CORRELATED RESPONSES RESULTING FROM SELECTION FOR SOCIAL AGGRESSIVENESS IN THE DOMESTIC CHICKEN

by

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B. S., Kansas State University, 1959

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Poultry Science

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1962

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INTRODUCTION

Schjelderup-Ebbe's initial observations (1922, 1923, 1924, 1935) on the social hierarchy in chickens established the peck-order as the basis of group behavior in adult birds. His findings have since been verified by a number of observers. Sanctuary (1932) studied the order of dominance in chickens and related it to certain physiological traits (items of productivity). Masure and Allee (1934) studied the social hierarchy in domestic fowl and compared it to that found in pigeons. Guhl (1953) found evidence of the peck-order when working with a flock of 96 White Plymouth Rock hens, although he was not able to observe all possible relationships. Both Guhl (1953) and Wood-Gush (1955) have published comprehensive reviews of social behavior in the domestic fowl.

This social hierarchy, or peck-order, indicates that levels of aggressiveness vary among individuals. Techniques for the measurement of aggressiveness have been developed by Collias (1943), Guhl (1953, 1960), McBride (1958), and Siegel (1960). Collias (1943) was one of the early workers to use the pair-contest method of evaluation in which initial encounters are staged between pairs of chickens.

The purpose of this investigation was to examine possible genetic relationships between levels of aggressiveness, as produced by selection for high and low strains utilizing the pair-contest method, and certain seconday traits. These secondary traits, i.e., traits not under direct selection, were measured to determine if they would show significant changes as the selected strains diverged for levels of aggressiveness. The secondary traits measured were sexual behavior of males and females, semen volume and concentration, age at sexual maturity of the females, hen-day percentage egg production, and body weights of both sexes at 5 and 8 months of age.

REVIEW OF LITERATURE

Schjelderup-Ebbe (1922) studied groups of 2 to 25 and 25 to 100 chickens. He observed a peck-order or hierarchical relationship among the birds which was generally linear in groups of 10 hens or less, but which became more complex in numbers above 10. Masure and Allee (1934) were able to verify these observations and extend them to other species of birds (pigeons). Guhl (1953) discussed the formation of peck-orders and presented evidence of the social hierarchy from his studies of White Plymouth Rock pullets.

Schjelderup-Ebbe (1922, 1935) pointed out that the results of encounters between hens were not always determined by either aggression or strength. If one bird was afraid, there was no fight and the other bird was the victor. When both were frightened, the first to overcome its fear would be dominant. He also noted that the physiological state of the bird can affect the outcome of the encounter. Thus, a tired bird might lose an encounter it would normally win. He found that birds on strange territory were less pugnacious than birds on their home territory and a bird on its home ground had greater prospects of winning an encounter with a stranger.

Collias (1943) analyzed statistically the factors which lead to success in initial encounters. He controlled the variables of sex, territory, and numbers present by using two strange hens, one each from two flocks of White Leghorn females, which were placed into a neutral pen where they would settle their dominance relationship. Collias measured the size of each bird's comb, using it as an indicator of the amount of male hormone present. The weight of the bird gave an indication of general health. Its rank in its home flock was used as an indicator of possible success in initial encounters. Collias also compared the state of molt of loser and winner. He used the path-coefficient method to correlate these measured factors with the bird's success in the initial encounters. Their order of importance was found to be: absence of molt, comb size, social rank, and weight. The author pointed out that other factors were involved in his results in addition to those studied. He suggested that these might be experience in winning or losing, fighting skill, wildness, and others. Guhl and Ortman (1953) found the possession of a large comb to have psychological value in paired contests. Three pullets, which had been less successful in paired contests with eight other pullets, were given large dummy combs and, after suitable isolation, were allowed to meet the other pullets. They won more encounters than they had previously and were generally avoided by the other pullets. After another suitable period of isolation, the same pullets were paired again. The false combs were removed and the three pullets reverted to their previous dominance positions. Guhl (1953) hypothesized that under range conditions the peck-order is probably less stable as birds may fail to recognize one another when contact is less frequent.

The effects of social status on feeding, roosting, and other privileges in flocks of chickens have been recognized by Masure and Allee (1934), Collias (1944), and Guhl (1953). Sanctuary (1932) found that the individuals in the upper half of the peck-order laid more eggs than did those composing the lower social level. Generally, higher ranking individuals had precedence at food dispensers, roosts, nests, etc., and had greater freedom of movement within the flock. Guhl and Allee (1944) compared well-integrated flocks with an established hierarchy to flocks undergoing constant reorganization. The measurements used for the comparisons included the amount of pecking, food consumption, body weight, rate of egg production, and social status. They found that organized flocks pecked less than experimental flocks, food consumption was higher in the organized groups, and the organized groups produced more eggs than the experimental groups. When feeding was restricted, the organized groups maintained body weight better than the experimental groups. Tindell and Craig (1959) found significant correlations between social status within flocks and certain quantitative traits within strains and flocks, i.e., hens high in the social order tended to be heavier at five months of age, gained less thereafter, fed more often, matured earlier, and had higher egg production rates for the first four months. McBride (1958) also confirmed these results for pullets in organized flocks but he could find no apparent relationship between aggressiveness scores and egg production for pullets kept in individual cages.

The effects of social rank of sexual behavior have been investigated by Guhl, Collias, and Allee (1945). They tested four males singly and successively with the same group of hens and after several weeks placed all the males into the pen simultaneously for further observations. Data were collected to determine the frequencies of courting, crouching, treading, and avoidance of the male by the females. The variations observed when the males were tested singly showed no direct relationship to the social position of the cocks, nor did the rate of a given male in one category of behavior necessarily reflect his rate in another type of behavior. When the four males were placed together in the pen of hens and permitted to remain there, there was considerable interaction among the cocks. They found that the dominant cock did most of the mating and prevented the others from mating, although he might be tolerant to a certain inferior. Guhl and Warren (1946) continued this study to determine whether there was any relation between the social position of a cock and the number of offspring sired. They found that the dominant cock in each of two experimental groups sired the most chickens. Guhl (1949) formed two heterosexual experimental flocks, each consisting of one cock, several capons, and several hens. The normal males dominated the capons who, with few exceptions, dominated the hens. Most of the treading was done by the normal males and the more masculine capons. Later, two of the inferior capons were given estrogen injections to increase their sexual activity but not their aggressiveness. After this treatment, they trod and courted at relatively high rates, but mostly with socially inferior females. Superior hens often repulsed the small-combed capons when they tried to mate, and Guhl concluded that, although a male may mate with superior females, social dominance of the male facilitates mating. Guhl (1950) further investigated the influence of high social rank upon the receptivity of the hen. He found that high-ranking hens crouched less than the lower- and middle-ranking hens, although hens showing relatively high and low receptivity were found at all levels of the dominance orders. He then subdivided each flock into three levels of dominance and separated the three sub-flocks. The same males were used and rotated between the sub-flocks. The high ranking hens now crouched more frequently than, or approximately as much as, the hens forming the lowest level. In two of the subflocks, the middle- and low-ranking hens crouched less after sub-flocking than before. These results showed that hens, like cocks, differed in their sexual activity and that psychological factors resulting from the males present, and their own social rank, influenced their sexual activity. Grosse and Craig (1960) in their study of sexual maturity found that young males placed with older females, beginning at 11 weeks of age, were socially dominated by the females in many cases, and appeared to be suppressed in their display of sexual aggressiveness. Social dominance effects within pairs of males, kept together, suggested that socially-dominated males were later in sexual maturity than males socially superior to them. Guhl (1960) pointed out that the display of sexual behavior is influenced by social dominance among males and social dominance between the sexes and that successful matings are most frequent when the sexes are acquainted.

