weight, blood and liver fat concentration (Table 2)

Tube feeding increased the relative weight of the crop by more than two-fold in the full-fed chicks only ($T_{100} > V_{100}$). In the restricted groups its relative weight was about two-fold that of the V_{100} group, and tube feeding had no effect in this respect. Proventriculus and gizzard relative weights increased in the restricted-fed groups. Tube-feeding had no effect on these parameters. While the duodenum and jejunum relative weight was increased by tube feeding, but not by feed restriction, the ileum relative weight was depressed in the V_{75} and V_{50} groups, and increased by the tube feeding. This increase was greater in the T_{75} and T_{50} than in the T_{100} chicks. In the ad-libitum fed chicks, the ratio of jejunum:ileum weight was 1.16; it increased in the T_{100} chicks to 1.26. In the restricted chicks this ratio was 1.2 and 1.3 in the V_{75} and V_{50} groups, respectively, without an additive effect of tube feeding.

Caecum and colon relative weights were not affected by feed restriction or by tube feeding. Liver weight, liver and blood plasma lipids were increased by tube feeding in the T_{100} chicks only. In the restricted chicks these parameters tended to decrease with tube feeding. Kidney relative weight was not affected by feed restriction in the voluntarily fed groups. Tube feeding decreased the kidney's weight in the restricted chicks (statistically significant for the T_{50} group).

TABLE 2. ORGAN WEIGHTS (g/100 g BODY WEIGHT) AND LIVER AND PLASMA LIPID CONCENTRATION IN CHICKS FED AD LIBITUM OR RESTRICTED AMOUNTS OF FEED.

	V ₁₀₀	T ₁₀₀	V ₇₅	T ₇₅	V ₅₀	T ₅₀
Crop	0.40 ^c	0.92 ^a	0.78 ^b	0.76 ^b	0.74 ^b	0.75 ^b
Proventriculus	0.61 ^b	0.63 ^b	0.76 ^a	0.10 ^b	0.75 ^a	0.78 ^{ab}
Gizzard	2.39 ^c	2.57 ^{bc}	2.88 ^b	2.69 ^b	3.20 ^a	3.10 ^{ab}
Duodenum	0.42 ^b	0.45 ^b	0.38 ^{bc}	0.52 ^{ab}	0.32 ^a	0.54 ^a
Jejunum	1.17 ^b	1.34 ^a	1.07 ^b	1.41 ^a	1.12 ^b	1.39 ^a
Ileum	1.10 ^b	1.06 ^{ab}	0.89 ^c	1.17 ^a	0.87 ^c	1.05 ^b
Caecum	0.52	0.51	0.53	0.54	0.54	0.58
Colon	0.26	0.24	0.25	0.27	0.25	0.26
Kidneys	1.04 ^{ab}	1.12 ^a	1.00 ^{bc}	0.94 ^{bc}	1.01 ^b	0.91 ^c
Liver	2.56 ^b	3.14 ^a	2.90 ^{ab}	2.81 ^b	2.90 ^{ab}	2.70 ^b
Total Lipids						
Liver (g/kg)	53.0 ^{bc}	63.5 ^a	59.4 ^{ab}	53.7 ^{bc}	56.3 ^{ab}	47.0 ^c
Blood Plasma (g/l)	4.31 ^b	5.44 ^a	5.42 ^a	4.43 ^b	5.42 ^a	4.83 ^b

Values with common superscripts do not differ significantly ($p < 0.05$).

Pancreas weight, intestinal content and activity of digestive enzymes

The relative weight of the pancreas was slightly increased by feed restriction and decreased by tube feeding. In chicks fed voluntarily, the jejunal and ileal contents were increased by feed restriction. Tube feeding increased the relative weight of the jejunal and ileal contents. The effect of tube feeding on jejunal content (but not on ileal content) was negatively related to the degree of restriction. This could also be expressed by the ratio jejunal:ileal contents, which was about 1 in all the voluntarily fed and restricted tube-fed groups but attained a value of 1.9 in the T₁₀₀ chicks.

