GENETICS OF BEHAVIOR:
ENDOCRINE RESPONSES IN LINES SELECTED FOR MATING ABILITY

by

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INTRODUCTION

The study of behavior has interested scientists for decades but the problem of sexual behavior as a separate entity has only recently commanded extensive laboratory study. That differences in mating behavior are under genetic control has been well documented and responses to selection for the trait, mating ability, have been demonstrated in animals ranging from the insects to the mammals.

Genetic differences in testes and comb growth response to hormones have been found in cockerels. The effects of hormones on mating behavior have been reported for several species. However, investigation of the role of the endocrine system of chickens differing genetically for mating ability is lacking.

From the literature it is quite evident that genetic and endocrine factors influence the sex-drive of vertebrates. It is, however, unknown whether the genetic effects are mediated through endocrine pathways, through other pathways, or through a combination of both.

The objective of this thesis was to determine the effects of testosterone propionate and castration on the mating behavior of chickens selected bidirectionally for number of completed matings and on an unselected randombred control line.

REVIEW OF LITERATURE

Inheritance of Sexual Behavior

The inheritance of sexual behavior has been studied in several species during the past two decades. Examples are Drosophila, (Manning, 1959, 1961; Bastock, 1956); mice, (McGill, 1962; McGill and Blight, 1963; McGill and Tucker, 1964; Levine *et al*., 1966); guinea pigs, (Valenstein *et al*., 1954; Jakway, 1959; Goy and Jakway, 1959); and chickens, (Guhl, 1951; Wood-Gush and Osborne, 1956; Wood-Gush, 1959, 1960; Tindell and Arze, 1965).

Insects: Bastock (1956) reported a yellow mutation in *Drosophila melanogaster* which influenced the sexual motivation of mutant males and thereby reduced their success in the fertilization of normal females. Manning (1961) developed, through artificial selection, two strains of *Drosophila melanogaster* which differed in mating speed. After seven generations of divergent selection, average mating speed was 80 minutes for the slow line and three minutes for the fast line.

Differences in sexual behavior that prohibited the interbreeding of species of crickets was observed by Alexander (1961). These differences involved the calling song and chemo-tactile stimuli which prevented females from mating with males from a different species. He also noted that interspecific discordances in sexual encounters were more complete than differences in aggressive encounters.

Poultry: Measurable differences in the relative sexual activity of individual cockerels were observed by Guhl (1951), and Wood-Gush and Osborne (1956) reported significant differences among sire families for mating frequency. Subsequently, Wood-Gush (1959) observed that sons of high scoring males mated more frequently than sons of low scoring males and Siegel (1959) reported significant differences between inbred lines of chickens for sex-drive.

Bidirectional mass selection for cumulative number of completed mating (CNCM) by males produced lines of chickens which were significantly different for this trait (Siegel, 1965). Realized heritabilities, after six generations of selection were .18 ± .05 and .31 ± .11 for the high mating line (HML) and the low mating line (LML), respectively. It appeared that both additive and non-additive gene action influenced CNCM and, in time, the response was symmetrical due to greater selection pressure in the HML and higher heritability in the LML. Tindell and Arze (1965) reported significant differences in the mating behavior of selected lines by the F_2 generation. They and Siegel (1965) used the Athens-Canadian Randombreds (Hess, 1962) as the foundation stock.

Smyth and Leighton (1953) suggested that selection of toms on the basis of their actual mating ability would improve mating efficiency. Four generations of selection for sexual receptivity of female turkeys yielded a significant response for this trait (Smyth, 1955). In the F_4 generation the mean numbers of matings per hen were 10.7 and 4.8 in the high and low lines, respectively.

Mammals: Male guinea pigs from a heterogeneous stock had a higher sex-drive than those from an inbred stock (Valenstein et al., 1954). Significant differences in mating behavior of two strains of guinea pigs were found by Jakway (1959), who proposed that genetic factors influenced the sexual behavior of guinea pigs. Goy and Jakway (1959) studied the interaction of genetic and hormonal factors in the determination of sexual behavior patterns of guinea pigs. They suggested that the mating act was composed of several responses and that each component rather than mating behavior per se was genetically determined.