Upp (1928), and Parker, McKenzie, and Kempster (1940) reported that the maximum number of copulations took place in the afternoon. Guhl (1951) noted that males varied in the frequency at which they courted, in their ability to elicit the sexual crouch in hens, and in the rates at which they trod the females. These differences were substantiated by Wood-Gush and Osborne (1956) who described frequency of matings as well as courting behavior of males in measuring sex drive. Guhl (1953) reported that, in mating trials, females tended to become progressively satiated with each successive male tested. McDaniel (1960) found that eight males could be tested in a pen of 30 females during an afternoon without affecting either the frequency of crouching of the females or the frequency at which a male mates, i.e., sexual activity was not confounded with order of testing. McDaniel and Craig (1959) found significant and highly significant associations between social aggressiveness scores, sexual effectiveness scores, and crouches elicited from females.

Since Collias' (1943) early work with the use of paired contests as the criterion of measurement for aggressiveness, many workers have studied this problem. Guhl (1953) pointed out that in flocks of more than 30 birds the measuring of aggressiveness by peck-order rank may not necessarily reflect the full potentialities of the individual chickens. Where information is desired for a moderate number of birds, different estimates of relative aggressiveness may be necessary.

McBride (1958) described a method for measuring relative aggressiveness which involved the use of standard panels of test birds. Panels consisted of teams of hens against which the females under evaluation were tested. Since previous experience and age are important in determining the outcome of initial-paired encounters (Guhl, 1953), the possibility of conditioning effects on the birds in the panel might make this method unsuitable for testing large numbers of chickens unless many panels were used. Guhl (1960) noted that, although ranks in a peck-order might reflect levels of aggressiveness, encounters between unacquainted birds by pairs offered more reliable results and might be less time-consuming. He discussed the advantages and disadvantages of four methods involving contests (1) between birds kept in individual cages, (2) between members of different flocks, (3) between members of a team and birds to be tested, and (4) between a limited number of randomly selected individuals maintained in cages or in pens. Siegel (1960) used a technique involving two flocks. Flock A consisted of 20 cockerels and Flock B was composed of 18 cockerels. Dominance ranks were determined among members of each flock by engaging all cockerels in each flock in initial-paired contests with all other members of its respective flock as described by Guhl (1953). Members from Flock A were then engaged in initial-paired encounters with males from another flock of 20 cockerels. Similarly, males in Flock B were engaged in initial-paired contests with cockerels from still another flock which consisted of 18 cockerels. Coefficients of correlation were calculated between the number of initial-paired encounters won against cockerels in the other flock, and the dominance rank of a male as determined by initial-paired encounters within his home flock. The purpose of this was to determine the number of initial-paired encounters necessary to provide a reliable estimate of a cockerel's relative aggressiveness. In both Flocks A and B, the magnitude of the coefficient of correlation increased with the number of times a cockerel was tested. Correlations for a 2-male test (two initial-paired encounters) were highly significant in Flock A and significant in Flock B. Highly significant correlations were obtained in both flocks for 4-, 6-, and 8-male tests. The high correlation obtained from the 8-male test in both flocks (.95 and .87, respectively) and the small increase in the correlation coefficient between 6- and 8-male tests led Siegel to conclude that eight initial-paired encounters were sufficient to accurately measure the relative aggressiveness of a cockerel. These results agreed with Collias (1943) who found statistically significant correlations to exist between (1) number of birds pecked in the ontogenetic peck-order and the number of contests won in the first series of pair-contests, (2) between the two sets of paired encounters, and (3) between the second set of pair-encounters and the final peck-order. It further substantiated the investigations of Guhl (1953) who found the correlations between four sets of data (percent pecked in sub-flocks, percent of interflock contests won, percent of initial encounters won during isolations, and percent pecked in the reassembled flock) to be statistically significant at the 1 percent level and to range between +0.77 and +0.98.

The extent to which aggressiveness is inherited has not been as thoroughly investigated as have some of the other aspects of social behavior. Most of the work has been done in the last few years and results are suggestive but still inconclusive. Guhl and Eaton (1948), and Eaton (1949) carried a selection experiment for aggressiveness and non-aggressiveness to the F_4 generation but only the F_3 generation suggested a genetic background for aggressiveness. Komai, Craig, and Wearden (1959) used observations of the social status of daughters and dams within six strains of four breeds to estimate heritability for social aggressiveness in the domestic chicken. Social aggressiveness appeared to be genetically variable enough within strains (mean heritability estimates of 0.30 and 0.34) to allow effective selection. The social standing of six strains observed in intermingled flocks had a high repeatability (0.857) which also indicated that differences in aggressiveness among the strains were largely determined by hereditary differences. Siegel (1960) obtained a heritability estimate of 0.57 for relative aggressiveness. He pointed out that his estimate, while higher than that reported by Komai, Craig, and Wearden, was well within the confidence limits given for their estimate. Guhl, Craig, and Mueller (1960) conducted a selection experiment for high and low levels of aggressiveness based on the results of initial-paired encounters as a measure of relative aggressiveness. Ranks in the peck-order were used as supporting evidence for relative aggressiveness. Two different strains of White Leghorns were used in a one-way cross in the parental generation to reduce excessive inbreeding, and selection was carried to the F_4 generation. Beginning with the F_2 generation, the two lines showed significant differences in the percentage of encounters won or lost, as well as in high or low ranks in the peck-orders. Heritability estimates of 0.22 and 0.18 were obtained when based on the percentages of contests won and individuals dominated, respectively.

MATERIAL AND METHODS

Genetic Stocks Used

Generation 0. The foundation stocks of the strains used in this study were NC-47 Regional Cornell Randombred White Leghorns (see King, Carson, and Doolittle, 1959), and NC-47 Regional Randombred Rhode Island Reds obtained from the NC-47 Regional Poultry Breeding Laboratory located at Purdue University. Eggs were received from the laboratory in January, 1958, and hatched on February 12, 1958. All birds were wing-banded at hatching and intranasally vaccinated for bronchitis and Newcastle disease. They were reared in battery brooders until 3 weeks of age and then moved to brooding pens. At 8 weeks of age they were vaccinated for fowl pox and Newcastle by the wing-web method. Males and females were separated and confinement-reared until approximately 6 months of age. Males were then leg-banded and randomly assigned to individual cages in a mating house. A wire pen approximately 4' by 4' was constructed for holding initial-pair contests. This pen was placed in a small isolated room in a corner of the mating house where the cocks could be placed to settle their dominance relationships free from other distractions. Each bird met 10 other birds of the same breed in initial-pair contests, but no two birds met more than once. Furthermore, contests were arranged so that no bird was engaged in succeeding contests until an interval of at least 4 hours had elapsed. All birds were allowed 2 weeks in their individual cages before the contests started so that birds would no longer recognize former penmates (Schjelderup-Ebbe, 1935). Ten initial-pair contests were used to establish the relative ability of a bird to dominate other individuals. This ability to dominate others is termed "aggressiveness" in this study.

