

GENETICS, BEHAVIOR, AND DISEASE RESISTANCE IN CHICKENS

by

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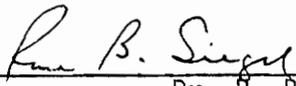
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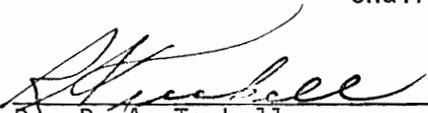
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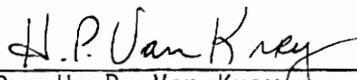
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## INTRODUCTION

Animal agriculture continues to become more intensive as we move into the final two decades of the 20th century. Concomitant to this is an increased concern about the potential for domestic animals to cope with current husbandry practices. Critics of intensive poultry production argue that there has been a molding of the chicken to fit the specifications of the engineers rather than a designing of equipment and housing to fit the biological needs of the chicken. The key to the understanding of this situation lies in the collection of objective data necessary to reveal relationships between husbandry practices and the biological responses of the chicken. The purpose of this dissertation was to evaluate genetic, behavioral, immunological, and disease factors associated with the adaptability of chickens to husbandry situations.

## REVIEW OF LITERATURE

### Behavior and Adaption

"Nearly all the behavior we observe in animals is adaptive" (Manning, 1972). Animals respond to appropriate stimuli in an effective manner and thereby feed themselves, find shelter, mate and rear offspring. The importance of the behavior of the animal in its ability to adapt to husbandry practices was recognized as early as the beginning of the domestication process (Hale, 1969; Ratner and Boice, 1975). Examples of behaviors favorable to the animal's ability to be domesticated were: (1) a large group structure regulated by a social hierarchy, (2) promiscuous sexual relationships with male dominance, (3) precocial young which the mother accepts quickly, (4) general dietary habits, (5) limited agility, and (6) adaptation to a wide range of environments (Hale, 1969). In numerous instances behavioral repertoires that initially favored domestication in the fowl have largely been ignored by those working with poultry (Siegel, 1976); their thinking has been channeled away from certain important points. For example, a preoccupation with peck orders has resulted in little consideration being given to territoriality which is important in the social organization of the fowl (Morejohn, 1968; Craig and Guhl, 1969; McBride et al., 1969; and McBride, 1971). The implications of territoriality should receive serious consideration in the location of equipment in the poultry house. The social organization, be it regulated by a hierarchical structure,

territoriality, or a combination of both, is a means by which chickens reduce social tension and conserve nonadaptive energy. A stable social order provides a framework for predictable relationships among members of a group (Siegel, 1976). This results in less strife (Siegel and Hurst, 1962) and the higher productivity that is observed in organized flocks rather than those kept from becoming organized (Guhl and Allee, 1944).

The dominance-subordinance relationships among flockmates are based upon behavior which includes attack, escape, avoidance and submissiveness (Guhl and Fischer, 1969). These activities vary in intensity and may be recognized by differences in posture and movement. In submission, a bird bows or crouches and thus yields to its despot. Avoidance involves motor activity as individuals tend to maintain distances. This results in low intensities of social interactions in well-regulated flocks.

The intensification of poultry production has caused sufficient concern to those involved with animal welfare to effect legislation either limiting or banning certain husbandry practices (Lindgren, 1976). This has spurred considerable discussion and the initiation of studies whereby behavioral measures are used to assess the welfare of farm animals (Bareham, 1972; Siegel and Gross, 1973; Black and Hughes, 1974; Duncan, 1974; Wood-Gush et al., 1975; Van Putten and Dammers, 1976; and Dawkins, 1976; 1977). Behaviors associated with the adaptation of poultry to husbandry practices have been described as comfort behavior (Hughes and Black, 1974); i.e. "fear" (Hughes and Black, 1974, Sefton, 1976; and Siegel et al., 1978) and head shaking (Duncan, 1970; Siegel

et al., 1978).

"Fear" may be considered in several contexts (Phillips and Siegel, 1966; Gallup, 1974; Murphy, 1977) and may be stimulus specific (Murphy and Duncan, 1977). In this dissertation "fear" is considered in the context of a response to humans. Head shaking, the flicking of the head from side to side, is a comfort movement (Duncan and Wood-Gush, 1972b). The incidence of head shaking is higher in caged than in floor flocks (Black and Hughes, 1974) and may be indicative of differences in stress (Hughes and Black, 1974). Considered as adaptive responses to stressors imposed by confinement and social interaction, "fear" and head shaking provide vehicles by which birds cope with their environment.

### Stress, the Pituitary-adrenocortical Axis, Disease and Heredity

#### The Stress Syndrome:

It is essential to understand the concept of stress before entering into a discussion of the relationships between strife and susceptibility to diseases and parasites. Selye (1950; 1956), in his monumental works, discussed stress as the common denominator of all adaptive reactions in the body and termed this the "General Adaptation Syndrome (GAS)". The GAS is manifested by an internal imbalance of the endocrine system which, although it may aid in resistance to some diseases, will increase susceptibility to other diseases. This ambivalence of resistance and susceptibility to disease will be discussed in greater detail later in this review.

Stress has been shown to increase the susceptibility to disease in a variety of animals, including man. A few examples are given below.

Friedman and Rosenman (1974) reported that people with "Type A" personalities were significantly more susceptible to heart disease than those with "Type B" personalities. He describes Type A people as aggressive, forceful, competitive, excitable and in a high degree of stress whereas Type B people were calmer and relaxed. Both Type A and B individuals were equally successful in their careers. Harker (1960) noted that cancer of the mid-gut would occur in cockroaches when their biological clocks were thrown out of sequence by transplantation methods. She concluded that the tumors were the result of internal stresses brought about by such change. Solomon (1969) reported a deterioration of the immune response in rats prechallenged with social stress and later challenged with flagellin.

#### Pituitary-adrenocortical Axis:

The pituitary-adrenocortical axis has been implicated as the physiological mechanism for the influence of stressor agents upon disease resistance. Freeman (1971; 1976) in a physiological appraisal of stress in the domestic fowl listed indicators of stress which are caused by increased adrenal activity. These include involution of lymphoid tissue (Thymus, spleen and the bursa of Fabricius) and changes in leucocyte and heterophil ratios.

Sidman et al. (1962) observed a positive correlation between the activity of the adrenal glands and the amount of social strife. An increased production of adrenocortical hormones due to the stressor effects of social strife has a pronounced influence upon the balance of the lymphoid and phagocytic defense responses. Increased population

densities, acting to increase the the number of aggressive confrontations between individuals is frequently correlated with an augmented production of adrenocortical hormones (Christian, 1955; Christian and Davis, 1960; Sidman et al., 1962; Bronson and Eleftheriou, 1965; Turner and Bagnara, 1976). This response occurs in the absence of physical injury, indicating that the stimulus is sociopsychological. The degree of response to social strife is not independent of the aggressiveness of the strain or species.

The main steroid hormone associated with stress in the chicken is corticosterone which is secreted from the adrenal gland (Turner and Bagnara, 1976). The secretion of corticosterone is the culmination of a neuro-endocrine chain (see Siegel, 1971 for review) in response to the stressors. This chain involves neural stimuli which stimulate the hypothalamus to secrete corticotropin-releasing hormone which then stimulates the anterior pituitary to secrete the hormone adrenocorticotropin. This, in turn, reaches the adrenal gland via the general circulation and causes an increase in its secretion of steroid hormones. Corticosterone, being the main hormone secreted in response to stress in chickens, has been measured to monitor the degree of stress in the environment by a host of experimenters. Other steroid changes, however, should be considered because of the various feedback mechanisms. Diurnal variations in plasma corticosterone have been documented (El-halawani et al., 1973), and Perry (1973) suggested that the maximum secretory rate is at the peak of the diurnal rhythm. Thus, if an animal is stressed at the time this peak is reached there will be no significant

increase in the concentration of corticosterone.

#### Immunological Responses:

The immune system which is involved in disease resistance may be influenced by social stress (Gross and Siegel, 1973). Riley (1975) studied mice maintained in a crowded environment and postulated that moderately chronic or intermittent stress may predispose them to an increased risk of mammary carcinoma. This may occur through a resultant compromise in their immunological competence or tumor surveillance system, and adequate protection from stress may reduce such risk. ACTH and corticosterone, hormones that reach high levels in stressed individuals, when injected into chickens caused a reduction in their ability to produce antibody (Glick, 1967). Also, Siegel and Latimer (1975) observed a decline in antibody titers associated with increased agonistic behavior in socially stressed birds. In a review paper, Clammans (1972) proposed that high steroid levels inhibited the interaction between bursa-derived lymphocytes and antigen. Thaxton and Siegel (1973), however, have shown that antibody production can also be impaired by stressors which do not even evoke a significant rise in plasma corticosterone.

#### Disease:

The role of social strife and the susceptibility to disease has been examined in chickens by a series of experiments (Gross and Siegel, 1965; Gross and Colmano, 1967; 1969; 1970; 1971; and Gross, 1972). A high degree of social strife resulted in an increased resistance to

infection with Escherichia coli and this resistance decreased when social interactions were reduced (Gross and Colmano, 1967). Although stress increased resistance to bacterial agents i.e., E. coli and Staphylococcus aureus, it was observed that there was decreased resistance to viral-type infections such as Mycoplasma gallusepticum and Newcastle Disease (Gross and Colmano, 1969); the opposite effect was noted in an environment where social stress was low. The administration of corticosterone and ACTH increased the resistance to E. coli infection in chickens (Gross and Colmano, 1970) which, in turn, corresponded with a reduction in the ability to produce antibody (Glick, 1967; Thaxton *et al.*, 1968). While the stress response can be demonstrated with relative ease, there is no way of determining whether this response will lead to a successful adaptation or death (Freeman, 1976).

#### Genotype-environment Interactions

The formulation of the problem whereby there may be differential responses of different genotypes in nonsimilar environments was presented by Haldane (1946). The implication that a population will not be superior to other populations under all possible environments is of concern to geneticists and agriculturalists. Recommendations regarding breeding practices for livestock by Hammond (1947) led to considerable experimentation on genotype-environment interactions. This was because Hammond's thesis held that genotype-environment interactions were not important for livestock and that heritabilities would be greatest in the best possible environments.

McBride (1958) provided a vehicle for studying specific types of

interactions when he partitioned environmental influences into macro- and micro-components and genotypic components into an intra- and inter-population basis. His four types were:

	<u>Micro- environments</u>	<u>Macro- environments</u>
Intra-population genotypes	Type A	Type B
Inter-population genotypes	Type C	Type D

Different climates and management practices are examples of macro-environmental items, while micro-environmental factors are those fluctuations which occur when all animals are treated alike. Inter- and intra-population differences refer to between and within population genotypic differences. The degree of interest in these types of interactions will depend on the particular vantage point that one is studying genotype-environment interactions. In the context of this dissertation primary, interest is in Type A and Type D; namely, the subtle influences of behaviors on selection and evaluating if there is a "right" environment for a given genotype.

Environmental factors may cause disruptions in the behavior exhibited by domestic animals. Such disruptions were categorized by Wood-Gush et al. (1975) as when (1) normal activities are 'frustrated' or prevented by some aspect of the physical or social environment, (2) artificial surroundings may lack some key releasing stimulus so that an important activity is not elicited, and (3) an environment may be so barren or, alternatively, so complex and changing, that an animal receives too little or too much general stimulation. Involved in this are thresholds for behaviors (Graves and Siegel, 1969) whereby the

threshold varies among genotypes. Thus, an environment that provides a stimulus to elicit a particular behavior in one genotype may not necessarily be of a sufficient stimulus to elicit the same behavior in another genotype. McBride (1962a) noted that different levels of social interaction may occur, depending upon genotype and environment, and that regulation of social order will contribute to a genotype-environment interaction. He alluded, in his paper, to relationships between social rank, environment and productivity of hens.

As stated earlier, genotype-environment interactions influence the estimation of genetic parameters. McBride et al. (1964) suggested that the heritability of growth in pigs may be strongly dependent upon husbandry conditions and questioned the practice of pig progeny testing schemes in single pens, since pigs are reared as groups commercially and the absence of genotype-environment interactions has not been demonstrated. McBride (1962b) compared the productivity of two populations of Australorps, one control and one selected, in three environments: (1) wire battery cages, (2) intensive housing, and (3) semi-intensive housing. Although he did not find a significant genotype-environment interaction, the selected line was only two generations removed from the unselected base population. Subsequently, Craig et al. (1956) bidirectionally selected for social dominance scores in initial cockerel encounters within each of two breeds of chickens. They found a large reservoir of additive genetic variation for agonistic behavior and suggested that genotypes responsible for differences in agonistic behavior under conditions of selection may not be equally effective in a different environment.