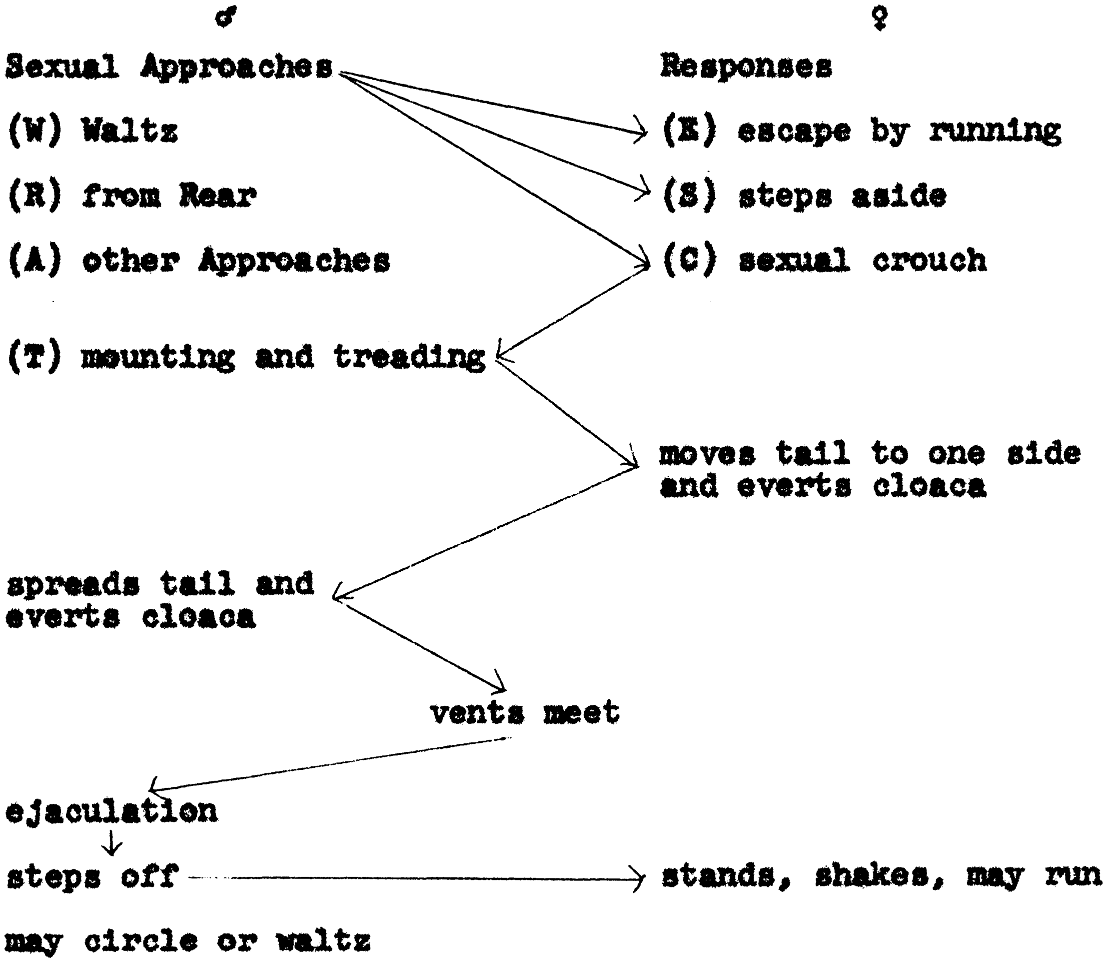
In studies of sexual selection in mice, Levine (1958) found that in groups of mixed mice an albino strain sired more litters than a black-agouti strain. He suggested that this was because albinos were superior in sexual competition to black-agouti mice. Subsequently, Levine et al. (1966) found that albinos performed fewer thrusts per mount and more genital licking per mating than the black-agouti males. Whalen (1961) reported strain differences in rats for intromission and concluded that intromission frequency was genetically controlled.

McGill (1962, 1965); McGill and Blight (1963a,b); and McGill and Tucker (1964) concluded from several studies with intact and castrated mice, that inheritance of sexual behavior was a complex phenomenon under several different modes of inheritance.

Courtship Behavior in Chickens

The mating act of chickens has been described by Williams and McGibbon (1955) and Guhl (1961). Mating is initiated by the male who approaches the female either from the rear or with a waltzing pattern. The female may respond by either avoiding or crouching for the male. The latter response may provide the stimulus to the male to mount, which is accomplished by placing his feet on the wings of the female and clasping her hackel with his beak. After a series of treading movements the female will move her tail aside to allow her vent to come into contact with the vent of the male. This allows for the transfer of semen and completion of the mating. Guhl (1961) referred to this as a signal-response sequence which is diagramed on page 10.