Generation 1. Seven of the most and seven of the least aggressive individuals from generation 0 were used as sires to produce high and low aggressiveness strains within each of the two breeds. Each male represented a different sire family and females within strains were assigned to males randomly, with the restriction that no relatives would be mated, i.e., inbreeding was avoided. Sires used to produce unselected controls were randomly selected with the single restriction that they be able to produce enough semen to inseminate five females (.30 cc.). The progeny of these sires represented the first selected generation. Approximately 2,000 of these generation 1 chicks were hatched on January 3 and January 10, 1959. Chicks were handled in the same way as those in generation 0, except that all birds were dubbed at hatching and dewattled at 4 weeks of age to avoid possible injuries when caged, and males and females were reared together within breeds. First-selected-generation males were caged in June, 1959. Approximately 70 males of each strain were tested in 10 initial-pair contests against randombred controls of their own breed to provide data for further selection. Testing procedures were the same as those used for generation 0. From these generation 1 males, seven sires, representing different families from the high and low strains within each breed, were used to produce the second selected generation. Again, females within strains were assigned to males, but no relatives were mated in order to avoid inbreeding.

Generation 2. On January 5, 1960, 1,945 birds were hatched from the four selected strains, plus controls. The controls for this year were procured from the same NC-47 White Leghorn and Rhode Island Red randombred populations sampled for foundation stocks in generation 0. These generation 2 males were handled in the same way as the generation 1 males, described previously. The males were caged in June, 1960. All males were tested against controls to establish the relative dominance of high and low strains, but only six initial-pair contests were used for this purpose. In addition, all high and low strain males were tested in 10 initial-pair contests on a within-strain basis, i.e., highs versus highs, etc., in order to intensify selection for the proposed third selected generation.

Correlated Responses

Characteristics (other than sexual behavior - see below) measured for indications of possible correlated responses included body weights of both sexes at 5 and 8 months of age; age at sexual maturity and hen-day percentage egg production of females; and semen volume and concentration of males. Body weights were taken to the nearest 0.1 pound. Age at production of the first egg was used as the criterion of age at sexual maturity of females. The females were trapnested 3 days per week and the number of eggs laid on trap-days was divided by the total number of trap-days from the first egg to 265 days of age. This was the criterion for hen-day percentage egg production. All males of the first and second selected generations were artificially ejaculated in June, 1959, and June, 1960, respectively, at approximately 5½ months of age. Each male was given two preliminary or "conditioning" ejaculations and then two more ejaculations where semen was collected, volume measured, and concentration recorded. Volume was measured to the nearest 0.01 cc. and the means presented are based on the sum of the last two readings, i.e., the third and fourth ejaculations. Parker, McKenzie, and Kempster (1942) have shown that semen varies in appearance; semen that is viscous and white has a high spermatozoa concentration, while semen that has a watery appearance is low in spermatozoa concentration. McDaniel and Craig (1959) have devised the following scoring system for the rating of semen appearance: watery or clear, 0; watery with white streaks, 1; medium, 2; thick white, 3; very viscous and chalk-white, 4. These same observers obtained a highly significant correlation (0.76) between concentration as determined by one individual with the aid of a hemocytometer, and appearance scores as assigned independently by the other observer. The same scoring system was used in this investigation by the observer in assigning scores to semen concentration.

Sexual Behavior

The tester females used in the first year of this investigation were housed during the month of May, 1959. The females were progeny of the selected breeders from generation 0 of the aggressiveness selection experiment (see previous discussion). Twenty-four females were housed in each of six pens, approximately 12' by 12'. Breeds were alternated by pen, i.e., pens 1, 3, and 5 had White Leghorn females; pens 2, 4, and 6 had Rhode Island Red females. Each pen contained eight high, eight low, and eight control females.

The males to be tested with these females were also progeny of generation 0 sires. Seventy-two males were tested, consisting of 12 highs, 12 lows and 12 controls of each breed. Thus, both males and females were unselected progeny of high, low, and control aggressiveness strains derived from the same stock, within breeds.

Guhl and Warren (1946) had noted that one of the factors responible for the rate at which males mate was experience in the mating act (see McDaniel and Craig, 1959, and Guhl, 1961 for later studies of this problem). The males in the 1959 test had been reared with females of their own breed until they were caged at approximately 5½ months of age in June. These tests for sexual behavior took place in late August and early September, 1959. The males had thus been isolated from females for approximately 3 months, therefore each male was allowed to run with the females he was to be tested with for one 24-hour "conditioning" period. After the conditioning period, the males were caged individually and held for a 3-day period, prior to testing, on the floor within the pen of females with which they were to be tested. Thus the males and females were partially isolated but visible to each other, also sharing the trough-type waterers which were attached to the male cages. During the observation periods, sacks were placed over and around the cages so that the males being tested could not see the remaining males.

Sexual effectiveness scores, as used in this study, followed essentially the method used by McDaniel and Craig (1959). That is, they included such behavior patterns as the ability of the male to tread and to follow through in the act of mating. Responsiveness or receptivity of the females, as demonstrated by sexual crouching and completed matings, was also recorded. Sexual effectiveness observations were carried out during afternoons. The observations involved the releasing of one male at a time and the recording of the number of crouches elicited and number of matings completed in a 10-minute period. Four such observations were given each male on 4 different days and the periods for each were randomized so that no male would be tested twice within the same hour of the afternoon. Rhode Island Red males were always tested with females of their own breed and White Leghorns were tested only with White Leghorn females.

The number of males tested per pen in any one afternoon was limited to six to avoid possible confounding of the results because of sexual satiation of the tester females (see Guhl, 1953 and McDaniel, 1960). Sexual effectiveness scores for the males were then calculated as the total number of completed matings in four 10-minute observation periods. Sexual receptivity of the females was first estimated by the total number of crouches displayed by a female during the complete test period, and secondly, by the total completed matings participated in by the female during the complete test period. All females were exposed to the same number of males for the same periods of time during the course of the entire experiment.

The second year of sexual behavior observations on generation 2 individuals utilized the progeny of the first-selected-generation high and low strains and controls obtained from the NC-47 Regional Laboratory, and was carried out during the late summer of 1960. The second year observations on sexual behavior followed the same pattern as used in the first year, except for the number of males tested (96) and a change in the conditioning period. Since all males in both years of the study had been individually caged and isolated from females for approximately 3 months prior to testing, the decision had been made in the first year of this experiment to give them a 24-hour conditioning period with females. This was to insure that each male had some mating experience before testing. However, at the conclusion of the first year (1959) of the experiment, doubts arose as to the efficacy of a 24-hour period. A 6-week experiment (unpublished data) led to the conclusion that a

1-week conditioning period would lead to more nearly optimum observations on a male's sexual effectiveness. Therefore, all males in the second year of this experiment were given a 1-week conditioning period rather than the 24-hour conditioning period of the first year of the experiment.