Pancreas enzymes activity (amylase excepted) was lower in the tube-fed groups than in the voluntarily fed ones. The feeding level had no significant effect on this respect. The effect of tube feeding or degree of restriction on pancreatic amylase activity was not consistent.

The overall effect of tube feeding on the enzymes total activity in the two parts of the small intestine was an increase as compared with the voluntarily fed birds in the jejunum, their activity was higher than in the ileum. In the voluntarily fed chicks, the activity of the enzymes in the jejunum and the ileum increased with feed restriction. The same was found for the tube-fed birds in the ileum but not the jejunum.

DISCUSSION

Body weight gain and composition, and energy and nitrogen utilization

Intubation of the same amount of food consumed voluntarily caused a consistent increase in energy utilization, but the diversion of energy to fat or lean tissue varied according to the feeding level. When tube fed the amount consumed ad libitum (T₁₀₀), the excess of available energy was

diverted to body fat (Table 1). This finding confirms previous data on tube-fed chicks (Nir et al., 1979) and meal-fed rats (Fabry, 1967).

In the T_{75} and T_{50} chicks, the excess of available energy was probably diverted to lean tissue formation since their carcass did not contain more fat than their voluntarily fed counterparts. It seems that the contribution of tube-feeding to energy retention increases with the degree of food restriction. While the tube feeding increased energy retention by 9% in the T_{100} birds, this improvement was 12% and 56% in the T_{75} and T_{50} chicks, respectively. The improved energy retention was concomitant to nitrogen retention in the restricted groups. The reduced variation in growth rate of the tube-fed chicks could also contribute to the improvement in energy retention. In the tube-fed chicks the CV for the final body weight was 2.7, 4.6 and 4.3 for the T_{100} , T_{75} and T_{50} birds respectively. For the voluntarily fed chicks, these values were 4.9, 6.7 and 19.4 for V_{100} , V_{75} and V_{50} birds, respectively. With tube-feeding, two major sources of variation, appetite and competition for food, were abolished. The CV increased markedly with the degree of restriction in the voluntarily fed groups, as food restriction increased competition for food. The remaining sources of variation found in the tube-fed chicks were quite similar at the different feeding levels. This remaining variation was apparently due to unidentified factors which, despite their quantitative similarity at all tube-feeding levels, were not necessarily identical. Nitrogen retention in the voluntarily fed chicks decreased with feed restriction due to utilization of part of the dietary protein as energy source. Improvement of energy utilization by the restricted tube-fed chicks, probably decreased the diversion of dietary protein to energy and hence improved protein retention.

This work confirms an earlier finding (Nir & Nitsan, 1979) that with

up to 75% restriction, the strategy of light-breed chicks is to maintain a body composition similar to ad libitum-fed chicks at the expense of growth. At 50% restriction, in the present work, body fat concentration decreased. The critical feeding level under which body composition is still maintained in the light-breed chicks is yet to be determined.

The importance of the gut microflora in digestion and absorption (Coats, 1976), can aid in the understanding of the response of chickens to meal feeding. Meal feeding reduced the bacterial count/g intestinal chyme and also probably changed its composition, since ad lib.-fed chicks responded differently to dietary supplementation of neomycine sulfate than meal-fed counterparts (authors' unpublished results).

Organ Weights

Feed restriction drives the voluntarily fed birds to consume the daily ration during a short period. This is concomitant with the increase in weight of the storage organs, mainly the crop and the gizzard. However, intestinal segment size was associated with the total amount of food consumed, as it was smaller in the restricted birds than in the ad libitum-fed ones. Tube feeding of equal amounts affected the storage organs similarly, but also increased the weight of the intestinal segments. The tube-fed chicks were offered their daily ration in two meals. Learned anticipatory control could cause acceleration of gastric emptying to the fore intestine in order to evacuate food from the storage organs before the expected meal. Enlargement of the intestine was also obtained in overfed chicks (Nir et al., 1974). In the present study, the mash for the tube-fed chicks was finely ground and mixed with water. According to Patrick & Shaible (1980), the rate of passage of food through the digestive tract is accelerated by the amount of food consumed and by the size of the particles. Heuser (1945) stated that wet mash passes from the crop faster than dry mash. Since in meal-