It is well-documented that there are differences among populations of chickens for susceptibility to various diseases. Some examples include pullorum disease (Scholes and Hutt, 1942), infectious coryza (Lerner et al., 1950), and coccidiosis (Edgar et al., 1951; Rosenberg et al., 1951). Comparisons of various populations for susceptibility to disease in different environments indicate the importance of genotype-environment interactions. Hyre (1955) observed a genotype-environment interaction for keel deformities in two strains of White Leghorns where perches were present and absent. Hutt (1958) reported a high incidence of pendulous crops in Bronze turkeys maintained at high temperatures whereas the condition was never observed in Bourbon Reds. A comparison between these populations in a cool environment precluded an expression of this condition in the Bronze turkeys. Siegel and Gross (1977) reported that when cocks in two lines of White Plymouth Rocks that had undergone divergent selection for high and low juvenile body weight were maintained in large all male flocks, the incidence of systemic infection from Staphylococcus aureus was essentially nil. When transferred from this environment to a low stress situation consisting of housing in single-bird cages with wire partitions, mortality from S. aureus was 3% for the low weight line and 45% for the high weight line. From this they concluded that a certain amount of social strife was beneficial to survival in the high weight line.

Susceptibility to disease may be considered a threshold trait. Falconer (1965; 1967) showed that the methodologies developed in quantitative genetics for dealing with threshold characters were applicable for studying liabilities to disease. Through the use of such procedures

one can obtain answers to the question of the relative importance of heredity and environment on the liability of specific populations to the disease. Fundamental to the experimentation in this area is an interfacing of various disciplines. An example of this is when Gross and Colmano (1971) divergently selected for high and low plasma corticosterone responses to social stress. Chickens selected for low plasma corticosterone levels, as a reaction to social stress, were more resistant to Marek's Disease and Mycoplasma gallusepticum infection and produced more antibody than chickens selected for a high plasma corticosterone reaction. Subsequently, Edens and Siegel (1975) reported significant line-heat stress interactions in chickens as measured by adrenal and plasma epinephrine and plasma corticosterone. The lines had undergone previous selection for high and low responsiveness to ACTH.

It is obvious that through selection one can develop populations for specific environments. Such may involve the role of secondary traits such as behavioral responses (eg. Tindall and Craig, 1959; Lowry and Abplanalp, 1970a; 1970b; 1972) and are probably the causes of the differences among various populations of chickens. Thus, the challenge is to develop the husbandry situation whereby an optimum amount of stress will favor the behavioral response that has the greatest biological advantage to the particular population (Siegel, 1978). Before this can be accomplished baseline data are necessary. Presently there is a dearth of such information.

## EXPERIMENT I: "FEAR", HEAD SHAKING AND PRODUCTION IN FIVE POPULATIONS OF CHICKENS MAINTAINED IN CAGES

This experiment was designed to obtain preliminary data on the behavioral responses and production performance of chickens maintained in single-bird cages. Of particular interest were the development of procedures for measuring "fear" of humans and head shaking in various populations of chickens, and relating these behaviors to production traits on a within and between population basis.

### Materials and Methods

#### Stocks and Husbandry:

Five lines of chickens were studied in each of two years. These lines consisted of the  $S_{18}$  and  $S_{19}$  generations of White Plymouth Rocks that had undergone bidirectional selection for high (HWS) and low (LWS) 8-week body weight (Siegel, 1962); two subpopulations (HWR and LWR) from the two weight-selected lines where selection was relaxed in the  $S_{13}$  generation (the relaxed lines were of the  $R_4$  and  $R_5$  generations), and the Athens-Canadian Randombreds (AC) population (Hess, 1962). All chicks, within a year, were hatched the same day (March 4, 1975 and March 2, 1976) and reared as floor flocks. Pullets were then placed singly in wire cages 46 cm high, 30 cm wide and 46 cm deep at 119 and 134 days of age in 1975 and 1976, respectively. The lighting regime consisted of 14 hr of light from 0700 to 2100 hr.

### Measurements and Analyses:

Fear in chickens may be considered in several contexts. For example, Gallup (1974) examined tonic immobility, Murphy (1977) and Murphy and Duncan (1977) considered the avoidance of humans, novel foods, and environments while Phillips and Siegel (1966) studied the response to sound. In this paper "fear" was considered as the response to humans in the context of the reaction to a caretaker. "Fear" was measured between 160 and 164 days after caging (279 to 283 and 294 to 298 days of age in 1975 and 1976, respectively). The method used was Sefton's (1976) modification of the procedure described by Hughes and Black (1974) where an observer faces the chicken and slowly moves a pencil from left to right across the front of the cage. Each pullet was given a cumulative score based on its response to the observer and pencil. The scoring criteria were:

- 1 - peck at pencil,
- 2 - face the front of the cage,
- 3 - face either side of the cage,
- 4 - face the rear of the cage, and
- 5 - flight.

The repeatability, calculated by the procedure outlined by Ehrman and Parsons (1976), of this score was 0.46. Thus, the value for each pullet was the cumulative score from four trials obtained on separate days. All scores were obtained by the same observer.

Head shaking, flicking the head from side to side, may be considered as a comfort movement (Duncan and Wood-Gush, 1972b) which has been observed to increase in frequency in caged birds as compared with those

in floor pens (Black and Hughes, 1974) and (Hughes and Black, 1974). The frequency of head shaking was measured for HWS and LWS pullets in 1976. The procedure consisted of observing a group of five pullets for five minutes and recording the cumulative number of times each individual shook its head from side to side. The repeatability of this measure was 0.20, and the decision was made to use a cumulative score based on seven 5-minute observation periods. All measurements were made on separate days between 1200 and 1700 hr by the same observer. Transformation of head shaking data to log 10 values prior to analysis removed the heterogeneity of variances noted from Bartlett's test (Snedecor and Cochran, 1967).

Data were also obtained for percentage hen-day egg production which was recorded daily from date of first egg to 302 and 296 days of age in 1975 and 1976, respectively. Other traits included age at first egg and body weights at 56, 168, and 266 days of age. All data were obtained on an individual bird basis. Since there were no year effects for any of the traits measured, the data were pooled across years for subsequent analyses.

Line effects for all traits, except head shaking, were analysed by analysis of variance using the model:

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

where,  $i = 1, 2$  lines and  $j = 1, 2 \dots n$  individuals. Product moment correlations between "fear" and the production traits were calculated within lines, tested for homogeneity, and an average correlation obtained using the  $z$  transformation (Snedecor and Cochran, 1967).

In 1976 "fear" and head shaking were also measured at three ages.

Data collection commenced at 162, 238, and 279 days of age (28, 104, and 145 days after caging). These data were analysed by multivariate analyses of variance (Kramer, 1972), since the multiple measures of behavior on a bird were correlated. The statistical model was:

$$y_{ij} = \mu + L_i + e_{ij}$$

where,  $i = 1, 2$  lines;  $j = 1, 2 \dots n$  observations per line, and 1, 2, 3 measurement ages. When significant differences were found, means were separated by Duncan's multiple range test for unequal numbers (Kramer, 1956). Product moment correlations between ages were also calculated within lines, tested for homogeneity, and an average correlation obtained using the  $z$  transformation.

### Results and Discussion

As expected for lines that had undergone many generations of divergent selection for body weight, highly significant differences were found for this trait (Table 1). Also, highly significant differences were found between lines for percentage hen-day egg production and age at first egg (Table 2). Egg production was greatest in the AC line, least in the LWS and LWR lines, with the HWS and HWR lines being intermediate. The pattern between lines for age at first egg showed that the AC line matured at the youngest age, the LWS line at the oldest age, with the LWR, HWS and HWR lines being intermediate.

"Fear" was greater in the LWS and LWR lines than in the HWS, HWR, and AC lines which did not differ (Table 2). The values obtained here for the HWS and HWR lines were intermediate to those obtained in a companion crossing experiment involving these populations (Siegel et al.,

Table 1. Means and standard errors among lines for body weight (g) at 3 ages

Line	N	Age in days		
		56	168	266
HWS	270	1155 ± 6 <sup>e</sup>	2707 ± 14 <sup>e</sup>	3431 ± 21 <sup>d</sup>
HWR	110	991 ± 12 <sup>d</sup>	2452 ± 24 <sup>d</sup>	3148 ± 36 <sup>c</sup>
LWS	251	413 ± 6 <sup>a</sup>	1232 ± 30 <sup>a</sup>	1730 ± 14 <sup>a</sup>
LWR	143	503 ± 7 <sup>b</sup>	1355 ± 19 <sup>b</sup>	1746 ± 18 <sup>a</sup>
AC	49	764 ± 12 <sup>c</sup>	2176 ± 34 <sup>c</sup>	2521 ± 49 <sup>b</sup>

Means within a column with the same superscript are not significantly different ( $P < .05$ ).

Since there were no significant differences among years, data were pooled for 1975 and 1976.

Table 2. Means and standard errors among lines for "fear" and reproductive traits

Line	N	"Fear"	N	% hen-day egg prod	Age at 1st egg
HMS	260	12.9 ± 0.2 <sup>a</sup>	268	68 ± 1 <sup>b</sup>	183 ± 1 <sup>b</sup>
HWR	113	12.8 ± 0.2 <sup>a</sup>	106	68 ± 2 <sup>b</sup>	182 ± 2 <sup>b</sup>
LWS	246	15.2 ± 0.2 <sup>b</sup>	244	64 ± 1 <sup>a</sup>	199 ± 1 <sup>d</sup>
LWR	143	15.5 ± 0.2 <sup>b</sup>	143	62 ± 1 <sup>a</sup>	187 ± 2 <sup>c</sup>
AC	49	12.9 ± 0.4 <sup>a</sup>	49	74 ± 1 <sup>c</sup>	173 ± 1 <sup>a</sup>

Means within a column with the same superscript are not significantly different ( $P \leq .05$ ).

Since there were no significant differences among years, data were pooled for 1975 and 1976.

1978). It is not clear why significant differences were found between the HWS and HWR lines in our previous study and not in the current one; however, scores were similar and minor differences may be explained in terms of different environmental factors.

Although there were differences between populations for "fear" and for production traits, the important consideration is the within-line phenotypic relationship between modest "fearfulness" and production traits. The correlations between "fear" and production traits were consistently low and not significant (Table 3), with the average correlations essentially zero. Only the correlation of "fear" with percentage hen-day egg production in the LWS line was significant and this was probably due to chance. These results are consistent with previous observations in single bird cages (Siegel et al., 1978) where only 1 out of 20 correlations between "fear" and production traits was significant. The situation, however, may be different in multiple bird cages where negative correlations were noted (Sefton, 1976).

Another consideration is the change in "fear" over time. "Fear" measured for 126 HWS and 109 LWS pullets at 162, 238 and 279 days of age (28, 104 and 145 days after caging) showed a consistent pattern between lines with values being greater for the LWS than for the HWS pullets. Means and standard errors of the cumulative score for four trials for the HWS pullets were:  $13.9 \pm 0.2$ ,  $12.8 \pm 0.2$ ,  $11.7 \pm 0.2$  at 162, 238 and 279 days of age respectively, while values for the LWS pullets were  $16.2 \pm 0.2$ ,  $16.0 \pm 0.3$  and  $14.8 \pm 0.3$ . There was a downward trend in both lines in "fear" over time. This was probably due to habituation to the cage environment rather than to the test situation since the

Table 3. Average correlations<sup>1</sup> between "fear" and production traits, by Line

Line	% hen-day egg prod	Age at 1st egg	Body weight at age (days)		
			56	168	266
HWS	.09	.10	.03	.04	.03
HWR	.02	0	.07	.02	.05
LWS	.17*	.02	-.03	.08	-.02
LWR	-.06	.10	-.05	-.01	.05
AC	-.22	.12	.18	.12	.07
Av r for lines	.06	.06	.01	.02	.03

<sup>1</sup>Years pooled.\*Significant at  $P \leq .05$ .

interval between tests was longer than two weeks.

The frequency of head shaking was also obtained for these same pullets at the same ages. Values for HWS pullets were consistently greater than those for LWS pullets at all ages. Means and standard errors for number of head shakes in seven 5-minute observation periods were  $25.2 \pm 2.4$ ,  $36.9 \pm 2.5$ , and  $33.1 \pm 2.2$  head shakes at 162, 238 and 279 days of age respectively, for HWS pullets. Respective values for the LWS pullets were  $1.4 \pm 0.3$ ,  $1.9 \pm 0.3$  and  $2.3 \pm 0.3$ . Thus, pullets in the HWS line while less "fearful" exhibited more head shaking than those in the LWS line. Product moment correlations between ages for these behaviors were highly significant within lines and for lines pooled (Table 4). This suggests that while "fear" measures are correlated in time and head shaking measures are correlated in time, the phenotypic relationship between the two behaviors is low.

The important consideration from a husbandry and an animal welfare view is that the correlations between modest "fearfulness" and head shaking with each other and with body weights and reproductive traits are of a low order and show no consistent pattern. Head shaking and similar movements may increase under confinement (Bareham, 1972; Black and Hughes, 1974; Hughes and Black, 1974; Duncan, 1970; Duncan and Wood-Gush, 1972a; Siegel *et al.*, 1978), as they provide a vehicle by which a bird copes with a situation to relieve strife. Although such supports Duncan's (1970) hypothesis that the chicken which head shakes may be "better off" than one that does not, there is a need to relate "fear" and head shaking with physiological and disease measures in an effort to obtain insights into the adaptive processes of the domestic chicken.

Table 4. Average correlations between "fear" and head shaking at 3 ages<sup>1</sup>

Behavior	"Fear"		Head shaking		
	Age in days				
	238	279	162	238	279
"Fear"					
162	.70**	.51**	-.22**	-.02	--
238		.67**	-.11	-.02	-.13
279			-.09	.02	-.04
Head shaking					
162				--	.41**
238					.37**

<sup>1</sup>Lines pooled.