Statistical Analyses

In the analyses of variance of the traits 5- and 8-month weights, semen volume and concentration, age at sexual maturity, and hen-day percentage egg production, account had to be taken of the disproportionate subclass numbers. Furthermore, since one of the error terms was sire family variation and sire family differences were to be tested, the control data could not be used because the controls were non-pedigreed birds. The decision was made to use the approximate method of disproportionate subclass numbers in an R x C table as outlined in Snedecor (1956: page 385). Snedecor pointed out that if the subclass numbers were only slightly unequal, especially if they were fairly large (10 or more), this approximation to the method of fitting constants was very close. The data met these criteria. Thus, the analyses of variance of the traits listed above are all based on an analysis by the approximate method of unweighted means. The individual source of variation, of course, was based on individual observations, not means. In order to transform this source of variation so that it could be used as an error term, the sum of squares was adjusted by using the harmonic mean. This was the reciprocal of the mean of the reciprocals of the lowest subclass numbers, i.e., of the sire families. After calculation of the harmonic mean, this value was used to divide the individual sums of squares to transform them to an essentially equivalent basis with the other sources of variation.

The two tables which follow show the general analysis of variance for the traits restricted to one sex (semen volume, semen concentration, age at sexual maturity for females, and hen-day percentage egg production) and the traits common to both sexes (5- and 8-month weights). The error or test term for each source of variation (Wearden, 1961) is presented. The controls used in this investigation were from unpedigreed, randombred populations. Thus, the analyses of variance of the various traits deal only with the high and low selected strains.

In order to determine if the high and low strains were diverging from the controls, the least significant difference (LSD) test for comparison among means was used (Snedecor, 1956, page 251).

The general formula for the computation of the LSD is:

$$LSD = t_{(.05)(2)}\sqrt{\frac{2\ EMS}{n}}$$

where EMS is the Stain: Breed error term, i.e., the G x S: B mean square in the original analysis of variance, and n equals the number of sub-classes in the Strain: Breed sum of squares.

In the analyses of variance of the sexual behavior traits, the Kruskal-Wallis one-way analysis of variance, as outlined by Siegel (1956), was used. This analysis makes no assumption of normality. The general formula for the H-statistic of the Kruskal-Wallis

General Analysis of Variance for Traits Restricted to One Sex.

Source	d.f.	Test Term
Breeds (B)	1	S: B
Strains: Breeds (S: B)	2	G x S: B
Generations (G)	1	G x S: B
G x B	1	G x S: B
G x S: B	2	Sires: G and S
Sires: G and S	40	Individuals
Individuals: Sires, S, B, G	$\Sigma(n_i-1)$	

General Analysis of Variance for Traits Common to Both Sexes.

Source	d.f.	Test Term
Breeds (B)	1	S: B
Strains: Breeds (S: B)	2	G x S: B
Generations (G)	1	G x S: B
G x B	1	G x S: B
G x S: B	2	Sires: G and S
Sires: G and S	40	SX x Sires: G and S: B
Sexes (SX)	1	SX x S: B
SX x B	1	SX x S: B
SX x S: B	2	SX x Sires: G and S: B
SX x G	1	SX x G and S: B
SX x G x B	1	SX x G and S: B
SX x G x S: B	2	SX x Sires: G and S: B
SX x Sires: G and S: B	40	Individuals
Individuals: Sires, S, B, G, SX	$\Sigma(n_i-1)$	

analysis of variance is:

$$H = \frac{12}{N(N+1)} \sum_{j=1}^{k} \frac{(R_j)^2}{n_j} - 3(N+1)$$

where k = number of samples

n_j = number of cases in j^{th} sample

$N = \sum n_j$; the number of cases in all samples combined

R_j = sum of ranks in j^{th} sample

$\sum_{j=1}^{k}$ = sum over the k samples

The H-statistic is distributed as chi-square with the degree of freedom equal to k - 1.

RESULTS

Selection for Aggressiveness and Non-Aggressiveness

Three selected generations have now been produced and tested against samples of the random bred populations from which they were derived. First-selected-generation males were all tested against random bred controls to provide data for further selection. Second- and third-selected-generation males were sampled and tested against controls to establish the relative dominance of high and low strains, but were tested also on a within-strain basis to provide information for further selection. For selection purposes, about 70 males of each strain are tested each generation and 10-15 percent of the most extreme individuals (either high or low, depending on the strain) are selected to sire the following generation.

Results obtained from initial-pair contests of selected strains versus unselected controls are presented in Table 1 (Craig, 1961). Although statistical analyses have not been completed on the data, the following observations might tentatively be made:

(a) Genetic variation exists for social aggressiveness within the two populations sampled.

(b) The high and low strains are different, not only in ability to dominate unselected controls, but also in the frequency with which social interactions are evoked in initial-pair contests. This is evident in encounters between selected strain and control individuals, but is even more strikingly apparent in intra-strain pair encounters, particularly for the Rhode Island Red strains (84.2% versus 56.7% contests resulting in social interactions for the high and low strain F_2 males, respectively).

Correlated Responses

Semen Volume. The analysis of variance for semen volume of the high and low strains is presented in Table 2. Semen volume readings represent the total volume produced in two artificial ejaculations after each male has had two conditioning ejaculations. The analysis shows a significant sire family difference, indicating that genetic variation is present. The analysis showed no breed difference and no strain differences, although the strains within breeds mean square approached significance. Upon partitioning the latter source of variance, the Rhode Island Red strains showed a

Table 1. Pair-contest behavior of White Leghorn and Rhode Island Red chickens selected for high and low aggressiveness levels. (Selected strains vs. controls)

			Measurements					
			% of Contests Won[1/]			% of Contests with Social Interactions[2/]		
Year	Generation	Sex	High	Low	High - Low	High	Low	High - Low
			White Leghorns					
1958	0	Male	--	--			87.1	
1959	1	Male	50.4	40.7	9.7	74.9	75.7	-0.8
1960	2	Male	45.5	38.5	7.0	84.3	79.3	4.0
1961	3	Male	62.0	48.8	13.2			
1960	2	Female	49.2	35.7	13.5	41.0	29.2	11.8
			Rhode Island Reds					
1958	0	Male	--	--			62.2	
1959	1	Male	66.7	40.6	26.1	55.8	43.0	12.8
1960	2	Male	71.8	56.2	15.6	74.0	58.7	15.3
1961	3	Male	64.2	51.8	12.4			
1960	2	Female	42.2	37.1	5.1	46.5	43.8	2.7

1/ % of Contests Won = number won/(number won + number lost).

2/ % with Social Interactions =

$$\frac{\text{(no. won + no. lost + no. no decisions)}}{\text{(no. won + no. lost + no. no decisions + no. no contests)}}.$$

significant difference, but no difference could be detected between the two White Leghorn strains. The error term for testing of breeds was strains within breeds. The variation between the Rhode Island Red strains was so large that the analysis was unable to show a breed difference. It will be noted that there are no significant differences among the White Leghorn strains nor is there a significant difference between the Rhode Island Red high and Rhode Island Red control strains (Table 3). The Rhode Island Red low strain was superior to the other two strains of the Rhode Island Reds. Calculated LSD values were .2090 and .4824 for the .05 and .01 probability levels, respectively.