fed birds the passage of the food through the whole gastrointestinal tract (determined by using ferric oxide as an indicator) was not accelerated (authors' unpublished results), the rapid passage of the food from the crop to the small intestine occurred concurrently with an accumulation of chyme, exceeding the normal capacity of the small intestine and causing its enlargement. The regulation of gastric emptying was discussed by Hunt & Knox (1968) and the constraints of the gastrointestinal tract by Booth (1979).

The kidneys' weight reflected nitrogen excretion :it was increased by tube feeding in the T_{100} birds and decreased in the T_{75} and T_{50} birds, parallel to nitrogen retention.

The liver's relative weight, its fat concentration and blood plasma lipids reflected the enhanced lipogenesis caused by tube feeding (or meal feeding) in the T_{100} birds, as reported earlier (Nir et al., 1979). An opposite effect of tube feeding, not significant for liver weight, but statistically significant for liver and plasma lipids, was found in the restricted birds. Food restriction is concurrent to meal feeding and meal feeding increases lipogenesis (Leveille et al., 1975). Assuming that lipogenesis is affected by the size of the meal, it is suggested that in the tube-fed restricted birds which received their daily ration in two meals, lipogenesis was lower than in the voluntarily restricted birds which were provided with "one meal"/day.

Digestive enzymes' activity

The higher amount of intestinal chyme in the tube-fed birds triggered a greater release of digestive enzymes from the pancreas into the intestine. This resulted in a lower pancreatic weight and enzymatic activities. The same results were observed in overfed birds (Nitsan et al., 1974). This confirms previous studies which showed that any alternation in the type or quantity of the diet (i.e., substrates) leads to an adjustment of specific

and total enzyme activities in the pancreatic tissue and in the pancreatic juice (Corring, 1980; Snook, 1968; Hulan and Bird, 1972).

In order to evaluate whether the treatments affected differentially the levels of the various enzyme activities, resulting from selective synthesis, secretion and/or disappearance, the activities of the amylase and chymotrypsin in the pancreas, jejunum and ileum were calculated as related to the trypsin activity at the same site. Trypsin appeared to be more stable in the small intestine, as compared with the other digestive enzymes, since it was the only enzyme whose activity in the ileum was close to that found in the jejunum. It was reported that pancreatic amylase is destroyed by bacterial action in the alimentary tract of chickens (Lepkovsky et al., 1964).

The ratio for lipase was not estimated, since the source of lipase activity is not the pancreas alone, but also the bile. The contribution of salivary amylase to intestinal amylase is negligible (Nitsan & Madar, 1978).

In all treatments, the ratios of amylase:trypsin (A:T) and chymotrypsin:trypsin (C:T) decreased from the pancreas to the jejunum, and decreased further in the ileum. In the feed-restricted voluntarily fed chicks, the A:T and the C:T ratios were similar to those found in the V_{100} chicks. In the tube-fed chicks, the C:T ratio was lower than in voluntarily fed chicks, in the pancreas and the jejunum, but higher in the ileum, at all feeding levels.

Tube feeding increased the A:T ratio in the pancreas of the restricted chicks. In the two segments of the intestine, this ratio followed the same trend as was obtained for the C:T ratio. There is much evidence that in different species, changes in diet composition are concurrent to a "purposeful adaptation" of pancreatic enzyme secretion (Hulan & Bird, 1972). In the present work, it was found that synthesis, secretion and/or stability of the pancreatic enzymes can also be affected differently by feeding regime.

D.2.6. Effect of intermittent feeding on blood plasma thyroxine and corticosterone in chickens of a heavy breed.