-- no value obtained since correlations between lines were heterogeneous; correlations between "fear" at 162 days of age and head shaking at 279 days of age was .50 for HWS and -.27 for LWS; correlations between head shaking at 162 and 238 days of age were .56 for HWS and .18 for LWS.

\* Significant at  $P \leq .05$ .

\*\* Significant at  $P \leq .01$ .

SUMMARY

Differences in "fear", head shaking and production traits were found between lines of chickens maintained in individual 46 X 30 X 46 cm cages. These differences were consistent across three ages. Although differences in "fear" and head shaking existed between lines that showed large differences for production traits, the within line relationships of production traits with modest "fearfulness and head shaking were not important.

EXPERIMENT II: BEHAVIOR AND DISEASE RESISTANCE IN TWO POPULATIONS OF CHICKENS WHERE THE SEX-LINKED DWARFING GENE HAS BEEN INTRODUCED

The liability of a social animal to disease has quantitative aspects which may be either enhanced or suppressed by environmental variables. Interwoven with this is a combination of behavioral and physiological processes which may serve as indicators of the adaptiveness of individuals and populations. In Experiment I the relationships of "fear" and head shaking with production characteristics were studied in five populations. No important phenotypic relationships were observed, suggesting plasticity in adjusting to a caging situation. Lacking, however, were data on the role of various physiological and immunological processes. Accordingly, the present experiment was designed to examine such processes in dwarf and nondwarf chickens in two lines selected for high and low juvenile body weight.

Materials and Methods

Stocks and Husbandry:

The dwarf gene, dw, (Hutt, 1959) was introduced from a commercial meat-population into the  $S_{13}$  generation of lines bidirectionally selected for high (HW) and for low (LW) juvenile body weight (Reddy and Siegel, 1977). Subsequent generations were produced by backcrossing Dwdw males to normal females of the respective selected line. The pullets used in the present experiments were obtained from the 4th and 5th

backcross (B<sub>4</sub> and B<sub>5</sub>) generations.

All chicks within a generation were hatched the same day (B<sub>4</sub> on March 4, 1975 and B<sub>5</sub> on March 2, 1976) and reared as floor flocks. Pullets were transferred to individual wire cages 46 cm high, 30 cm wide, and 46 cm deep at 119 and 134 days of age in 1975 and 1976, respectively. The lighting regime consisted of 14 hr of light from 0700 to 2100 hr.

#### Measurements and Analyses:

"Fear" responses to a human were measured between 160 and 164 days after caging (279 to 283 days of age in 1975 and 294 and 298 days of age in 1976). Also, in 1976, an early measure of "fear" was obtained between 24 and 28 days after caging (158 to 162 days of age). Head shaking was measured between 160 and 168 days after caging (279 and 288 days of age in 1975 and between 294 and 302 days of age in 1976). "Fear" and head shaking were measured by the procedures outlined in Experiment I.

Antibody titers to sheep red blood cells were measured by the injection of 0.1 ml of a 0.5% solution of sheep red blood cells (SRBC) in physiological saline. Injections of SRBC were given 289 and 316 days after caging (408 and 450 days of age) in 1975 and 1976, respectively. Five days after the injection of the SRBC, 0.5 ml of blood was removed via the brachial vein from each bird to test the antibody titers using the microdilution procedure. Plasma corticosterone levels were measured at 321 days after caging (455 days of age), in 1976 by a modification of Murphy's (1967) procedure where the competitive binding protein consisted of plasma obtained from humans over 70 years of age.

The E. coli challenge was made by injecting 0.1 ml of a 10<sup>-4</sup>

diluted 24-hr incubated serotype 01 K1 in tryptose broth in the posterior-thoracic air sac at 294 and 321 days after caging (413 and 455 days of age) in 1975 and 1976, respectively. Mortality and abnormal droppings (a diarrhea typical of that observed with an E. coli infection) were recorded for five days postchallenge, after which the survivors were sacrificed and scored for the presence or absence of heart and air sac lesions.

Line and genotype effects for "fear", number of head shakes, antibody titers to SRBC, and plasma corticosterone levels were analyzed by analysis of variance using the model:

$$Y_{ijk} = \mu + L_i + G_j + (LG)_{ij} + e_{ijk}$$

where,  $i = 1, 2$  lines;  $j = 1, 2$  genotypes; and  $k = 1, 2 \dots n$  individuals. Since multiple measures of a behavior on an individual are correlated, the two measures of "fear" were analyzed by multivariate procedures (Kramer, 1972) using the model:

$$Y_{ijk} = \mu + L_i + G_j + (LG)_{ij} + e_{ijk}$$

where,  $i = 1, 2$  lines;  $j = 1, 2$  genotypes;  $k = 1, 2 \dots n$  individuals; and 1, 2 measurement ages. Product moment correlations between "fear" and head shaking were calculated within lines, tested for homogeneity, and averaged using the  $z$  transformation (Snedecor and Cochran, 1967). Mortality, lesions, and droppings data were analyzed by Chi square where  $T = 2$  (Jensen et al., 1968).

## Results and Discussion

### "Fear" and Head Shaking:

Line-dwarf genotype interactions for "fear" were not significant, suggesting that genotypes within lines responded similarly. There was a highly significant difference between genotypes with the dwarf pullets exhibiting greater "fear" than the normal ones (Table 5). Also, pullets from the LW line consistently exhibited significantly greater "fear" than those from the HW line, an observation consistent with that reported previously for these lines (Experiment I and Siegel *et al.*, 1978).

There were significant line-dwarf genotype interactions each year for the frequency of head shaking (Figure 1). Accordingly, comparisons were made between genotypes within lines.

In the B<sub>4</sub> generation the differences between normal and dwarf pullets were highly significant in both lines with the normal pullets having more head shakes than the dwarf pullets. The same pattern existed in the B<sub>5</sub> with the differences being significant in the LW line only. Correlations between "fear" and head shaking were -.02 in the B<sub>4</sub> and 0 in the B<sub>5</sub>, suggesting no phenotypic relationship between the traits.

### Antibody and Plasma Corticosterone Titers:

The line-dwarf genotype interactions were significant for antibody titers to SRBC in both years (Figure 2). Within the HW line, dwarf pullets had significantly higher antibody titers than normal pullets in both years. In contrast, differences between dwarf and nondwarf genotypes were not significant in the LW line. These results demonstrate that the influence of the dw gene varies with the genetic background of the

Table 5. Cumulative "fear" values, by line, genotype, and generation.

	Days after caging		
	160 to 164		24 to 28
	B <sub>4</sub>	B <sub>5</sub>	B <sub>5</sub>
Line			
HW	13.3 ± 0.2	11.3 ± 0.2	11.8 ± 0.2
LW	14.0 ± 0.2	14.3 ± 0.3	15.3 ± 0.2
Diff.	-0.7**	-3.0**	-3.5**
Genotype			
<u>Dw</u>	13.0 ± 0.3	13.1 ± 0.4	11.9 ± 0.4
<u>dw</u>	14.6 ± 0.4	13.9 ± 0.4	13.9 ± 0.4
Diff.	-1.6**	-0.8**	-2.0**

\*\* P ≤ .01.

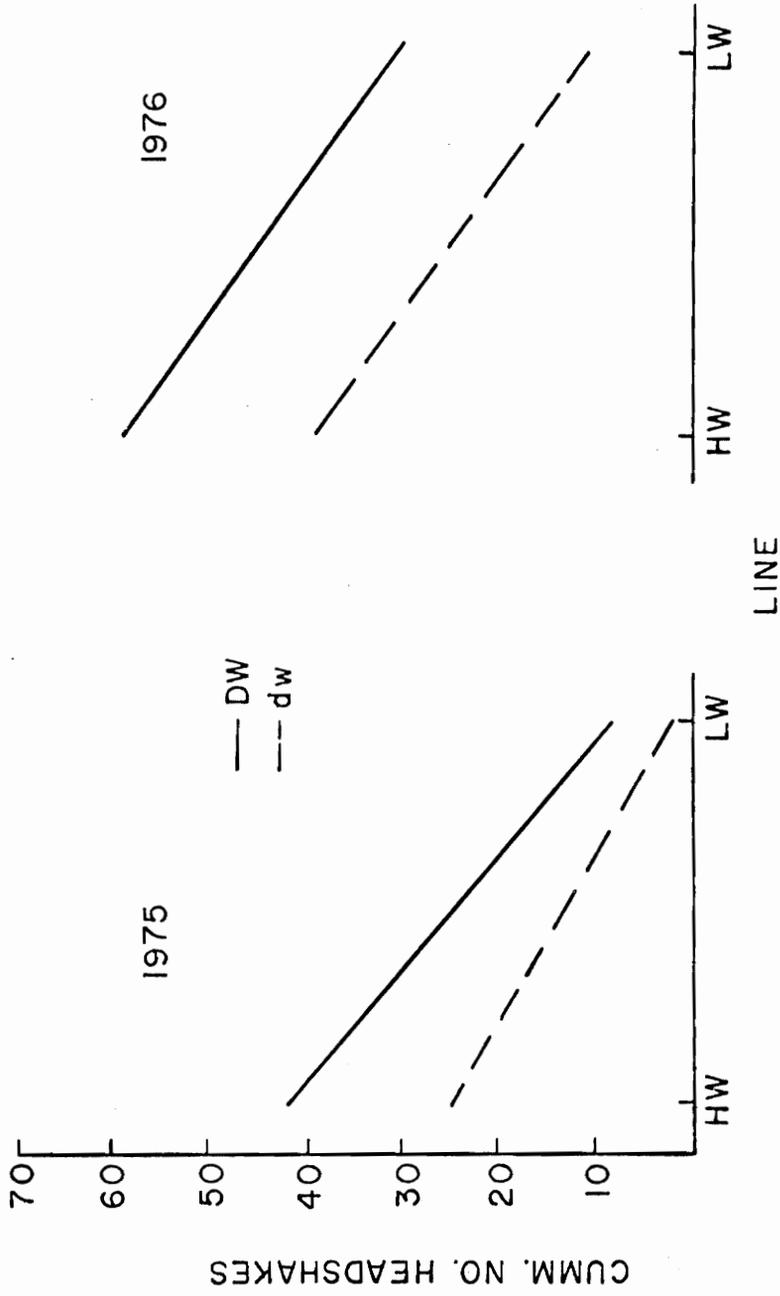


Figure 1. Cumulative frequency of head shaking between 160 and 168 days after caging in 1975 and 1976, respectively, by line and genotype.

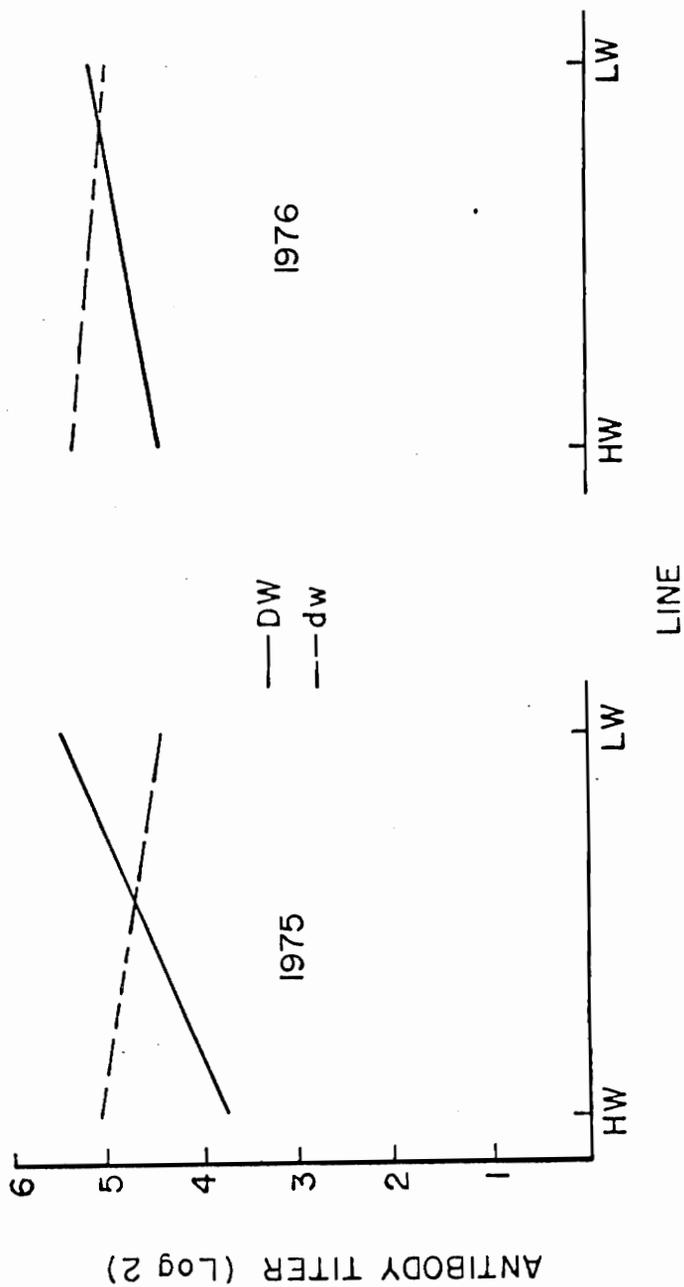


Figure 2. Antibody titers to SRBC by lines and genotypes at 289 and 316 days after caging in 1975 and 1976, respectively.

population.