Semen Concentration (Appearance). Parker, McKenzie, and Kempster (1942) have shown that semen that is viscous and white has a high spermatozoa concentration, while semen that has a watery appearance is low in spermatozoa concentration. McDaniel and Craig (1959) devised the following scoring system for the rating of semen appearance: watery or clear, 0; watery with white streaks, 1; medium, 2; thick white, 3; very viscous and chalk-white, 4. These same observers obtained a highly significant correlation (0.76) between concentration as determined by one individual with the aid of a hemocytometer, and appearance scores as assigned independently by the other observer. The same scoring system was used in this investigation. The analysis of variance given in Table 4 shows significant breed, generation, and generation by breed interaction differences. The generation and generation by breed differences are thought to be caused by observer differences. The subjective

Table 2. Analysis of variance of semen volume of high and low strains in White Leghorn and Rhode Island Red breeds.

Source	d.f.	M.S.	F
Breeds	1	30, 158.71	11.43
Strains: Breed	2	2, 687.79	18.91
WL low vs. high	1	318.57	2.24
RIR low vs. high	1	5, 057.33	35.58*
Generation	1	113.99	.802
G x B	1	678.98	4.78
G x S: Breed	2	142.12	.187
Sires: G and S	40	761.52	1.453*
Ind: Sire, S, B, G	477	524.06	

*$P \leq 0.05$

Table 3. Least significant difference table for high, low, and control strains - semen volume means in cc.

White Leghorn				Rhode Island Red			
Strain	$\bar{x}$	$\bar{x}$ - .9209	$\bar{x}$ - .9573	Strain	$\bar{x}$	$\bar{x}$ - 1.3825	$\bar{x}$ - 1.4003
High	1.0243	.1034	.0670	Low	1.6537	.2712*	.2534*
Low	.9573	.0364		Control	1.4003	.0178	
Control	.9209			High	1.3825		

*$P \leq 0.05$

ratings were scored by two different observers in 1959 and 1960.

Table 5 gives the means for the high, low, and control strains of the two breeds. The White Leghorn strains all scored higher than the Rhode Island Red strains. The calculated LSD critical levels were 0.70 and 1.62 (P = .05 and .01). The LSD table showed a significant difference between the White Leghorn control strain and White Leghorn high strain and the difference of the control strain over the low strain approaches significance (0.69). The apparent superiority of the controls over the other two strains might be due to the restriction placed on the control breeders for 1959, i.e., each control breeder produced at least 0.30 cc. of semen.

Age at Sexual Maturity. The means for the number of days to sexual maturity for the high, low, and control strains of both breeds are given in Table 7. The calculated LSD's for sexual maturity were 7.06 and 16.28 (P = .05, .01). The differences among all strains were nonsignificant. The analysis of variance (Table 6) showed no differences between the high and low lines, nor was there any breed difference. The analysis of variance does show a significant sire family difference, indicating that genetic variation does exist for this trait.

Hen-Day Percentage Egg Production. This trait failed to respond as a correlated trait to selection for aggressiveness as did age at sexual maturity. The analysis of variance (Table 8) showed a significant sire family difference but no breed or strain difference. This was substantiated in Table 9 where no significant

Table 4. Analysis of variance of semen concentration of high and low strains in White Leghorn and Rhode Island Red breeds.

Source	d.f.	M.S.	F
Breeds	1	6.21	34.5*
Strains: Breed	2	.18	1.125
Generations	1	25.04	156.5**
G x B	1	3.55	22.19*
G x S: B	2	.16	.0675
Sires: G and S	40	.237	.675
Ind: Sire, S, B, G	477	.351	

*$P \leq 0.05$
**$P \leq 0.01$

Table 5. Least significant difference table for high, low, and control strains - semen concentration (appearance) means.

White Leghorn				Rhode Island Red			
Strain	$\bar{x}$	$\bar{x}$ - 4.45	$\bar{x}$ - 4.47	Strain	$\bar{x}$	$\bar{x}$ - 3.70	$\bar{x}$ - 3.97
Control	5.16	.71*	.69	Control	4.28	.58	.31
Low	4.47	.02		Low	3.97	.27	
High	4.45			High	3.70		

*$P \leq 0.05$

differences were detected among the high, low, or control strains. The calculated LSD's were 15.45 and 35.63 (P = .05, .01). The indication is that neither age at sexual maturity nor hen-day percentage egg production are influenced by selection for and against aggressiveness.

Five-Month Body Weight. Table 10 gives the analysis of variance for 5-month body weight. As was expected, highly significant breed and sex differences were detected. The analysis further shows significant and highly significant differences for the sex by breed and sex by generation interactions, respectively. This indicates that the differences between sexes were greater in one breed than in the other, and that the relative differences between the sexes were greater in one year than in the other. No sire family differences were detected nor was there any apparent difference between the high and low strains. The means for 5-month body weights by strain are presented in Table 11. The calculated LSD's were .166 and .382 (P = .05, .01). No significant strain differences among high, low, and control strains within breeds were detected.

Eight-Month Body Weight. Table 12 gives the analysis of variance for 8-month body weights. Again, highly significant breed and sex differences were obvious. The highly significant sex by breed interaction indicated that the difference between sexes was greater in one breed than in the other. There was no significant difference between high and low strains nor among sire families. Table 13 shows the 8-month weight means for the six strains. No detectable differences were found within breeds among the high, low, and

Table 6. Analysis of variance of age at sexual maturity (age at first egg) of high and low strains.

Source	d.f.	M.S.	F
Breed	1	277.92	4.416
Strains: Breed	2	62.94	3.880
Generations	1	5.63	.347
G x B	1	32.74	2.018
G x S: B	2	16.22	.312
Sires: G and S	40	51.97	1.483*
Ind: Sires, S, B, G	479	35.04	

*$P \leq 0.05$

Table 7. Least significant difference table for high, low, and control strains - age at sexual maturity of females.

White Leghorn				Rhode Island Red			
Strain	$\bar{x}$	$\bar{x}$ - 167.77	$\bar{x}$ - 170.09	Strain	$\bar{x}$	$\bar{x}$ - 166.78	$\bar{x}$ - 167.09
Low	173.82	6.05	2.73	Control	172.60	5.82	5.51
Control	170.09	2.32		High	167.09	.31	
High	167.77			Low	166.78		

Table 8. Analysis of variance of hen-day percentage egg production of high and low strains.

Source	d.f.	M.S.	F
Breeds	1	17.62	.106
Strains: Breeds	2	165.93	2.137
Generations	1	28.83	.371
G x B	1	313.04	4.030
G x S: B	2	77.63	1.530
Sires: G and S	40	50.85	1.990**
Ind: Sires, S, B, G	511	25.60	

**P ≤ 0.01

Table 9. Least significant difference table for high, low, and control strains - hen-day percentage egg production.

White Leghorn				Rhode Island Red			
Strain	$\bar{x}$	$\bar{x}$ - 61.37	$\bar{x}$ - 62.68	Strain	$\bar{x}$	$\bar{x}$ - 63.52	$\bar{x}$ - 64.69
Low	67.57	6.20	4.89	Low	67.11	3.59	2.42
High	62.68	1.31		High	64.69	1.17	
Control	61.37			Control	63.52		

Table 10. Analysis of variance of 5-month weight for high and low strains of both sexes.