INTRODUCTION

Intermittent feeding of heavy breed chicks (White Rock) was accompanied by a daily fluctuation of GH and prolactin. GH was higher in the restricted birds than in the ad libitum fed counterparts, it was higher after food deprivation than after food restoration. Blood plasma prolactin concentration was depressed after food deprivation and resumed the ad libitum fed counterparts concentration after food restoration (Nir et al., 1983).

In the present study the effect of intermittent feeding on blood plasma concentration of thyroidal hormones and corticosterone concentration was investigated. The birds used were the ones on which GH and prolactin were determined.

MATERIALS AND METHODS

The experimental protocol was published recently (Nir et al., 1983). One-day-old cockerels from a heavy breed (White Rock) were obtained commercially. From 12d of age and on they were reared in individual cages. The chicks were divided into three groups: One control group was fed ad libitum and two groups were intermittently-fed: Depleted birds in which food was removed every odd day, and Repleted birds in which food was provided every even day. At 20, 33, 56 and 83d of age, blood samples were obtained by cardiac puncture, using heparinized syringes. Blood samples were collected and centrifuged at 5°C and the plasma samples were stored deep frozen (-20°C).

Plasma glucose was determined by the glucose oxidase method (Hestrin-Lerner and Ben-Yonah, 1963). Total lipids were determined by the method of Zollner and Kirsch (1962). Plasma T3 and T4 were determined by radioimmunoassay in single assays as described by Seth et al (1976). Concentration of plasma corticosterone were determined in duplicate by a sensitive radioimmunoassay as described by Harvey et al (1980). The data were analyzed statistically by t-test and, where indicated, by analyses of variance.

RESULTS

Food intake and body weight of the birds were published recently (Nir et al., 1983). Food intake of the intermittently-fed birds during repletion days was higher than that of control but their food intake per 48h was less than control. As a result of reduced food intake the body weight and growth rate of the intermittently-fed birds was lower than that of the controls.

Variance analysis of data (Table 2) demonstrated significant effects of age ($P < .01$) on plasma concentrations of T4, corticosterone, glucose and total lipids but not on T3. Feeding regimes had significant effect on the plasma concentrations of all the above parameters (Table 2). Plasma glucose in the restricted birds, following the days of depletion was markedly lower than in the control and repleted groups. Statistically significant difference between the control and depleted groups was evident on day 20 only, while the difference between the depleted and repleted groups was significant on days 20, 56 and 83 of age. The differences in plasma glucose concentration at the different ages were not consistent.

Plasma total lipid concentration was higher in the treated than in the control birds. The highest level was observed after repletion (Statistically different from the control $P < .05$). The lipemia in the depleted group was

Table 1.

T3, T4, Corticosterone, Glucose and Total lipids concentrations in the plasma of chicks fed ad-libitum (control) or fed intermittently on alternate days. Blood samples were taken from the intermittently-fed birds 24h after food removal (Depleted birds) and 24h after refeeding (Repleted birds).