The highly significant line-dwarf genotype interaction for plasma corticosterone level was of the cross-over type. That is, the values were higher for dwarf than for normal pullets in the HW line ( $3.8 \pm 0.5$  ng/ml vs  $3.0 \pm 0.4$  ng/ml), while the inverse was the case for the LW line ( $3.2 \pm 0.5$  ng/ml vs  $4.3 \pm 0.7$  ng/ml). Correlations between antibody and plasma corticosterone titers were positive, but not significant, being .05, .15, .30, and .11 for HW normal, HW dwarf, LW normal, and LW dwarf pullets, respectively, suggesting that stress was not a sufficient factor in this experiment to cause lymphoid involution.

#### E. coli Challenge:

The percentage of mortality plus survivors with heart lesions due to the E. coli challenge was significantly greater in the HW than in the LW line, and greater for normal than dwarf genotypes in the B<sub>4</sub> generation (Table 6). The percentage of survivors exhibiting air sac lesions and abnormal droppings was significantly greater in the HW line than in the LW line. Also, normal pullets had a significantly higher percentage of abnormal droppings than their dwarf counterparts, while there was no difference between genotypes for the incidence of air sac lesions.

Results of the E. coli challenge were quite different in the B<sub>5</sub> generation (Table 7), with the LW pullets being significantly more affected than the HW pullets. This inconsistency is not surprising in view of the disease history of the flocks. There was no history of disease in the B<sub>5</sub> generation, while in the B<sub>4</sub> an outbreak of E. necatrix at about 13 weeks of age in the LW line caused approximately 30% mortality. Since there was no evidence of the E. necatrix outbreak in the HW line, the LW survivors

Table 6. Mortality, lesions and abnormal droppings from E. coli challenge by lines and genotypes, 1975 (B<sub>4</sub>)

	N	% dead + heart lesions	N	Surviving with	
				% air sac lesions	% abnormal droppings
Line					
HW	84	41.7	49	69.4	57.1
LW	66	27.3	48	41.7	37.5
Diff.		14.4*		27.7*	19.6*
Genotype					
<u>Dw</u>	85	44.7	47	53.2	59.6
<u>dw</u>	65	23.1	50	68.0	28.0
Diff.		21.6*		14.8	31.6*

Analyses made on actual numbers.

\*  $P \leq .05$ .

Table 7. Mortality, lesions and abnormal droppings from *E. coli* challenge by lines and genotypes, 1976 (B<sub>5</sub>)

	N	% dead + heart lesions	N	Surviving with	
				% air sac lesions	% abnormal droppings
Line					
HW	76	2.6	74	9.5	6.8
LW	83	24.1	63	20.6	20.6
Diff.		21.5*		11.1	13.8
Genotype					
<u>Dw</u>	74	13.5	64	17.6	11.8
<u>dw</u>	85	12.9	74	12.0	12.0
Diff.		0.6		5.6	0.2

Analyses made on actual numbers.

\*  $P \leq .05$ .

were probably those with the greatest resistance to bacterial and parasitic infections. This is because the individuals with the best phagocytic defense system should have survived the E. necatrix outbreak and would thus have the greatest resistance to the E. coli. This reasoning is consistent with the results of Gross and Colmano (1969; 1970; 1971) and Gross (1972) who showed that individuals with a strong phagocytic response were generally resistant to bacterial and parasitic infections (i.e., E. coli and E. necatrix) and susceptible to viral and tumor diseases (i.e., M. gallusepticum and Marek's disease).

The mortality and lesion data of the E. coli challenge in 1976 (B<sub>5</sub> generation) were consistent with those of Reddy et al. (1975) who studied the B<sub>2</sub> generation which also had no history of disease outbreaks prior to challenge. Furthermore, it is interesting to note that in this generation the HW normal pullets (the subclass with the highest percentage of mortality and heart lesions) also had the lowest antibody titers of any of the groups.

Line-dwarf genotype interactions have been reported for production traits such as body weight, percentage hen-day egg production, and age at first egg (Reddy and Siegel, 1977; Cherry and Siegel, 1978). These observations, plus the line-dwarf genotype interactions noted for head shaking, antibody titers, and plasma corticosterone levels indicate that the phenotypic expression of the dw gene is modified by the genetic background of the population. This, in turn, means that caution should be exercised in making inferences across populations on the influence of the dw gene on various traits.

### Summary

Investigated were several behavioral and physiological traits associated with the adaptability of dwarf and nondwarf pullets in populations of White Plymouth Rocks that had undergone selection for high (HW) and for low (LW) juvenile body weight. The traits measured were "fear", head shaking, antibody titers to sheep red blood cells, plasma corticosterone titers, and resistance to E. coli infection. Significant line-dwarf genotype interactions were found for all traits except "fear". There was significantly greater "fear" noted in the LW than in the HW line and in dwarf than in normal pullets in both generations. Head shaking was significantly greater for normal than for dwarf pullets in both lines in the B<sub>4</sub> generation; however, in the B<sub>5</sub> generation this difference was significant in the LW line only. Both generations the antibody titers to sheep red blood cells were greater in dwarf than in normal pullets from the HW line while no significant differences were noted between genotypes in the LW line. Percentages of mortality plus heart lesions, air sac lesions, and abnormal droppings to an E. coli challenge were greater in the HW line than in the LW line in the B<sub>4</sub> generation. In contrast, the response to the E. coli challenge in the B<sub>5</sub> generation was greater in the LW than in the HW line pullets. The inconsistency between generations may be explained by differences in the disease histories of the pullets as there was an outbreak of E. necatrix in the B<sub>4</sub>, but not in the B<sub>5</sub> generation.

EXPERIMENT III: THE RELATIONSHIP BETWEEN THE DWARFING GENE (dw) AND  
E. COLI INFECTION IN TWO POPULATIONS OF CHICKENS

Genetic influences on the disease resistance of organisms are well documented with numerous specific examples for the fowl (Hutt, 1949, 1959). The influence of the sex-linked recessive dwarfing gene (dw) on nutritional, physiological and disease factors has been the subject of recent intensive investigation in chickens (Haas et al., 1975; Guillame, 1976; and Reddy et al., 1977), and its influence on resistance to E. coli infection was studied in Experiment II. Lacking, however, were (a) an evaluation of male genotypes and (b) an environment where social interaction was present. The purpose of this experiment was to measure antibody production and resistance to E. coli challenge in flocks of dwarf and nondwarf pullets and cockerels during the period of peck-order formation.

Materials and Methods

The sex-linked recessive gene, dw, was introduced into lines divergently selected for high (HW) and low (LW) juvenile body weight by mating Dwdw males to S<sub>13</sub> generation females of each selected line (Reddy and Siegel, 1977). The Dwdw progeny were backcrossed to normal females in the respective selected generations. The birds used in this experiment were males from the B<sub>6</sub> and both sexes from the B<sub>7</sub> generations.

All chicks, within a generation, were hatched on the same date (B<sub>6</sub> on March 1, 1977 and B<sub>7</sub> on January 13, 1978) and reared as floor flocks.

At 47 days of age, they were moved to wire-floor cages 41 cm high, 76 cm wide and 76 cm deep, where they were maintained as small flocks of 8 to 12 birds each. Food and water were provided ad libitum, lighting was continuous, and the temperature maintained between 20 and 21°C.

At the time of moving each bird was given, via the brachial vein, 0.1 ml of a 0.5% solution of sheep red blood cells (SRBC) in physiological saline. Five days later, 0.5 ml of blood was removed from the brachial vein to test for antibody titers using the microdilution procedure. The chicks were also inoculated at this time with 0.1 ml of a 24-hr incubated serotype of O1 K1 E. coli in tryptose broth via the posterior-thoracic air sac. The E. coli cultures were diluted to  $10^{-5}$  in the B<sub>6</sub> generation and  $10^{-3.5}$  in the B<sub>7</sub> generation. Mortality was measured for five days post E. coli challenge, after which the survivors were sacrificed and scored for either the presence or absence of heart and air sac lesions.

Mortality plus heart lesions were analyzed by Chi square and since the same data were used to test for differences between lines and between genotypes (Jensen et al., 1968)  $\tau$  was = 2. The association between genotype and E. coli infection was analyzed in males using a procedure proposed by Norwood and Hinkelman (1978) which consisted of a Chi square analysis with tests for nonrandom mating (A x A), independence of allele and infection (A x D), and for an allele interaction effect on the incidence of infection (A x A x D).

Antibody titers were analyzed within sexes by analysis of variance using the model:

$$Y_{ijk} = \mu + L_i + G_j + (LG)_{ij} + e_{ijk}$$

where,  $i = 1, 2$  lines;  $j = 1, 2, 3$  genotypes (for males) and 1, 2

genotypes (for females); and  $k = 1, 2 \dots n$  individuals. Lines and genotypes were considered as fixed effects.

### Results and Discussion

#### Response to E. Coli Challenge:

The difference between lines for mortality plus heart lesions was not significant in the  $B_6$  generation, whereas, among survivors there were significantly more air sac lesions in the HW than in the LW line (Table 8). When the dosage of E. coli was increased from a  $10^{-5}$  dilution in the  $B_6$  to a  $10^{-3.5}$  dilution in the  $B_7$  generation, mortality was increased several fold in both lines with the HW line having significantly greater mortality plus heart lesions, and air sac lesions of survivors than in the LW line. This effect was common to both sexes (Tables 8 and 9).

Chi square analysis revealed no significant differences among dwarf, heterozygous and normal genotypes for resistance to E. coli as measured by mortality and lesions (Table 8). The Norwood and Hinkelman (1978) procedure enables a further evaluation of the effect of genes at a single locus on disease resistance (Table 10). The greatest portion of the variation in all comparisons, however, was due to the interaction between the two alleles ( $A \times A$ ) which indicated nonrandom mating. This result was not surprising because individual males had been mated to individual females. The associations of most interest, however, were  $A \times D$  (association between the dw allele and the disease) and  $A \times A \times D$  (the interaction between the two alleles with the disease). Variation due to  $A \times D$  was not significant for any comparison, while that for

Table 8. Mortality plus heart lesions and air sac lesions in males, by generation, line and genotype<sup>1</sup>

Line	B <sub>6</sub>				B <sub>7</sub>				
	n	% mortality plus heart lesions	Survivors % air sac lesions	n	% mortality plus heart lesions	Survivors % air sac lesions	n	% mortality plus heart lesions	Survivors % air sac lesions
HW	58	15.5 <sup>a</sup>	49	30.2 <sup>b</sup>	46	78.3 <sup>b</sup>	10	50.0 <sup>b</sup>	
LW	59	13.6 <sup>a</sup>	51	11.9 <sup>a</sup>	56	51.8 <sup>a</sup>	27	14.8 <sup>a</sup>	
Genotype									
DwDw	41	12.2 <sup>a</sup>	36	19.4 <sup>a</sup>	41	58.5 <sup>a</sup>	18	27.8 <sup>a</sup>	
Dwdw	36	11.1 <sup>a</sup>	32	28.1 <sup>a</sup>	27	74.1 <sup>a</sup>	7	28.6 <sup>a</sup>	
dwdw	40	20.0 <sup>a</sup>	32	21.9 <sup>a</sup>	34	64.7 <sup>a</sup>	12	16.7 <sup>a</sup>	

<sup>1</sup>Analysis made on actual numbers.

Means within a column for a main effect with the same superscript are not significantly different ( $P \leq .05$ ).

Table 9. Mortality plus heart lesions and air sac lesions in B<sub>7</sub> generation females, by line and genotype<sup>1</sup>

	n	% mortality plus heart lesions	Survivors	
			n	% air sac lesions
Line				
HW	53	73.6 <sup>b</sup>	14	35.7 <sup>b</sup>
LW	79	30.4 <sup>a</sup>	44	13.6 <sup>a</sup>
Genotype				
Dw -	61	49.2 <sup>a</sup>	31	16.1 <sup>a</sup>
dw -	71	62.0 <sup>a</sup>	27	22.2 <sup>a</sup>

<sup>1</sup>Analysis made on actual numbers.

Means within a column for a main effect with the same superscript are not significantly different ( $P \leq .05$ ).

Table 10. The association of the dw allele with E. coli infection, by generation and line<sup>1</sup>

Source of variation	df	B <sub>6</sub>		B <sub>7</sub>	
		HW	LW	HW	LW
A x A <sup>2</sup>	1	6.89**	10.56**	5.52*	20.43**
A x D <sup>3</sup>	1	0.35	0.42	0.20	0
A x A x D <sup>4</sup>	1	2.81	4.70*	0.13	0.69
Total <sup>5</sup>	3	10.05*	15.68**	5.03	21.12**

<sup>1</sup>Analysis made on actual numbers.

<sup>2</sup>A x A tests for nonrandom mating.

<sup>3</sup>A x D tests for independence of allele and disease.

<sup>4</sup>A x A x D tests for an allele interaction effect on incidence of disease.

<sup>5</sup>Total tests for total degree of variation in the population for the above components.

\*  $P \leq .05$ .

\*\*  $P \leq .01$ .