Source	d.f.	M.S.	F
Breeds	1	6,730.33	266.58***
Strains: Breeds	2	25.25	14.19
Generations	1	8.11	4.56
G x B	1	9.36	5.26
G x S: B	2	1.78	.19
Sires: G and S	40	9.28	.61
Sexes	1	4,483.63	606.72***
SX by B	1	258.49	34.98*
SX by S: B	2	7.39	2.04
SX by G	1	104.72	119.00**
SX by G and B	1	.37	.42
SX by G by S: B	2	.88	.24
SX by Sire: G and S: B	40	3.63	.24
Ind: Sire, S, B, G, SX	1045	15.25	

*$P \leq 0.05$
**$P \leq 0.01$
***$P \leq 0.005$

Table 11. Least significant difference table for high, low, and control strains - 5-month weight for both sexes.

White Leghorn				Rhode Island Red			
Strain	$\bar{x}$	$\bar{x}$ - 3.839	$\bar{x}$ - 3.852	Strain	$\bar{x}$	$\bar{x}$ - 5.423	$\bar{x}$ - 5.483
High	3.945	.106	.093	High	5.502	.079	.019
Control	3.852	.013		Low	5.483	.060	
Low	3.839			Control	5.423		

control strains. The calculated LSD's were .361 and .832 ($P = .05$, .01).

Sexual Behavior

Sexual effectiveness mean scores for 72 males in 1959 and 96 males in 1960, as determined by the number of completed matings in four 10-minute observation periods, are presented in Table 14. It should be noted that the means for 1960 are relatively higher than those for 1959. This is attributed to the change from a 24-hour conditioning period in 1959 to a 1-week conditioning period in 1960. No significant differences were found among the strains for either year. A significant breed difference ($P < .05$) was noted in 1959, with the White Leghorn males having consistently higher rates of mating. The analyses of variance of these data are presented in Table 15. The method of analysis used was the Kruskal-Wallis one-way analysis of variance as described by Siegel (1956). This method of analysis makes no assumption of normality, i.e., data may or may not be normally distributed.

Table 16 shows the number of completed matings for high, low, and control females. The effect of the 1-week conditioning period of the males is again apparent in these data, as the 1960 mean scores are consistently higher than those for 1959. Table 17 shows the analyses of variance of these data with no apparent strain differences detected, but significant breed differences for both years.

Crouching response of females was the third sexual behavior

Table 12. Analysis of variance of 8-month weight for high and low strains of both sexes.

Source	d.f.	M.S.	F
Breeds	1	10,082.72	2,301.99***
Strains: Breeds	2	4.38	.52
Generations	1	111.93	13.26
G x B	1	.05	.006
G x S: B	2	8.44	.42
Sires: G and S	40	20.14	.71
Sexes	1	8,846.97	3,061.24***
SX by B	1	1,189.49	411.59***
SX by S: B	2	2.89	.61
SX by G	1	8.33	.95
SX by G and B	1	.47	.05
SX by G by S: B	2	8.81	1.87
SX by Sire: G and S: B	40	4.72	.17
Ind: Sire, S, B, G, SX	993	28.51	

***$P \leq 0.005$

Table 13. Least significant difference table for high, low, and control strains - 8-month weight for both sexes.

White Leghorn				Rhode Island Red			
Strain	$\bar{x}$	$\bar{x}$ - 4.496	$\bar{x}$ - 4.626	Strain	$\bar{x}$	$\bar{x}$ - 6.393	$\bar{x}$ - 6.484
High	4.720	.224	.094	High	6.729	.336	.245
Low	4.626	.130		Low	6.484	.091	
Control	4.496			Control	6.393		

trait studied. The number of crouches observed was taken as a measurement of female sexual receptivity. Table 18 shows the mean number of crouches for the high, low, and control females. Once more, the means are higher for the year 1960, apparently because of the relatively greater male mating experience. Strain differences were not significant, but breed differences were observed in 1960. The analyses (Table 19) did not reveal a breed difference for 1959, although the means were 7.3 for White Leghorn females versus 4.7 for Rhode Island Red females.

DISCUSSION

Falconer (1960) has pointed out that the genetic cause of correlation is chiefly pleiotropy, though linkage is a cause of transient correlation, particularly in populations derived from crosses between divergent strains. Pleiotropy is the property of a gene whereby it affects two or more characters. It is often important and of particular interest to the poultry and animal breeder to know whether the change brought about by selection in one character will cause simultaneous changes in other characters. Falconer (1960, pages 312-322) gives a comprehensive review of the methods of estimating genetic correlations. Among other methods (analysis of half- and full-sib families, offspring-parent relationship) he shows how genetic correlations can be estimated from responses to selection for trait X where the correlated response of trait Y is given by the formula:

$$CR_Y = i\ h_X\ h_Y\ r_A\ \sigma_{PY}$$

Table 14. Mean sexual effectiveness scores of high, low, and control males as measured by completed matings.

Strain	1959	1959 Average All Males	1960	1960 Average All Males
WL				
High	4.67		5.4	
Low	5.67	5.2	9.1	7.8
Control	5.25		8.9	
RIR				
High	2.83		5.8	
Low	2.00	2.5	4.9	5.5
Control	2.75		5.7	

Table 15. Analyses of variance of sexual effectiveness scores of high, low, and control males as determined by number of completed matings.

Source	d.f.	H-statistic	P
1959			
WL high, low, control	2	.586	>.50
RIR high, low, control	2	.530	>.75
WL versus RIR	1	4.900	<.05
1960			
WL high, low, control	2	4.62	>.10
RIR high, low, control	2	.19	>.90
WL versus RIR	1	3.26	>.05

Table 16. Mean number of completed matings for high, low, and control females.

Strain	1959	1959 Average All Females	1960	1960 Average All Females
WL				
High	2.9		5.0	
Low	3.8	3.8	5.8	5.4
Control	4.7		5.3	
RIR				
High	2.3		4.0	
Low	1.6	1.8	3.8	3.7
Control	1.7		3.2	

Table 17. Analyses of variance of number of completed matings for high, low, and control females.

Source	d.f.	H-statistic	P
1959			
WL high, low, control	2	2.06	>.25
RIR high, low, control	2	1.38	>.50
WL versus RIR	1	6.60	<.025
1960			
WL high, low, control	2	.93	>.50
RIR high, low, control	2	1.19	>.50
WL versus RIR	1	9.10	<.005

Table 18. Receptivity levels as indicated by mean number of crouches for high, low, and control females.

Strain	1959	1959 Average All Females	1960	1960 Average All Females
WL				
High	4.4		11.0	
Low	8.4	7.3	10.8	10.3
Control	8.9		9.1	
RIR				
High	5.5		7.7	
Low	3.9	4.7	8.5	8.0
Control	4.8		7.8	

Table 19. Analyses of variance of number of crouches for high, low, and control females.