Age (d)	Control		Depleted		Repleted		Age mean	
T3 (ng/ml)								
20	1.63	0.31(5)a	0.48	0.06(5)b	2.16	0.14(5)a	1.43	0.22(15)
33	1.41	0.33(4)	0.73	0.19(5)	0.83	0.22(5)	0.96	0.15(14)
56	1.44	0.34(5)a	0.46	0.12(4)b	2.53	0.28(5)a	1.55	0.27(14)
83	1.87	0.42(5)	0.79	0.10(5)	1.86	0.46(4)	0.84	0.21(14)
T4 (ng/ml)								
20	16.32	1.10(5)b	24.88	1.03(5)a	15.80	1.48(5)b	19.00	1.29(15)
33	15.10	1.46(4)b	22.68	1.06(5)a	13.32	1.13(5)b	17.17	1.32(15)
56	19.86	2.13(5)	22.15	1.70(4)	22.72	1.85(5)	21.54	1.09(14)
83	17.46	0.22(5)b	26.22	1.08(5)a	23.05	1.65(2)ab	16.52	1.00(12)
Corticosterone (ng/ml)								
20	6.09	0.85(5)	8.20	1.80(5)	3.39	0.51(5)	5.89	0.82(15)a
33	3.58	0.98(4)	5.97	0.42(5)	4.08	1.02(5)	4.62	0.53(14)ab
56	3.14	0.21(5)	4.18	0.53(3)	3.53	0.84(5)	3.53	0.35(13)bc
83	2.71	0.37(5)	2.52	0.51(5)	1.78	0.06(4)	2.46	0.21(14)c
Glucose (mg/ml)								
20	2.87	0.10(5)a	2.17	0.11(5)b	2.69	0.05(5)a	2.58	0.09(15)ab
33	2.63	0.04(4)	2.67	0.08(5)	2.86	0.13(5)	2.73	0.06(14)a
56	2.73	0.07(5)ab	2.06	0.09(4)b	3.02	0.09(5)a	2.64	0.12(14)ab
83	2.41	0.18(5)ab	2.13	0.11(5)b	2.80	0.12(4)a	2.42	0.08(14)b
Total lipids (mg/ml)								
20	7.46	0.35(5)	7.52	0.54(5)	7.86	0.42(5)	7.61	0.24(15)a
33	7.70	0.34(4)	7.38	0.56(5)	6.44	0.63(5)	7.14	0.33(14)a
56	5.65	0.17(5)b	6.87	0.29(4)ab	8.63	0.43(5)a	7.06	0.39(14)a
83	5.21	0.17(5)b	6.28	0.28(5)ab	7.55	0.50(4)a	6.17	0.25(14)b

Values are mean+SEM, those with different superscripts are significantly different ($P \leq 0.05$) by t-test. The analysis was carried out between the different feeding status in each age.

Table 2.

Analysis of variance of T3, T4, Corticosterone, Glucose and Total lipids concentrations in the plasma of chicks versus three feeding regimes (ad-libitum, depleted and repleted birds) and four experimental periods (20, 33, 56, and 83d of age). Data present the significance of F-values.

	Plasma concentrations of				
	T3	T4	corticosterone	glucose	lipids
	(Significance of F-value)				
Effect of Age	.066	.001	.001	.019	.004
Effect of Feeding-regimes	.001	.001	.008	.001	.003
Interaction of Age versus Feeding-regimes	.016	.007	.106	.002	.001
Birds n	60	57	60	61	61

between that observed in the control and the repleted ones and did not differ from either of them significantly. Plasma total lipids declined with age, it was lower at 83d than at younger ones.

Plasma T3 concentration was lowest in the treated birds following depletion, while the control and repleted birds did not differ from each other in this respect. No age effect was observed on T3 blood plasma concentration.

Plasma T4 concentration was negatively related to T3 concentration, the highest level was found in the depleted birds, and the repleted birds resumed the control T4 concentration. Age had no consistent effect on T4 concentration.

Corticosterone mean plasma was higher in the restricted chicks after depletion than in the control ones. Following repletion, corticosterone level regressed to a slightly lower level that was found in the controls. The difference between the concentration of corticosterone in depleted and repleted birds was statistically significant ($P < .05$). Plasma corticosterone level regressed with age (Table 1).

DISCUSSION

The decrease in the concentration of plasma T3 and the increase of plasma T4 during days of depletion may be related to the reduction in the metabolic rate. Earlier studies with chickens (Klandorf et al., 1981a; Klandorf et al., 1981b) reported also that the concentration of plasma T3 and T4, may be regulated by the feeding pattern and fasting was associated with high levels of plasma T4 and low levels of plasma T3. The inverse relationship between T3 and T4 is in accordance with the suggestion that T3 in the chicken is partly derived from T4 by peripheral deiodination (Klandorf et al., 1978), fasting could affect this process and cause an accumulation of T4 in the blood plasma.