A x A x D was significant in only one for four analyses (the LW line in the B<sub>6</sub> generation) suggesting that the relationship in this experiment was minor. Although this is inconsistent with our observations with adult hens in the B<sub>2</sub> and B<sub>5</sub> generations (Experiment II and Reddy et al., 1975) there are several reasons that may be offered as explanation. The birds in the present experiment were in recently assembled flocks and peck orders were being formed at the time of the E. coli challenge. Accordingly, social strife was near its maximum as measured by blood plasma corticosterone levels (Williams et al. 1977). In contrast, the adult birds had been maintained in individual cages for over 250 days and were under very low social strife. Gross and Colmano (1969) have shown that the degree of social interaction will markedly influence susceptibility or resistance to infectious agents. They found that a high degree of social interaction resulted in an increased resistance to E. coli and Staphylococcus aureus infection (bacterial infections) and a decreased resistance to Mycoplasma gallusepticum and Newcastle disease (viral infections). A low degree of social interaction had the opposite effect. Increased levels of plasma corticosterone due to social stress causes lymphoid involution (Selye, 1956) resulting in a decreased resistance to viral infections but, on the other hand, social stress enhances phagocytic responses which are the main defense against bacterial and parasite infections (Gross, 1976). The complexity of the relationships among genotype, social strife and disease have been discussed (Gross, 1976; Gross and Colmano, 1969; Reddy and Siegel, 1977; Siegel, 1976) and indicates that the prior history of a population is important in understanding genetic-disease relationships.

### Antibody Response to SRBC:

Antibody titers to SRBC were significantly higher in the LW line than in the HW line in all comparisons (Table 11). Although the dwarf males in the B<sub>6</sub> generation had significantly higher antibody titers to SRBC than either heterozygous or homozygous normal males, which were not significantly different from each other, no differences among genotypes were noted in the B<sub>7</sub> generation. These results are inconsistent with our previous study using the B<sub>4</sub> and B<sub>5</sub> generations of these same lines where adult chickens were used (Experiment II). The previous study revealed a line by dwarf-genotype interaction for antibody titers to SRBC in the B<sub>4</sub> and B<sub>5</sub> generations. Analyzed within lines, the dwarf hens had significantly greater antibody titers than the normal hens in the HW line in both generations. Normal LW line hens in the B<sub>4</sub> generation produced more antibody to SRBC than the dwarf hens; there were no significant differences due to genotype in the LW line in B<sub>5</sub>. However, as mentioned earlier, prior histories of the populations used in the two studies were different, and the importance of population-history and degree of social strife on the ability of chickens to produce antibody have been pointed out (Gross and Siegel, 1973; Siegel and Latimer, 1975). It is quite probable that the high level of social strife due to the formation of peck rights masked the interactions between genotype and antibody titers. Such considerations are important in the design of experiments involving disease resistance in social organisms.

In view of the present results, another trial should be conducted where the challenge with SRBC will be made at an early age, during peck-order formation and the establishment of the social hierarchy. The

Table 11. Means and standard errors of antibody titers (log 2 values) to SRBC by sex, generation, line and genotype

	Males				Females	
	B <sub>6</sub>		B <sub>7</sub>		B <sub>7</sub>	
	n	titer	n	titer	n	titer
<b>Line</b>						
HW	58	5.6 ± 0.2 <sup>a</sup>	56	4.8 ± 0.2 <sup>a</sup>	53	4.8 ± 0.2 <sup>a</sup>
LW	59	6.6 ± 0.2 <sup>b</sup>	66	6.2 ± 0.2 <sup>b</sup>	79	6.0 ± 0.2 <sup>b</sup>
<b>Genotype</b>						
DwDw	41	5.2 ± 0.2 <sup>a</sup>	42	5.8 ± 0.2 <sup>a</sup>		
Dwdw	36	5.9 ± 0.2 <sup>a</sup>	47	5.2 ± 0.2 <sup>a</sup>		
dwdw	40	7.2 ± 0.2 <sup>b</sup>	33	5.8 ± 0.3 <sup>a</sup>		
Dw -					61	5.6 ± 0.2 <sup>a</sup>
dw -					71	5.4 ± 0.2 <sup>a</sup>

Means within a column for a main effect followed by a common superscript are not significantly different ( $P \leq .05$ ).

challenge to E. coli should be made after establishment of the social hierarchy. Under such a situation social stress should be at a low level resulting in a balance between the lymphoid and phagocytic components of disease resistance. Change in body weight should also be measured post-E. coli challenge since it has been shown to be a good indicator of stress (see Experiment IV),

### Summary

Resistance to an E. coli challenge and antibody production in response to sheep red blood cells were studied in the 6<sup>th</sup> and 7<sup>th</sup> backcross generations after the introduction of the sexed-linked recessive dwarf gene (dw) into two populations of White Plymouth Rock chickens that had undergone bidirectional selection for juvenile body weight.

Males and females responded similarly to E. coli and SRBC challenges. The HW line birds had significantly lower antibody titers to SRBC than those from the LW line. Also, the dwarf genotypes had significantly higher antibody titers to SRBC than heterozygous and homozygous normal genotypes. Mortality plus heart lesions and air sac lesions due to the E. coli challenge were significantly greater in birds from the HW than from the LW line. There were no differences in susceptibility to E. coli between dwarf, heterozygous and normal genotypes. Inconsistencies of results of E. coli challenge in the present experiment using the B<sub>6</sub> and B<sub>7</sub> generations and in previous experiments (Experiment II and Reddy et al., 1975) using the B<sub>2</sub>, B<sub>4</sub> and B<sub>5</sub> generations are explained by the different life histories of the birds in a particular generation.

EXPERIMENT IV: INTERFACING OF GENETICS, BEHAVIOR AND HUSBANDRY TO AN  
E. COLI CHALLENGE IN WHITE LEGHORN CHICKENS

The first three experiments involved the influence of genetics and husbandry on behavior, production traits and bacterial infections in the fowl. In Experiment IV, the interfacing of these factors was examined in an effort to evaluate resource allocations as measured by body weight, immunological responses, blood characteristics, and behaviors in White Leghorn chickens.

Materials and Methods

Stocks and Husbandry:

The females used in this experiment were from the  $S_3$  and  $S_4$  generations of two lines divergently selected for persistence (P) and nonpersistence (NP) of antibody production. Selection in the P and in the NP lines were for a small and a large change, respectively, in antibody titers between 5 and 21 days postchallenge to sheep red blood cell antigen (SRBC). The antigen was given when the pullets were 51 days of age. The base population for the selected lines was the Cornell Randombred White Leghorn population (King et al., 1959).

Chicks from the  $S_3$  and  $S_4$  generations were hatched March 2, 1976 and October 26, 1976, respectively. They were reared as floor-flocks until 134 days of age in the  $S_3$  generation and 242 days of age in the  $S_4$  generation, after which each bird was placed into a wire cage 46 cm high, 30 cm wide and 46 cm deep. The lighting regime consisted 14 hr of

light from 0700 to 2100 hr. Food and water were provided ad libitum.

Movement Scheme:

At 295 days of age in the  $S_3$  generation and 394 days of age in the  $S_4$  generation females from each line were subjected to the following movement scheme:

- (a) one-third remained in the same cages (not moved, NM)
- (b) one-third were moved into different, but essentially identical single cages (single moved, SM), and
- (c) one-third were paired in neutral, but essentially identical cages with females from the other line (paired, PM).

The experiment involved 48 pullets in the  $S_3$  generation (24/line) and 78 pullets in the  $S_4$  generation (39/line).

Measurements:

"Fear" of humans and head shaking were measured via the procedures outlined in Experiment I, and based on the repeatability estimates of "fear" and head shaking obtained in Experiment I cumulative values of four "fear" trials and seven head shaking trials were obtained. "Fear" was measured during the period from three to seven days premovement and one to four days postmovement while head shaking was measured during the period from one to seven days premovement and from one to seven days postmovement. Changes in "fear" and head shaking were considered as premovement minus postmovement values. All head shaking data were transformed to log 10 values prior to analysis.

The size of the comb was considered as the product of the length times the height at the highest point expressed as  $\text{mm}^2$ . Measurements

were obtained just prior to movement in the  $S_3$  generation, whereas, in the  $S_4$  generation a second measure was obtained seven days postmovement. Change in comb size was the premovement minus the postmovement value. Social rank was determined daily by the dominance-subordinance relationship of each pair in an effort to evaluate the stability of the social hierarchy.

Individual body weights were obtained in the  $S_3$  generation on the day of movement and five days postmovement. In the  $S_4$  generation weights were recorded on the day of movement and 2, 4 and 7 days postmovement. Change was considered as premovement minus postmovement weight.

One day postmovement each bird was given, via the brachial vein, 0.1 ml of a 0.5% suspension of SRBC in physiological saline. Seven days later, 0.5 ml of blood was removed from the brachial vein and tested for antibody titers using the microdilution procedure. Plasma samples were collected for corticosterone titer determinations 1 and 7 days postmovement in the  $S_3$  generation and on the day of movement plus 1 and 7 days postmovement in the  $S_4$  generation. The method used consisted of a modification of Murphy's (1967) procedure. The modification in the  $S_3$  generation involved using a competitive binding protein from plasma obtained from humans over 70 years of age. In the  $S_4$  generation the competitive binding protein consisted of plasma from chickens fed exogenous corticosterone. The feeding of corticosterone was terminated two days prior to obtaining blood plasma from the donors. Their adrenals had undergone considerable atrophy and the level of corticosterone in their plasma was zero.

Differential and total leucocyte counts were made from blood

obtained from each  $S_3$  generation female on the day of movement and 1 and 7 days postmovement. In addition, measurements were obtained on the size of lymphocytes and heterophils. Data were expressed as:

- (1) number of lymphocytes/mm<sup>3</sup>,
- (2) diameter ( $\mu$ ) of lymphocytes,
- (3) lymphocytes ( $\mu^2$ /mm<sup>3</sup>),
- (4) number of heterophils/mm<sup>3</sup>,
- (5) diameter ( $\mu$ ) of heterophils,
- (6) heterophils ( $\mu^2$ /mm<sup>3</sup>), and
- (7) ratio of heterophil to lymphocyte numbers.

Females were inoculated seven days after movement in both generations with 0.1 ml of a 24-hr incubated serotype of O1 K1 E. coli in tryptose broth via the posterior-thoracic air sac at a dilution of  $10^{-5}$ . Social rank was determined each day postchallenge by the dominance-subordinance relationship of each pair. Individual body weights were obtained on the day of challenge and at 1, 3 and 5 days postchallenge to determine the effect of the challenge on body weight. Mortality and abnormal droppings (diarrhea typical of that observed due to an E. coli infection) were measured five days post-E. coli challenge, after which the survivors were sacrificed and scored for either the presence or absence of heart and air sac lesions.

#### Analyses:

All premovement measures for comb size, plasma corticosterone levels, lymphocyte and heterophil characteristics plus "fear" and head shaking were analyzed to test line effects using a completely randomized design.

The statistical model was:

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

where,  $i = 1, 2$  lines and  $j = 1, 2 \dots n$  individuals per line.

Changes in body weight postmovement and postchallenge with E. coli, plus postmovement values of "fear", head shaking, comb size and antibody titers to SRBC were analyzed by analyses of variance using a randomized block design where:

$$Y_{ijk} = \mu + L_i + G_j + (LG)_{ij} + e_{ijk}$$

where,  $i = 1, 2$  lines;  $j = 1, 2, 3$  movement groups; and  $k = 1, 2 \dots n$  individuals.

Since multiple measures of a given trait are correlated, multivariate analyses of variance (Kramer, 1972) were used to analyze postmovement measures of plasma corticosterone levels and leucocyte characteristics. The statistical model was:

$$Y_{ijk} = \mu + L_i + G_j + (LG)_{ij} + e_{ijk}$$

where,  $i = 1, 2$  lines;  $j = 1, 2, 3$  movement groups; and  $k = 1, 2 \dots n$  individuals; and 1, 2 measures of each parameter.

Product moment correlations were obtained in the PM group for the following combinations:

- (1) premovement comb size and postmovement social rank,
- (2) first and last measures of social rank postmovement, and
- (3) first measure of social rank postmovement and last measure of social rank postchallenge.

Data for mortality, lesions, droppings, and social rank were analyzed by Chi square where  $\tau = 2$  (Jensen et al., 1968) since the data were used twice (once for analysis of line effects and once for analysis of

movement group effects).

### Results and Discussion

#### "Fear" and Head Shaking:

There were highly significant differences between lines in both generations for "fear" with the NP line having higher values than the P line (Table 12). The pattern between lines was the same when comparisons were made premovement and postmovement. Although differences in "fear" among various populations of chickens have been observed in several experiments (Sefton, 1976; Murphy, 1977; Murphy and Duncan, 1977; 1978; and Experiments I and II), such responses may be stimulus specific. For example, Murphy and Duncan (1977) observed greater withdrawal in response to a mechanical scraper in a strain considered docile to humans than one that was considered flighty.

There were no significant differences between movement groups for "fear" responses (Table 12). Generalization of this observation to other situations may not be appropriate because Sefton (1976) noted physical and social effects on "fear" at various cage sizes and flock densities, and Hughes and Black (1974) observed differences in "fear" when chickens were maintained at varying light intensities and population densities.