Source	d.f.	H-statistic	P
1959			
WL high, low, control	2	4.83	>.05
RIR high, low, control	2	1.47	>.25
WL versus RIR	1	2.10	>.10
1960			
WL high, low, control	2	.98	>.50
RIR high, low, control	2	.54	>.75
WL versus RIR	1	4.30	<.05

where:

i = selection intensity

h_X = square root of the heritability of trait X

h_Y = square root of the heritability of trait Y

r_A = the genetic correlation between X and Y

σ_{PY} = the standard deviation of the phenotype of trait Y

X = the selected trait

Y = the unselected trait.

Thus, the response of a correlated character can be predicted if the genetic correlation and the heritabilities of the two characters are known. And, conversely, if the correlated response is measured by experiment, as was done in the investigation, and the heritabilities are known, the genetic correlation can be estimated.

This investigation did not detect any significant strain differences in body weights at 5 and 8 months of age, semen concentration, or sexual behavior characteristics. The implication is that genes affecting these traits and aggressiveness are apparently not linked, nor are they pleiotropic in nature. There is some evidence of a negative genetic correlation between aggressiveness and semen volume in the Rhode Island Reds. Comparable data from the White Leghorn strains do not support these results, however.

The results of the analyses of 5- and 8-month body weights did not agree with those of Guhl, Craig, and Mueller (1960) who were able to show significant and highly significant differences in body weights in their F_1, F_2, and F_4 males and their F_3 and F_4 females in lines selected for high and low aggressiveness. This investigation has only been carried through the second selected generation. The discrepancy between the results of the two investigations may be due to the fact that the first investigation used relatively higher selection pressure by selecting on both sides, i.e., selection was on both the male and female sides, while this investigation was conducted by selection only of the male side.

Reports in the literature of the relationship of sexual behavior to aggressiveness are contradictory. Guhl, Collias, and Allee (1945) found no significant phenotypic relationship between the social rank of a cock and his sexual activity when placed alone in a flock of chickens. McDaniel and Craig (1959) found significant and highly significant phenotypic associations between social aggressiveness scores, sexual effectiveness scores, and crouches elicited from females. Wood-Gush and Osborne (1956) studied the mating frequencies of 30 cockerels belonging to six sire families and 15 full-sib pairs. They found significant differences between sire families, indicating that mating frequency has a genetic basis. Wood-Gush (1960) continued his studies with another group of 30 cockerels belonging to six sire families and again found differences among families with respect to mating frequency. He produced F_1 and F_2 generations from the highest and lowest scoring males and was able to maintain this difference with the high males always superior to the low males. Wood-Gush tested his F_1 and F_2 strains in initial encounters with other birds from panels trained to fight. He could find no evidence of genetically correlated response between the scores for aggressiveness and the scores for mating frequencies, i.e., the two strains did not differ in their aggressiveness toward other males.

Falconer (1960) has pointed out that if both characters have low heritabilities, then the phenotypic correlation is determined chiefly by the environmental correlation; if they have high heritabilities, then the genetic correlation may be the more important. In view of the relatively low to moderate heritability estimated for aggressiveness as found by Guhl and Eaton (1948), Komai, Craig, and Wearden (1959), Guhl, Craig, and Mueller (1960), but not by Siegel (1960), environmental correlations would be expected to make up a large part of the phenotypic correlations found between aggressiveness and other traits as found by McDaniel and Craig (1959). In this investigation, in order to avoid inbreeding, selection pressure was not as strong as it might have been. However, strain differences in aggressiveness are apparent. The presently available evidence suggests therefore that any genetic correlations between aggressiveness and other traits studied which may be present are not of large enough magnitude to be detected from two generations of selection for high and low levels of aggressiveness.

SUMMARY

Randombred White Leghorns (Cornell controls) and Rhode Island Reds (NC-47 Regional Red controls) were sampled in 1958 from populations maintained at the Regional Poultry Breeding Laboratory, Purdue University, to provide foundation stocks for aggressiveness selection experiments. Two selected generations of aggressive and

non-aggressive strains have been produced by the use of initial-pair contests. A high and low strain of each breed, selected on the basis of relative success in dominating other individuals, have been shown to diverge from each other by testing them with the randombred controls. Secondary traits were measured in order to estimate the importance of possible genetic correlations with the traits under selection (aggressiveness and non-aggressiveness). The traits measured were semen volume and appearance, female age at sexual maturity and hen-day percentage egg production, 5- and 8-month body weights of both sexes, and sexual behavior of both sexes.

Strain differences for semen volume were observed in the Rhode Island Red breed with the low strain producing significantly more semen than the other strains of the same breed. No strain differences were detected in other secondary traits. Breed differences were apparent for semen concentration with the White Leghorn breed having the greater scores. Breed differences were shown for male sexual effectiveness scores as measured by number of completed matings for 1959 and the differences approached significance for 1960 ($P < .10$) with the White Leghorn breed mating at a greater rate. White Leghorn females showed greater sexual receptivity than the Rhode Island Red females as measured by completed matings in both 1959 and 1960. The White Leghorn females also showed a higher level of crouching response in 1960, but no difference was observed in 1959. Significant sire family differences were observed in semen volume, female age at sexual maturity, and hen-day percentage egg production.

ACKNOWLEDGMENT

The author expresses his sincere gratitude to Dr. J. V. Craig, Poultry Geneticist and major advisor, for his technical advice and assistance, as well as the personal guidance he extended throughout this study and for his numerous suggestions in analyzing the data and constructive criticism of this thesis.

Grateful appreciation is extended to Dr. A. M. Guhl for his aid in planning the experiments and his active interest in all phases of the investigation.

The author especially wishes to express his thanks to Dr. S. Wearden for his advice on the statistical treatment of the data in this study.

Appreciation is also expressed to Professor T. B. Avery, Head of the Department of Poultry Science, for his encouragement of and interest in the investigation.

Thanks are extended to the National Science Foundation, whose Grant No. G-7069 financed this investigation and whose National Science Foundation Research Fellowship award to the author made his participation possible.

Acknowledgment is also given to the graduate students of the Department of Poultry Science as well as members of the Poultry Farm staff who aided in the collection of the data.

LITERATURE CITED

Collias, N. E.
Statistical analysis of factors which make for success in initial encounters between hens. Amer. Nat. 77: 519-538. 1943.

Collias, N. E.
Aggressive behavior among vertebrate animals. Physio. Zool. 17: 83-123. 1944.

Craig, J. V.
Department of Poultry Science, Kansas State University, Manhattan, Kansas. Personal communication. 1961.

Eaton, R.
Breeding for aggressiveness in the fowl. M. S. Thesis, Kansas State University, Manhattan, Kansas. 1949.

Falconer, D. S.
Introduction to quantitative genetics. The Ronald Press Co. New York. 1960.

Grosse, A. E., and J. V. Craig.
Sexual maturity of males representing twelve strains of six breeds of chickens. Poultry Sci. 39: 164-172. 1960.

Guhl, A. M.
Heterosexual dominance and mating behavior in chickens. Behavior 2: 106-120. 1949.

Guhl, A. M.
Social dominance and receptivity in the domestic fowl. Physiol. Zool. 23: 361-366. 1950.