Thyroidal hormones in the chickens affect carbohydrate metabolism (Hazelwood, 1976; Scanes and Harvey, 1982). Administration of triiodothyronine to chickens reduces liver glycogen (Arrondo et al., 1978), and increases glucose uptake by heart muscle cells (Segal et al., 1977). Furthermore, it was concluded that in hens (Klandorf et al., 1981a), the feeding pattern plays an important role in the regulation of the daily rhythm of plasma thyroid hormones concentration.

It is well established that the deprivation of food, increases the concentration of corticosterone of chickens (Freeman et al., 1981; Scanes et al., 1980; Harvey et al., 1983). The increase in corticosterone concentration in the intermittently-fed birds after depletion may be related to its effect on carbohydrate and protein metabolism (Scanes and Harvey, 1982). Food restoration caused a reduction of plasma corticosterone concentration. This result is confirmed by Harvey et al. (1983) who showed a rapid decline in the corticosterone concentration following refeeding, which occurred in response to neural stimuli. In the present experiment, the plasma glucose concentration increased following repletion, while the corticosterone decreased. The corticosterone pattern could be related to its glucogenic effect, and the adrenocortical suppression here may be involved in the glucostatic mechanism as a metabolic stimulator.

Intermittent feeding induced considerable changes in the hormone patterns of the chicken which are characterized by low plasma T3 level consequent to food removal and high T4 and corticosterone. During the repletion days high level of nutrient are consumed and the pattern of those hormones were inverse. At this feeding status a marked increase in the plasma glucose and total lipids level was noticed.

It was shown previously (Nir et al., 1983) that the concentration of plasma GH in intermittently-fed birds increased while prolactin decreased after 24h of food deprivation. These alterations were related to their effect on protein, lipids and carbohydrate metabolism (Scanes and Harvey, 1982). GH appear to stimulate lipolysis and inhibit lipogenesis. King and King (1976) suggested that thyroidal influence on growth may be mediated by decreased GH secretion. The glucagon increases the already high plasma concentration of glucose while insulin exerts an opposite effect (Heald et al., 1965; Hazelwood 1976). The glucagon and insulin depress the plasma concentration of GH in the young chickens (Harvey et al., 1978). From hormone and metabolite pattern in the present study it can be assumed that in the intermittently-fed birds during days of depletion, there was lipolysis while during repletion an extensive lipogenesis.

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E. EVALUATION OF RESEARCH ACHIEVEMENTS WITH RESPECT TO THE ORIGINAL RESEARCH PROPOSAL

1. Aspects of body development in broiler females that must reach critical levels for onset of sexual maturity were defined (Sections D.1.1, D.1.2, D.1.4).

2. Estimate of phenotypic and genetic variation in minimum body weight for onset of sexual maturity were obtained (Section D.1.5) and two-way selection program for high and low body weight requirement for onset of sexual maturity were established (D.1.6).

3. Effect of different degrees of early feed restriction and of feed composition on critical factors were defined (Section D.1.1, D.1.2).

4. Different factors affecting growth of light and heavy breeds were compared (D.2.5) and phenotypic and genetic correlations of early growth-rate and minimum weight for onset of sexual maturity were obtained (Section D.1.5).

5. The dwarf gene was found to affect weight for onset of sexual maturity in proportion to its effect on mature body weight (Section D.1.4).

6. Physiological studies of response of light and heavy breeds to food restriction were carried out (Section D.2.5, D.2.6).

7. Selection studies of gain under restricted uniform food intake suggest a possible interaction of growth-rate factors (maintenance requirements and body composition) and minimum weight for onset of sexual maturity (Section D.1.6).

8. Allometric studies of developmental patterns in heavy and light breeds in relation to feed restriction were carried out, but are not yet fully evaluated. (Ph.D. Thesis, Judy Plotkin, in preparation).