There were no significant differences between lines or among movement groups for frequencies of head shaking (Table 12). Head shaking has been considered as a vehicle by which a bird adapts to strife (Siegel et al., 1978), and a chicken which head shakes may be better off than one that does not (Duncan, 1970). Such, however, may be long term

Table 12. Means and standard errors for "fear" and head shaking, pre- and postmovement, by generation, line and movement treatment

Line	S <sub>3</sub>		Fear		S <sub>4</sub>		Head Shaking		S <sub>4</sub>	
	Premove	Postmove	Premove	Postmove	Premove	Postmove	Premove	Postmove	Premove	Postmove
P	11.9 ± 0.6 <sup>a</sup>	11.2 ± 0.5 <sup>a</sup>	12.3 ± 0.2 <sup>a</sup>	13.0 ± 0.2 <sup>a</sup>	6.0 ± 1.7 <sup>a</sup>	8.4 ± 2.4 <sup>a</sup>	10.4 ± 1.8 <sup>a</sup>	10.3 ± 2.4 <sup>a</sup>		
NP	15.6 ± 0.4 <sup>b</sup>	13.9 ± 0.4 <sup>b</sup>	14.5 ± 0.3 <sup>b</sup>	15.0 ± 0.3 <sup>b</sup>	2.1 ± 0.4 <sup>a</sup>	5.7 ± 0.3 <sup>a</sup>	7.4 ± 1.4 <sup>a</sup>	6.1 ± 0.9 <sup>a</sup>		
Movement group										
NM		12.4 ± 0.7 <sup>a</sup>		13.8 ± 0.4 <sup>a</sup>		5.1 ± 1.2 <sup>a</sup>		9.8 ± 3.3 <sup>a</sup>		
SM		13.1 ± 0.6 <sup>a</sup>		14.0 ± 0.4 <sup>a</sup>		5.4 ± 1.1 <sup>a</sup>		6.5 ± 1.3 <sup>a</sup>		
PM		11.9 ± 0.7 <sup>a</sup>		14.2 ± 0.4 <sup>a</sup>		10.3 ± 3.9 <sup>a</sup>		8.2 ± 1.7 <sup>a</sup>		

Any two means in a column within a main effect with the same superscript are not significantly different ( $P \leq .05$ ).

adaptations and would not necessarily be exhibited in situations such as those in this experiment where primary concern is with short term adaptiveness.

#### Comb Size and Social Rank:

Mean premovement comb size in the  $S_3$  generation was 4,709 mm<sup>2</sup> for the P line and 4,968 mm<sup>2</sup> for the NP line. The respective values in the  $S_4$  generation were 4,500 and 5,190 mm<sup>2</sup>. Although the trend between lines was the same in both generations, the difference was significant in the  $S_4$  generation only. Differences between lines and between movement treatments for comb size seven days postmovement were not significant; however, the line-movement treatment interaction was highly significant. Subsequent comparisons of comb size among movement treatments showed no significant differences within the P line, whereas, in the NP line the PM females had significantly smaller combs than the NM and SM birds (Table 13).

There were no significant differences between lines in either generation for social rank in the PM treatment. Product moment correlations between the first and last measures of postmovement social rank were highly significant being 1.00 and 0.85 in the  $S_3$  and  $S_4$  generations, respectively, revealing that once established, the peck rights were predictable. Product moment correlations between social rank and comb size were positive in both generations being 0.26 and 0.73 in the  $S_3$  and  $S_4$  generations, respectively. These positive relationships between social rank and comb size agree with the observations of Allee et al. (1939), Collias (1943), Guhl and Ortman (1953), Marks et al. (1960),

Table 13. Means and standard errors for comb size ( $\text{mm}^2$ ) postmovement in the  $S_4$  generation, by line and movement group

Movement group	Line	
	P	NP
NM	4525 $\pm$ 401 <sup>a</sup>	5200 $\pm$ 179 <sup>b</sup>
SM	4384 $\pm$ 257 <sup>a</sup>	5512 $\pm$ 387 <sup>b</sup>
PM	4781 $\pm$ 342 <sup>a</sup>	4030 $\pm$ 311 <sup>a</sup>

Any two means in a column with the same superscript are not significantly different ( $P \leq .05$ ).

and Siegel and Dudley (1963) who found that individuals with larger combs had the advantage in initial social encounters.

#### Changes in Body Weight:

There were no significant differences between lines for 5-day post-movement body weight in the  $S_3$  generation or at 2 and 4 days postmovement in the  $S_4$  generation (Table 14). By seven days postmovement, however, the females from the NP line had lost significantly more weight than those from the P line. This was because the P line females had returned to their premovement weights within seven days after moving, whereas the NP birds continued to lose body weight. This suggests that the adjustments to the new environment were faster in the P than in the NP line.

The effects of movement on body weight were highly significant. In all comparisons the PM females lost more weight than the NM females with the weight loss of the SM birds being intermediate. These data suggest that the effect of moving, even to a different but essentially identical cage, is sufficient to cause a short term loss in body weight. Also, the influence was more severe when individuals were caged in pairs suggesting that the physical and social effects imposed by the movement scheme were cumulative.

#### Plasma Corticosterone and Antibody Titers:

Lines, movement treatment and the line-movement treatment interaction were not significant for plasma corticosterone levels. Time trends, however, were highly significant in the  $S_4$  generation with the lowest values being premovement, the highest values one day postmovement and the 7-day values, intermediate (Table 15).

Table 14. Means and standard errors for change in body weight (g), by generation line and movement group

	$S_3$	$S_4$		
	5-days postmovement	days postmovement		
		2	4	7
Line				
P	$-37 \pm 14^a$	$-12 \pm 16^a$	$-12 \pm 13^a$	$2 \pm 12^b$
NP	$-20 \pm 9^a$	$-3 \pm 9^a$	$-21 \pm 11^a$	$-26 \pm 13^a$
Movement group				
NM	$0 \pm 8^b$	$26 \pm 4^b$	$37 \pm 6^c$	$52 \pm 8^c$
SM	$-19 \pm 15^{ab}$	$2 \pm 12^b$	$0 \pm 12^b$	$-18 \pm 12^b$
PM	$-55 \pm 17^a$	$-34 \pm 11^a$	$-76 \pm 14^a$	$-70 \pm 14^a$

Any two means in a column within a main effect with the same superscript are not significantly different ( $P \leq .05$ ).

Table 15. Means and standard errors for plasma corticosterone (ng/ml) by generation and time of measurement

Time of measurement	Generation	
	S <sub>3</sub>	S <sub>4</sub>
Premove	-	4.4 ± 0.3 <sup>a</sup>
Postmove (1 day)	7.4 ± 0.6 <sup>a</sup>	6.7 ± 0.4 <sup>c</sup>
Postmove (7 days)	5.9 ± 0.6 <sup>a</sup>	5.8 ± 0.3 <sup>b</sup>

Any two means in a column with the same superscript are not significantly different ( $P \leq .05$ ).

Differences between lines for antibody production in response to SRBC were not significant in either generation. Although no significant differences in antibody titers were noted among movement treatments in the  $S_4$  generation ( $9.8 \pm 0.5$ , NM;  $9.7 \pm 0.5$ , SM; and  $9.9 \pm 0.4$ , PM), there were significant differences in the  $S_3$  generation. The NM group had significantly higher titers than the PM group ( $9.1 \pm 0.4$  vs  $7.0 \pm 0.4$ ), while titers for the SM treatment were intermediate ( $8.2 \pm 0.4$ ) and not significantly different from either of the other treatments. These  $S_3$  results are consistent with those of Siegel and Latimer (1975) and Gross and Siegel (1965) who observed a depletion of antibody titers when social interactions were increased and support the theory that stress (social or physical) will cause lymphoid involution (Selye, 1950) resulting in lower antibody production.

#### Leucocyte Characteristics:

None of the differences between lines for leucocyte parameters was significant except for the premovement diameter of lymphocytes where values were significantly greater for the NP ( $6.5 \pm 0.1 \mu$ ) than for the P line ( $6.2 \pm 0.1 \mu$ ). This, in turn, caused a difference when lymphocytes were expressed as  $\mu^2/\text{mm}^3$  ( $990 \pm 53$  for the NP line and  $777 \pm 50$  for the P line). Differences between movement treatments were not significant for any of the measures of either lymphocytes or heterophils.

When measured over time lymphocytes were a more sensitive assay than heterophils. The number of lymphocytes/ $\text{mm}^3$  was significantly reduced one day postmovement with evidence of recovery noted by seven days (Table 16). Also, the diameter of lymphocytes were significantly

Table 16. Means and standard errors for the times of measurement of lymphocytes and heterophils in the S<sub>3</sub> generation

Time of measurement	Lymphocytes			Heterophils			No. het. ÷ no. lymph. x 10 <sup>2</sup>
	no./mm <sup>3</sup> x 10 <sup>-2</sup>	diameter (μ)	μ <sup>2</sup> /mm <sup>3</sup> x 10 <sup>3</sup>	no./mm <sup>3</sup> x 10 <sup>-2</sup>	diameter (μ)	μ <sup>2</sup> /mm <sup>3</sup> x 10 <sup>3</sup>	
Premove	140 ± 5 <sup>c</sup>	6.3 ± 0.1 <sup>a</sup>	883 ± 39 <sup>b</sup>	61 ± 5 <sup>a</sup>	8.8 ± 0.1 <sup>a</sup>	703 ± 50 <sup>a</sup>	44 ± 5 <sup>b</sup>
Postmove (1 day)	84 ± 6 <sup>a</sup>	6.6 ± 0.1 <sup>b</sup>	640 ± 43 <sup>a</sup>	62 ± 5 <sup>a</sup>	9.0 ± 0.1 <sup>ab</sup>	824 ± 60 <sup>a</sup>	39 ± 4 <sup>b</sup>
Postmove (7 days)	109 ± 5 <sup>b</sup>	6.5 ± 0.1 <sup>ab</sup>	746 ± 41 <sup>a</sup>	66 ± 5 <sup>a</sup>	9.1 ± 0.1 <sup>b</sup>	858 ± 50 <sup>a</sup>	27 ± 2 <sup>a</sup>

Any two means in a column with the same superscript are not significantly different (P ≤ .05).

greater one day postmovement than prior to movement with the values at seven days intermediate. This general pattern was, in turn, reflected when lymphocytes were expressed as  $\mu^2/\text{mm}^3$ . These results are consistent with the reduction in lymphocytes caused by stress (Wolford and Ringer, 1962; Ben Nathan et al., 1977) and by the administration of exogenous corticoids (Dougherty et al., 1964). The reduction in lymphocytes and the increased plasma corticosterone titers observed in this experiment may be an explanation for the reduction in antibody titers noted in the  $S_3$  generation. Accordingly, the greater lag in recovery of antibody production in comparison to lymphocytes is not surprising.

#### E. coli Challenge:

There was no significant difference between lines for postchallenge social rank of the PM treatment in either the  $S_3$  or the  $S_4$  generation. Although there were high correlations between measures of postmovement social rank prior to the E. coli challenge, the correlations between those measures and postchallenge social rank were not significant ( $r = 0.26$  and  $-0.09$  in the  $S_3$  and  $S_4$  generations, respectively). This suggests that the postchallenge social rank depended upon the degree of resistance to the E. coli rather than on the prechallenge social rank.

Mortality in the  $S_3$  generation was of such a high magnitude (Table 17) that it precluded meaningful interpretations of the data. In the  $S_4$  generation there was a significant difference between lines with the incidence of air sac lesions being greater in the P than the NP line. Likewise, there was a significantly lower incidence of air sac lesions in the PM group than the NM group with the SM birds being intermediate.

Table 17. Mortality, lesions and abnormal droppings due to *E. coli* challenge, by generation, line and movement group<sup>1</sup>

	S <sub>3</sub>		S <sub>4</sub>	
	% dead + heart lesions	% dead + heart lesions	% air sac lesions	% abnormal droppings
Line				
P	75 <sup>a</sup>	41 <sup>a</sup>	87 <sup>b</sup>	35 <sup>a</sup>
NP	79 <sup>a</sup>	54 <sup>a</sup>	56 <sup>a</sup>	44 <sup>a</sup>
Movement group				
NM	81 <sup>a</sup>	42 <sup>a</sup>	93 <sup>b</sup>	33 <sup>a</sup>
SM	81 <sup>a</sup>	46 <sup>a</sup>	86 <sup>ab</sup>	57 <sup>a</sup>
PM	69 <sup>a</sup>	58 <sup>a</sup>	40 <sup>a</sup>	18 <sup>a</sup>

<sup>1</sup>Analysis was made on the actual numbers.

Any two means in a column within a main effect with the same superscript are not significantly different ( $P \leq .05$ ).

Further insights may be obtained from examination of body weight changes to the challenge with E. coli. Differences between movement groups were not significant until five days postchallenge when the SM birds lost significantly more weight than the PM ones (Table 18). Body weights for the NM females at this time were intermediate and not significantly different from the other two groups. This is in contrast with the changes in body weight observed among movement treatments prior to the E. coli challenge. It will be recalled (Table 14) that there were highly significant differences among movement groups with the weight loss being larger in the PM than in the SM treatment, and that NM pullets exhibited no loss in weight. Thus, the severity of the E. coli challenge was influenced by the prior history of the birds in that the influence of movement seven days prior to challenge aided the bird in its resistance to E. coli infection. This reasoning is in agreement with that of Gross and Colmano (1969; 1970; 1971) and Gross (1972) who found that high levels of social strife may aid in phagocytic responses and confer increased resistance to bacterial infections.