Guhl, A. M.
Measurable differences in mating behavior of cocks. Poultry Sci. 30: 687-693. 1951.

Guhl, A. M.
Social behavior of the domestic fowl. Kansas Agr. Expt. Sta. Tech. Bul. 73. 1953.

Guhl, A. M.
The development of social organization in the domestic chick. Ani. Behavior 6: 92-111. 1958.

Guhl, A. M.
The measurement of aggressiveness in cocks and hens. Poultry Sci. 39: 1255. 1960.

Guhl, A. M.
The effects of acquaintance between the sexes on sexual behavior in White Leghorns. Poultry Sci. 40: 10-21. 1961.

Guhl, A. M., N. E. Collias, and W. C. Allee.
Mating behavior and the social hierarchy in small flocks of White Leghorns. Physiol. Zool. 18: 365-390. 1945.

Guhl, A. M., J. V. Craig, and C. D. Mueller.
Selective breeding for aggressiveness in chickens. Poultry Sci. 39: 970-980. 1960.

Guhl, A. M., and R. C. Eaton.
Inheritance of aggressiveness in the fowl. Poultry Sci. 27: 665. 1948.

Guhl, A. M., and L. L. Ortman.
Visual patterns in the recognition of individuals among chickens. Condor 55: 287-297. 1953.

Guhl, A. M., and D. C. Warren.
Number of offspring sired by cockerels related to social dominance in chickens. Poultry Sci. 25: 460-472. 1946.

King, S. C., J. R. Carson, and D. P. Doolittle.
The Conneticut and Cornell randombred populations of chickens. World's Poul. Sci. J. 15: 139-159. 1959.

Komai, T., J. V. Craig, and S. Wearden.
Heritability and repeatability of social aggressiveness in the domestic chicken. Poultry. Sci. 38: 356-359. 1959.

Masure, R. H., and W. C. Allee.
The social order in flocks of the common chicken and the pigeon. Auk 51: 306-327. 1934.

McBride, G.
The measurement of aggressiveness in the domestic hen. Ani. Behaviour 6: 87-92. 1958.

McDaniel, G. R.
A phenotypic and genetic study of factors affecting male fertilizing capacity in the domestic chicken. Ph. D. Thesis, Kansas State University, Manhattan, Kansas. 1960.

McDaniel, G. R., and J. V. Craig.
Behavior traits, semen measurements, and fertility of White Leghorn males. Poultry Sci. 38: 1005-1014. 1959.

Parker, J. E., F. F. McKenzie, and H. L. Kempster.
Observations on the sexual behavior of New Hampshire males. Poultry Sci. 19: 191-197. 1940.

Parker, J. E., F. F. McKenzie, and H. L. Kempster.
Fertility in the male domestic fowl. Missouri Agr. Expt. Sta. Bul. 347. 1942.

Sanctuary, W. C.
A study of avian behavior to determine the nature and persistency of the order of dominance in the domestic fowl and to relate these to certain physiological reactions. M. S. Thesis, Mass. State College, Amherst, Mass. (unpublished). 1932.

Schjelderup-Ebbe, T.
Beitrage zur Social-Psychologie des Haushuhns. Zeitschr. f. Psychol. 88: 225-252. 1922.

Schjelderup-Ebbe, T.
Weitere Beitrage zur Social und Individual Psychologie des Haushuhns. Zeitschr. f. Psychol. 92: 60-87. 1923.

Schjelderup-Ebbe, T.
Zur Socialpsychologie der Vogel. Zeitschr. f. Psychol. 95: 36-84. 1924.

Schjelderup-Ebbe, T.
Social behavior in birds. Chapter XX in Murchinson's Handbook of Social Psychology, pp. 947-972. Clark University Press, Worcester. 1935.

Siegel, P. B.
A method for evaluating aggressiveness in chickens. Poultry Sci. 39: 1046-1048. 1960.

Siegel, S.
Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill Book Co., Inc. New York. 1956.

Snedecor, G. W.
Statistical Methods. Iowa State College Press, Ames. 1956.

Tindell, L. D., and J. V. Craig.
Effects of social competition on laying house performance in the chicken. Poultry Sci. 38: 95-105. 1959.

Upp, C. W.
Preferential mating of fowls. Poultry Sci. 7: 225-238. 1928.

Wearden, S.
Personal communication. 1961.

Wood-Gush, D. G. M.
The behaviour of the domestic chicken: A review of the literature. British. Jour. Anim. Behaviour 3: 81-110. 1955.

Wood-Gush, D. G. M.
A study of sex drive of two strains of cockerels through three generations. Ani. Behaviour 8: 43-53. 1960.

Wood-Gush, D. G. M., and R. Osborne.
A study of differences in the sex drive of cockerels. British Jour. Anim. Behaviour 4: 102-110. 1956.

CORRELATED RESPONSES RESULTING FROM SELECTION FOR SOCIAL AGGRESSIVENESS IN THE DOMESTIC CHICKEN

by

WAYMAN PATRICK JUSTICE

B. S., Kansas State University, 1959

AN ABSTRACT OF A THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Poultry Science

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1962

Randombred White Leghorns (Cornell controls) and Rhode Island Reds (NC-47 Regional Red controls) were sampled in 1958 from populations maintained at Purdue University to provide foundation stocks for aggressiveness selection experiments. Approximately 70 randomly selected males were tested within each breed by means of 10 initial-pair encounters to establish relative ability to dominate other individuals (aggressiveness - the "high" line) or lack of this ability (non-aggressiveness - the "low" line). Four selected strains (high and low for each breed) were then established, using seven of the most and seven of the least aggressive individuals as sires to produce high and low aggressiveness strains within each of the two breeds. Selection was restricted to males and inbreeding was consciously avoided.

Two selected generations have been produced and tested against samples of the randombred populations from which they were derived. First-selected-generation males were tested against randombred controls to provide data for further selection. Second-generation males were sampled and tested against controls to establish the relative dominance of high and low strains, and were also tested on a within-strain basis to provide information for further selection. For selection purposes, about 70 males of each strain were tested each generation and 10-15 percent of the most extreme individuals (highs and lows of each breed) were selected to sire the following generation. Results were presented which indicated success in separating the strains and which suggested that genetic variation exists for social aggressiveness.

Secondary traits, i.e., those not under direct selection, were measured to determine whether they would also show changes as the behavioral patterns of the selected populations changed.

No correlated changes were detected in semen appearance, at sexual maturity for females, hen-day percentage egg production, 5-month weight, 8-month weight, or sexual effectiveness as measured by completed matings and female crouching responses. A strain difference was detected in the Rhode Island Red breed for semen volume with the low strain producing the greatest volume of semen. Breed differences were apparent for semen concentration with the White Leghorn breed having the greater scores. Breed differences were shown for male sexual effectiveness scores as measured by number of completed matings for 1959 and the differences approached significance for 1960 ($P < .10$), with the White Leghorn breed mating at a greater rate. White Leghorn females showed greater sexual receptivity than the Rhode Island Red females as measured by completed matings in both 1959 and 1960. The White Leghorn females also showed a higher level of crouching response in 1960, but no difference was observed in 1959. Sire family differences were observed in semen volume, age at sexual maturity for females, and hen-day percentage egg production.