9. Theoretical and experimental studies of growth-rate components were carried out (Section D.2.1, D.2.2, D.2.3).

F. DESCRIPTION AND RESULTS OF COOPERATION

Cooperation was close and fruitful. Drs. Siegel and Cherry visited Israel at the start of the program to plan the research. Dr. Nir spent a sabbatical year at Blacksburg and carried out joint research with Dr. Siegel and Cherry. Judy Plotkin (Ph.D. student) spent two weeks at Blacksburg consulting on methods for the analysis and presentation of her data. Prof. Soller and Dr. Brody visited Blacksburg for useful exchanges on interpretation of experimental data and interacted with graduate students. The investigators also interacted in several research efforts as evidenced by joint publications. A further example of the interaction between the investigators is that Drs. Nir and Siegel will be presenting invited plenary papers at the World Poultry Science meeting in Helsinki in 1984 on the topic of fat in broilers. Dr. Nir will cover the nutritional aspects and Dr. Siegel the genetic aspects.

G. THESES

1. Ph.D. Thesis: Developmental patterns of light and heavy breed chicks in relation to feed restriction. Judy Plotkin (in preparation).
2. M.Sc. Thesis: Minimum body weight at sexual maturity and weight gain under restricted feeding. Tatiana Agursky.

H. BENEFIT TO AGRICULTURE

1. By defining weight and age factors determining onset of sexual maturity in broiler strain females, the research shows how more effective utilization of feed restriction during the growing period can be carried out, while avoiding a delay in onset of lay.

2. Observations on food intake after restriction in young chicks carried out as a part of the Ph.D. research of Judy Plotkin suggested a novel food restriction program: skip-2-days. In this program, birds are allowed full feed one day out of three and fast the remaining two days. This allows food restriction to be implemented while avoiding problems of aggressive competition between birds. The program has been successfully implemented in a number of breeding flocks, and has good chances of becoming the industry standard.

3. Minimum weight for onset of sexual maturity has been defined as a new genetic trait and possible breeding objective in poultry.

4. A comprehensive model of growth-rate in relation to its components has been developed which should allow more precise design of breeding programs to improve feed efficiency and decrease fat deposition in broilers.

I. INVESTIONS

None

J. PUBLICATIONS

1. Soller, M., T. Brody, Y. Eitan and T. Agursky. (1982). Growth and the onset of sexual maturity in chickens. 2nd World Congress on Genetics Applied to Livestock Production. Madrid, October 1982. Volume 5: 690-698.
2. Eitan, Y., T. Agursky and M. Soller. (1982). Genetic aspects of feed efficiency under food intake restriction in broiler chickens. 2nd World Congress on Genetics Applied to Livestock Production. Madrid, 1982. Volume 7: 417-423.
3. Eitan, Y., Y. Zarchi and M. Soller. (1983). Effect of severe quantitative food restriction from day of hatch through the rearing period on reproductive performance of White Rock broiler strain females. British Poultry Science (in press).
4. Soller, M. and Y. Eitan. (1984). Why does selection for liveweight gain increase fat deposition? A model. World's Poultry Science Journal (in press).
5. Soller, M., Y. Eitan and T. Brody. (1983). Effect of diet and early quantitative food restriction on the minimum weight requirement for onset of sexual maturity in White Rock broiler breeders. Poultry Science (in press).
6. Dunnington, E.A., P.B. Siegel, J.A. Cherry and M. Soller. (1983). Relationship of age and body weight at sexual maturity in selected lines of chickens. Arch. Geflugelk. (in press).
7. Nir, I., S. Harvey, Z. Nitsan, Y. Pinchasov and A. Chadwick. (1983). Effect of intermittent feeding on blood plasma growth hormone and prolactin in chicks of heavy breed. British Poultry Science 24: 63-70.
8. Nitsan, Z., I. Nir and I. Petihi. (1983). The effect of meal feeding and food restriction on body composition, food utilization and intestinal adaptation in light-breed chicks. British J. Nutrition (in press).

9. Zelenka, D.J., J.A. Cherry, I. Nir and P.B. Siegel. (1982). Body composition at the onset of lay in Japanese quail. Poultry Sci. 61: 1571-1572.