#### Summary

Adult females from the S<sub>3</sub> and the S<sub>4</sub> generations of lines which had undergone previous selection for persistence and nonpersistence of antibody production to sheep red blood cells were placed in the following situations: (1) one-third remained in the same cages they were placed in at the time of caging, (2) one-third were moved to different but essentially identical cages, and (3) one-third were paired in neutral

Table 18. Means and standard errors for change in body weight (g) of survivors post-*E. coli* challenge in the S<sub>4</sub> generation, by line and movement group

	Days post- <i>E. coli</i> challenge		
	1	3	5
<b>Line</b>			
P	-75 ± 8 <sup>a</sup>	-143 ± 26 <sup>a</sup>	-172 ± 23 <sup>a</sup>
NP	-70 ± 10 <sup>a</sup>	-107 ± 22 <sup>a</sup>	-129 ± 32 <sup>a</sup>
<b>Movement group</b>			
NM	-68 ± 11 <sup>a</sup>	-116 ± 27 <sup>a</sup>	-149 ± 32 <sup>ab</sup>
SM	-76 ± 10 <sup>a</sup>	-166 ± 22 <sup>a</sup>	-205 ± 24 <sup>a</sup>
PM	-75 ± 12 <sup>a</sup>	-90 ± 40 <sup>a</sup>	-92 ± 42 <sup>b</sup>

Any two means in a column within a main effect with the same super-script are not significantly different ( $P \leq .05$ ).

but essentially identical cages with females from the other line. Characteristics measured were: "fear", head shaking, social rank, comb size, body weight, antibody titers, plasma corticosterone levels, and the number and size of heterophils and lymphocytes. Although differences between lines were not significant for most characteristics measured, the pullets from the persistent line exhibited significantly less "fear", had smaller lymphocytes and lost less body weight when moved than those from the nonpersistent line. When comparisons were made between premovement, one-day postmovement and seven-day postmovement times, significant differences were found for plasma corticosterone levels, antibody titers, number and size of lymphocytes, and size of heterophils. Significant differences were noted among movement treatments for changes in body weight and for number of air sac lesions to an E. coli challenge. It appears that the physical and social effects on most of the traits were cumulative in both lines.

## GENERAL SYNTHESIS

This dissertation consists of four interrelated experiments designed to examine the interfacing of behavior, genetics, physiology and disease resistance in the domestic fowl. My desire was to develop a coordinated approach that would contribute to the general understanding of how chickens adjust to various husbandry practices.

I. Experiment I consisted of a survey of the variability of several traits in five diverse populations of adult chickens. Significant differences were found among the populations for "fear" (as measured by the response to humans), head shaking, body weight at three ages, percentage hen-day egg production and age at first egg. There was a temporal effect on "fear" which declined over time suggesting habituation to a husbandry procedure that consisted of maintaining the chickens singularly in wire cages. The lack of significant phenotypic correlations between "fear" and head shaking with production traits in any of the five populations is of prime consideration because it suggested that there was general behavioral adaptation to the single-bird caging environment. Caution should be exercised in drawing inferences from these data to situations where layers are maintained in colony cages.

Additional insights were obtained from Experiment IV which was designed to examine the influence of short term social and physical changes on behavioral, immunological and blood characteristics. The populations studied were two lines of White Leghorns that had been

divergently selected for persistence and nonpersistence of antibodies over time to an antigen consisting of sheep red blood cells (SRBC). The short term social and physical environmental changes consisted of (1) moving laying hens that had been maintained singularly in cages into other cages that were essentially identical (single moved) and (2) pairing females, one from each line, into neutral but identical cages (pair moved). The control consisted of females that remained in their home cages (not moved). The treatments had no short term influence on "fear" and head shaking. The social influences of pairing females in a fixed area and the physical effects of moving were cumulative as measured by loss in body weight, reductions in lymphocyte number and size, lower antibody production, and a decreased incidence of air sac lesions following an E. coli challenge. The pattern was similar for both lines.

II. The relationships of specific loci in different genetic backgrounds with husbandry practices were studied in Experiments II and III. The sex-linked dwarfing gene (dw) did not influence "fear" even when there were highly significant differences between genetic backgrounds (LW>HW). Whether or not the dw gene influenced the frequency of head shaking, antibody titers to SRBC and plasma corticosterone levels depended on the genetic background of the particular population. This was evidenced by significant line-dwarf genotype interactions. The presence of these interactions required that consideration be given to the life history of the specific population under investigation.

The history of the group was collated with the dwarf genotype and population to ascertain how these variables influence immunological responses and challenges to E. coli infection (Table 19). Although the disease histories of the B<sub>4</sub> and B<sub>5</sub> generations were different, the pattern of antibody responses to SRBC of females maintained singularly in cages was similar in that the line-dwarf genotype interactions were significant in both generations. The pattern of the interaction was that there were no differences between dwarf and normal genotypes within the LW line, while in the HW line the normal birds had higher titers than their dwarf counterparts. When comparisons of antibody responses to SRBC were made for flocks of juveniles during the period of peck-order formation (B<sub>6</sub> and B<sub>7</sub> generations), the line-dwarf genotype interaction was not significant. Chickens from the LW line had significantly higher antibody titers than those from the HW line. The effect of the dwarf locus was inconsistent between caging environments and additional experimentation will be necessary to ascertain its role.

There was an inconsistency between the B<sub>4</sub> and B<sub>5</sub> generations in the response to the E. coli challenge (Table 19). Mortality in the B<sub>4</sub> generation was greater in the LW line than in the HW line and more for normal than for dwarf females, whereas in the B<sub>5</sub> generation, the line difference was reversed and there was no influence of the dwarf alleles. A reason for the inconsistency between generations may be attributed to an E. necatrix outbreak in the B<sub>4</sub> generation LW line at about 90 days of age. The survivors of this infection were probably those most resistant to bacterial infection and, hence, had a high resistance to the E. coli challenge given later in life. To the contrary, in the B<sub>5</sub> generation

Table 19. A summary of results where sheep red blood cells and *E. coli* were administered to normal and dwarf genotypes in the HW and LW lines (Experiments II and III)

Gen.	Line	Genotype	Husbandry	Antibody to SRBC				Resistant
				Challenge	Titer	Challenge	Challenge	
B <sub>4</sub>	HW	Dw- dw-	0 to 119 days in floor pens, then moved to single bird cages; outbreak of <i>E. necatrix</i> in the LW line at about 90 days; social strife low	at 289 days after caging	Line-genotype interaction with: Dw>dw in HW line Dw=dw in LW line	294 days after caging	LW>HW dw>Dw	
	LW	Dw- dw-						
B <sub>5</sub>	HW	Dw- dw-	0 to 134 days in floor pens, then moved to single bird cages; social strife low	at 316 days after caging	Line-genotype interaction with: Dw>dw in HW line Dw=dw in LW line	321 days after caging	HW>LW Dw=dw	
	LW	Dw- dw-						
B <sub>6</sub>	HW	DwDw Dwdw dwdw	0 to 47 days in floor pens, then moved to colony cages; period of peck order formation	same day as caging	LW>HW dw>Dw>DwDw=Dwdw	5 days after caging	mortality too low to make meaningful conclusions	
	LW	DwDw Dwdw dwdw						
B <sub>7</sub>	HW	DwDw Dwdw dwdw	0 to 47 days in floor pens, then moved to colony cages; period of peck order formation	same day as caging	LW>HW DwDw=Dwdw=dwdw Dw=dw	5 days after caging	LW>HW DwDw=Dwdw=dwdw Dw=dw	
	LW	DwDw Dwdw dwdw						

where there was no history of an infectious disease, the result to the E. coli challenge was consistent with that obtained in previous experimentation with these lines (Reddy et al., 1975).

It may be appropriate to speculate on the responses observed when the E. coli challenge was given to adults maintained singularly in cages and to juveniles assembled in small flocks. The best data for such a comparison are the B<sub>5</sub> and B<sub>7</sub> generations since there was the E. necatrix outbreak in the B<sub>4</sub> generation and low mortality in the B<sub>6</sub> generation. Birds from the LW line were more resistant than those from the HW line in the B<sub>5</sub> generation while the opposite was observed in the B<sub>7</sub> generation (Table 19)--Why? First, there was a large difference in the ages of the birds at the time of E. coli challenge. The B<sub>5</sub> birds were challenged at 455 days of age (321 days after caging) while those from the B<sub>7</sub> generation birds were challenged at 52 days of age (5 days after caging). Thus, one group was challenged with E. coli after being in the single cages for a long period and the other was challenged at the time of peck order formation. Second, husbandry was different in that the B<sub>5</sub> generation chickens were maintained singularly in cages while those from the B<sub>7</sub> generation were housed as small flocks in colony cages. Siegel and Gross (1977) showed that in the HW line a moderate amount of social strife was beneficial to birds in the defense against the bacterium (Staphylococcus aureus) while in the LW line the defense against S. aureus was not readily visible. Third, there may be differences in the way chickens from the two lines perceive their environment. Individuals that perceive a particular environment to be stressful will exhibit manifestations of the GAS while animals perceiving the same environment

not to be stressful will not exhibit such manifestations. Graves and Siegel (1969) observed that chickens from the HW line were more than twice as responsive as those from the LW line in their response and approach to an imprinting stimulus indicating differences in the way they perceived their environment. Additional research is necessary to ascertain differences in perception by the chickens and the relationship between perceptiveness and resistance of infectious diseases. Fourth, the response to natural and artificial bacterial challenges may or may not be comparable. This concept has generally been ignored and needs experimental verification.

Antibody titers to SRBC were poor predictors of the responses by the chickens to E. coli challenges. This is not surprising because antibody responses and resistance to bacterial infections are, in the short term, due to two different defense mechanisms. Antibody production is dependent upon the integrity of bursa-derived lymphocytes while resistance to E. coli is dependent upon a phagocytic response. This would suggest breeding programs and husbandry practices should be geared toward obtaining a balance of the lymphoid and phagocytic components of the chicken's defense against disease. Such plasticity would be an important survival mechanism.

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## APPENDIX

Experiment I	Tables 1 and 2
Experiment II	Tables 3 and 4
Experiment III	Table 5
Experiment IV	Tables 6 to 14 and Plasma Corticosterone Assay

Appendix Table 1. Analysis of variance for "fear", percentage hen-day production, age at first egg, and body weight at 56, 168 and 266 days of age by year in five diverse populations of chickens (Experiment I)

Sources of variation	Mean squares										
	"fear" (1975)	% hen-day egg prod. (X10 <sup>-2</sup> )	age at 1st egg (X10 <sup>-2</sup> )	body weight (days of age)							
	1975	1976	1975	1975	1976	1975	1975	1976	1975	1976	
Among Lines	105**	23**	44**	17**	162**	11538**	36456**	2594**	1855**	2998**	3061**
Within Lines	6	2	2	3	5	8	243	2	2	3	4

\*\*P ≤ .05.

Appendix Table 2. Multivariate analysis of variance for "fear" and head shaking at three ages in the HWS and LWS lines of chickens in 1976<sup>1</sup> (Experiment I)

Sources of variation	Mean squares		
	"fear" (age in days)	head shaking (age in days)	
	238	279	279
	162	162	238
Among Lines	322**	527**	105.2**
	562**	7	116.0**
Within Lines	6	7	0.2
			0.3
			0.2
			0.2

<sup>1</sup>Head shaking data transformed to log 10 values prior to analysis.

\*\*P ≤ .01.

Appendix Table 3. Analysis of variance for "fear", head shaking, antibody titer to SRBC and plasma corticosterone levels in dwarf and nondwarf genotypes in the high and low weight lines in the B<sub>4</sub> and B<sub>5</sub> generations<sup>1</sup> (Experiment II)

Sources of variation	B <sub>4</sub>		B <sub>5</sub>		plasma corticosterone level
	"fear"	head shaking	antibody titer	antibody titer	
Line	27.78**	89.1**	2.6	0.6	416
Genotype	7.87**	13.8**	0.1	4.4	23
LXG	.03	3.8**	9.8*	9.0*	2417*
Error	3.91	0.3	2.0	1.6	632

<sup>1</sup>Head shaking data transformed to log 10 values prior to analysis.

\* P ≤ .05.

\*\* P ≤ .01.

Appendix Table 4. Multivariate analysis of variance for "fear" in dwarf and nondwarf genotypes in the high and low weight line in the B<sub>5</sub> generation (Experiment II)

Source of variation	df	Days after caging	
		24 to 28	160 to 164
Line	1	91.3**	51.9**
Genotype	1	4.0*	22.6**
LXG	1	0.5	2.0
Error	145	5.5	5.6

\*  $P \leq .05$ .

\*\*  $P \leq .01$ .

Appendix Table 5. Analysis of variance of antibody titers to SRBC of dwarf and nondwarf genotypes in the high and low weight lines in the B<sub>6</sub> and B<sub>7</sub> generations by sex and generation (Experiment III)

Sources of variation	Mean squares		
	Males		Females (B <sub>7</sub> )
	B <sub>6</sub>	B <sub>7</sub>	
Line	33**	62**	47**
Genotype	44**	2	2
LXG	1	2	1
Error	2	2	3

\*\* P ≤ .01.

Appendix Table 6. Analyses of variance for premovement measures of "fear", head shaking, comb size and plasma corticosterone levels in the P and NP lines by generation<sup>1</sup> (Experiment IV)

Source of variation	Mean squares				plasma corticosterone level (S <sub>4</sub> )
	"fear" S <sub>3</sub>	head shaking S <sub>3</sub>	head shaking S <sub>4</sub>	comb size (10 <sup>-5</sup> ) S <sub>4</sub>	
Between Lines	178**	0.68	1.1	6	90*
Within Lines	7	0.30	0.5	14	12
					2.6
					5.2

<sup>1</sup>Head shaking data transformed to log 10 values prior to analysis.

\* P ≤ .05.

\*\* P ≤ .01.

Appendix Table 7. Analysis of variance for postmovement measures of "fear" and head shaking in the P and NP lines by generation<sup>1</sup> (Experiment IV)

Sources of variation	Mean Squares							
	"fear"		head shaking ( $\times 10^2$ )		antibody titer to SRBC		S <sub>3</sub>	S <sub>4</sub>
	S <sub>3</sub>	S <sub>4</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>3</sub>	S <sub>4</sub>
Line	102	76	61	15	4.1	4.6		
Movement Group	6	1	6	7	18.2**	0.3		
LXG	1	3	4	46	0.2	2.1		
Error	5	3	25	45	3.3	6.3		

<sup>1</sup> Head shaking data transformed to log 10 values prior to analysis.

\*\* P  $\leq$  .01.

Appendix Table 8. Analysis of variance for postmovement measures of changes in body weight in the P and NP lines in the S<sub>3</sub> and S<sub>4</sub> generations (Experiment IV)

Source of variation	Mean squares for change in body weight (days postmovement) X10 <sup>-3</sup>		
	$\frac{S_3}{5}$	$\frac{2}{4}$	$\frac{S_4}{7}$
Line	3	0.7	4
Movement Group	13*	23.5**	86**
LXG	5	4.0	4
Error	3	2.4	3
			3.6

\* P ≤ .05.

\*\* P ≤ .01.

Appendix Table 9. Analysis of variance for premovement leucocyte characteristics in the P and NP lines in the S<sub>3</sub> generation (Experiment IV)

Sources of variation	Mean squares						
	no./mm <sup>3</sup> X10 <sup>-7</sup>	lymphocytes diameter (μ)	μ <sup>2</sup> /mm <sup>3</sup> X10 <sup>-10</sup>	no./mm <sup>3</sup> X10 <sup>-6</sup>	heterophils diameter (μ)	μ <sup>2</sup> /mm <sup>3</sup> X10 <sup>-11</sup>	no. het. ÷ no. lymph X10 <sup>-2</sup>
Between Lines	4	1.6*	54**	15	0.9	0.7	8
Within Lines	1	0.4	6	13	0.5	12.0	4

\* P < .05.

\*\* P < .01.

Appendix Table 10. Multivariate analysis of variance for postmovement lymphocyte characteristics in the P and NP lines in the S<sub>3</sub> generation (Experiment IV)

Source of variation	Mean squares for lymphocyte characteristics (days postmovement)					
	no./mm <sup>3</sup> X10 <sup>-6</sup>	diameter (μ)	μ <sup>2</sup> /mm <sup>3</sup> X10 <sup>-10</sup>			
	7	7	7	7		
Line	48	3	0.02	0.54	14	11
Movement Group	49	14	0.12	0.48	2	12
LXG	6	24	0.32	1.18*	1	27*
Error	14	11	0.14	0.30	9	7

\* P ≤ .05.

Appendix Table 11. Multivariate analysis of variance for postmovement heterophil characteristics and no. heterophils ÷ no. lymphocytes in the P and NP lines in the S<sub>3</sub> generation (Experiment IV)

Source of variation	Mean squares						
	heterophil characteristics (days postmovement)		heterophil characteristics (days postmovement)		no. het. ÷ no. lymph X10 <sup>-2</sup>		
	no./mm <sup>3</sup> X10 <sup>-5</sup>	diameter (μ)	μ <sup>2</sup> /mm <sup>3</sup> X10 <sup>10</sup>	μ <sup>2</sup> /mm <sup>3</sup> X10 <sup>10</sup>			
	7	7	7	7	7	7	
Line	3	47	0.51	0.31	0.7	0.02	0.02
Movement Group	46	253	0.05	0.65	31.0	0.03	0.04
LXG	164	160	0.46	0.56	26.0	0.02	0.01
Error	143	91	0.22	0.65	16.4	0.03	0.01

Appendix Table 12. Means and standard errors for measures of lymphocytes and heterophils, by line in the S<sub>3</sub> generation (Experiment IV)

Trait	Measure	Treatment <sup>a</sup>	Line		Diff.
			Persistent	Nonpersistent	
Lymphocytes A	no./mm <sup>3</sup> X10 <sup>-2</sup>	I	131 ± 7	149 ± 8	-17
		II	74 ± 7	94 ± 9	-20
		III	113 ± 7	107 ± 7	6
B	diameter (μ)	I	6.2 ± 0.1	6.5 ± 0.1	-0.3*
		II	6.6 ± 0.1	6.6 ± 0.1	0
		III	6.6 ± 0.1	6.4 ± 0.1	0.2
C	μ <sup>2</sup> /mm <sup>3</sup> X10 <sup>-3</sup>	I	777 ± 50	990 ± 53	-213**
		II	586 ± 54	694 ± 65	-108
		III	795 ± 59	698 ± 58	97
Heterophils D	no./mm <sup>3</sup> X10 <sup>-2</sup>	I	66 ± 8	55 ± 6	11
		II	61 ± 9	63 ± 6	-2
		III	69 ± 8	63 ± 5	6
E	diameter (μ)	I	8.6 ± 0.1	8.9 ± 0.2	-0.3
		II	8.9 ± 0.1	9.1 ± 0.1	-0.2
		III	9.1 ± 0.1	9.2 ± 0.2	-0.1
F	μ <sup>2</sup> /mm <sup>3</sup> X10 <sup>-3</sup>	I	742 ± 61	664 ± 79	78
		II	812 ± 90	836 ± 80	-24
		III	884 ± 73	831 ± 70	53
Het:lymph	(D:A) X10 <sup>2</sup>	I	51 ± 5	37 ± 3	14
		II	89 ± 4	66 ± 3	23
		III	61 ± 3	88 ± 2	3

<sup>a</sup>I = premovement measures; II and III = measures obtained 1 and 7 days postmovement, respectively.

\* P ≤ .05.

\*\* P ≤ .01.

Appendix Table 13. Analysis of variance for times of measurement for leucocyte characteristics and plasma corticosterone levels by generation (Experiment IV)

Source of variation	Mean squares								
	lymphocytes no./mm <sup>3</sup> X10 <sup>-8</sup>	lymphocytes diameter ( $\mu$ )	$\mu^2$ /mm <sup>3</sup> X10 <sup>-10</sup>	no./mm <sup>2</sup> X10 <sup>-6</sup>	heterophils diameter ( $\mu$ )	$\mu^2$ /mm <sup>2</sup> X10 <sup>-10</sup>	(S <sub>2</sub> )no. het ÷ no. lymph X10 <sup>-2</sup>	S <sub>3</sub> plasma corticosterone titer	S <sub>4</sub> plasma corticosterone titer
Among Times	4**	0.99*	72**	6	1.5*	63	14**	52	217**
Within Times	1	0.30	8	12	0.5	14	3	16	8

\* P ≤ .05.

\*\* P ≤ .01.

Appendix Table 14. Analysis of variance for changes in body weight postchallenge with E. coli in the P and NP lines in the S<sub>4</sub> generation (Experiment IV)

Source of variation	Mean squares for changes in body weight (days postchallenge)X10 <sup>-2</sup>		
	1	3	5
Line	5	150	127
Movement Group	5	232	367
LXG	41	76	200
Error	28	140	134

## Appendix (Experiment IV)

## PLASMA CORTICOSTRONE ASSAY

- I. Corticosterone Standards
  - A. Dissolve nonradioactive corticosterone in small amount of benzene
  - B. Dilute with 95% ethanol so that the following amounts can be put in test tubes--0, 0.1, 0.3, 1, 2, and 4 nanograms
  - C. Dissolve off the benzene and ethanol
  
- II. Protein precipitation from samples
  - A. Put 0.1 ml aliquots of plasma samples into small test tubes
  - B. Add 2 ml of 95% ethanol
  - C. Vortex 10 seconds
  - D. Centrifuge on desk top centrifuge for 5 minutes
  - E. Pour off supernatant into new test tubes (discard old ones)
  - F. Evaporate off the ethanol
  
- III. Addition of  $^3\text{H}$ -corticosterone, competitive binding protein, and scintillation
  - A. Add 1 ml of the following solution to each test tube:  
4 micro Ci  $^3\text{H}$ -corticosterone/100 ml of double distilled  $\text{H}_2\text{O}$  + 1 ml of the competitive binding protein (see pages 25 and 48 of this dissertation)
  - B. Vortex for 10 seconds
  - C.  $45^\circ\text{C}$  water bath for 5 minutes
  - D. Ice bath for 10 minutes
  - E. While still in ice bath, add 40 mg of activated floracil (very critical to place exactly same amount in each tube; can use a spatula which will hold a constant volume)
  - F. Vortex for 30 seconds
  - G. Take out 0.7 ml and put in scintillation vials
  - H. Add 10 ml of scintillation fluid
  - I. Scintillate
  - J. Multiply counts by 10 because 0.1 ml aliquots were taken from samples
  - K. Put standard data on a log scale
  - L. Data from samples should fit this log curve

## VITA

Joseph M. Mauldin, son of Mr. and Mrs. L. E. Mauldin, Jr., was born on a farm in Jones County, Mississippi. During his boyhood years there was activity in youth groups including a 4-H poultry judging team and the Boy Scouts where he achieved the rank of Eagle. He entered Mississippi State University in September, 1966 and received a B.S. degree in Poultry Science in August, 1970.

After teaching science in the public schools in Moss Point, Mississippi and spending six months on active duty in the Medical Training Corps in the army at Fort Sam Houston, Texas, he entered the Graduate School at Mississippi State University. Upon receipt of the M.S. degree in Animal Physiology under the direction of Dr. Bruce Glick in December, 1973, he accepted employment in the school of Pharmacy at the University of Mississippi. Responsibilities included the biological screening of potential human drugs on laboratory animals. In August, 1975, he entered the Graduate School at Virginia Polytechnic Institute and State University and is a candidate for the Ph.D. degree in Genetics.

Joe has been involved with many club activities since the beginning of his undergraduate training. He participated in Poultry Science Club activities in Mississippi and Virginia. In Mississippi he was active in CLEAN (Committee for Leaving the Environment of America Natural), was the President of the Choctaw group of the Sierra Club, and was on the Board of the Mississippi Conservation Council. The recipient

of the Quarles Memorial Scholarship in 1976, his membership in professional and honor societies include: Gamma Sigma Delta, Sigma Xi, Poultry Science Association, Animal Behavior Society, A.A.A.S., Genetics Society of America and the Virginia Poultry Federation.

The author is married to Nancy Musgrove of Jones County, Mississippi.

*Joseph M. Mauldin*

# GENETICS, BEHAVIOR AND DISEASE RESISTANCE IN CHICKENS

by

Joseph M. Mauldin

(ABSTRACT)

This dissertation consists of a series of four experiments designed to examine the interfacing of behavior, genetics, physiology and disease resistance in the domestic fowl. The principle objective was to obtain insights into the mechanisms involved in the responses of the domestic chicken to various husbandry situations. A second objective was to determine the degree of generalization of inferences which could be made to various populations of chickens that had different genetic backgrounds.

Differences were found among various lines for "fear", head shaking, body weight and reproductive traits. In all cases the association of "fear" with head shaking was of a low magnitude and neither behavior had, on a within line basis, a significant relationship with growth and reproductive traits. A temporal effect which declined over time was noted for "fear" of humans by females maintained individually in cages suggesting habituation to such a husbandry situation.

The effect of the sex-linked gene for dwarfing on the frequency of head shaking, antibody titers to sheep red blood cells, and plasma corticosterone levels was influenced by the genetic background of the population studied. Line differences were observed for the degree of

mortality, lesions, and abnormal droppings in response to a challenge with E. coli. The disease and social history of the populations would, however, mask differences due to the particular genome of the population studied. Therefore, the response of a population of chickens to E. coli depends upon its genetic background, previous history, and the current husbandry situation. The stability of the social hierarchy after an E. coli challenge was influenced more by the degree of resistance of the individual to infection than by social inertia.

The influence of short-term physical and social environmental changes were cumulative for traits such as antibody production, plasma corticosterone levels, plus changes in body weight, lymphocytes and heterophils. Lymphocytes were more responsive to the short term changes than heterophils. It appears from the data that "fear" and head shaking behaviors are vehicles by which chickens adapt to long term environmental changes, but are not used for short term adaptations.

The data demonstrate specific relationships among the genome and mechanisms involved in the response of chickens to various husbandry situations. This implies that the adaptiveness of populations to various husbandry practices is greatly influenced by the genetic background of the specific population. The plasticity of populations, however, suggests that selection for various husbandry situations is feasible.