SIGNAL-RESPONSE SEQUENCE[1]



[1] Guhl (1961)

Hormones and Sex Behavior

The principle method used to study physiological influences on sexual behavior has been organ removal and the subsequent treatment with exogenous hormones. Almost thirty years ago Stone (1938) observed differences in the sexual response of rats administered male hormones, suggesting variation among individuals for the threshold of sexual activity. Stone also found that administration of testosterone propionate (T.P.) to castrates caused a return of sexual activity to precastration levels.

Hamilton and Golden (1939) reported that although androgen activated latent masculine behavior in female chickens, the response was less than that observed for normal males. Ball (1940) observed that female rats injected with testosterone exhibited masculine sexual behavior and concluded that the male copulatory pattern was present in a rudimentary form in females. Rats ovariectomized prior to puberty and given T.P. injections exhibited sexual behavior that differed from that of intact females injected with T.P. (Beach, 1942a). T.P. caused the expression of feminine sexual behavior in ovariectomized birds, whereas male sexual behavior was exhibited by the injected intact females. The behavior of ovariectomized females that did not receive T.P. was similar to that of sluggish males.

In another phase of the same experiment, estrogen administered to males castrated prior to puberty induced copulatory behavior comparable to that observed in intact male rats (Beach, 1942b).

Hart et al. (1946) found that injections of T.P. did not increase either the sex-drive or the copulatory behavior of irregularly breeding male cattle. Grunt and Young (1952) postulated, from results obtained with castrated guinea pigs, that differences between individuals were due to the reactivity of the tissues rather than to differences in hormone amounts. In a subsequent experiment, Grunt and Young (1953) restored normal sexual behavior in castrated guinea pigs through administration of 25 µg of T.P. When dosages were increased to 100 µg, the response was not significantly different from that at 25 µg. Riss and Young (1954), in an effort to stimulate low-sex-drive male guinea pigs, used 500 µg of T.P., a quantity twenty times greater than the 25 µg used by Grunt and Young (1953), but were unable to increase sex-drive.

Champlin, et al. (1963) reported that the lack of testicular androgens in castrated mice reduced sexual behavior to such a degree that the males failed to ejaculate. Daily injections of 32 µg of T.P. for two weeks were sufficient to cause the return of sexual behavior to pre-castration levels and to sustain such behavior. Dosages as great as 1024 μg did not produce measurable differences of the sexual patterns exhibited by normal mice.

Collias (1944, 1950) concluded that the reactivity of tissues and the chemicals secreted by them were inseparable. Thus, differences in behavior could be related both to the amount of hormone secreted and the sensitivity of the target organ to these hormones. Grunt and Young (1953) attributed the differences in sexual behavior, in part, to differences in the reactivity to hormones, of the tissues mediating that behavior. Riss and Young (1954) concluded that differences between high and low sex-drive animals was determined by the soma or substrate acted upon by the hormones.

Levy (1954) showed that immature male mice administered T.P. exhibited aggressive behavior at an earlier than normal age. Comparable responses were not evident in injected females. Similar results were obtained by Tollman and King (1956) who gave a single injection of 0.5 mg T.P. to castrated male and female mice and tested for aggressiveness during the succeeding ten days. These results suggest that sexual dimorphism in aggressiveness may be due to neural differences rather than those of hormone quantity. Recently, Caggiula and Hoebel (1966) found that male rats could be made to copulate by electrical discharges though platinum electrodes implanted in the hypothalamus. Systemic introduction of testosterone caused an increase of self-stimulation by these rats.

Androgen and Red Blood Cells

Numerous investigations have demonstrated a positive relationship between androgen and the number of red blood cells. Adams and Skevket (1929) found higher erythrocyte counts for males than for females in two strains of white rats. Comparisons, within four inbred strains of mice by Kamenoff (1937), showed that the percentage of red blood cells of males exceeded that for females in all strains. A comparable sexual dimorphism was found in rabbits by Rosahn *et al*. (1934), in cats by Lewis (1941), and in pigeons and doves by Riddle and Braucher (1934).

Juhn and Domm (1930) demonstrated a relationship between the gonads and erythrocyte values in chickens. Juveniles, poulards, capons, and mature females had comparable red blood cell counts. Transplantation of testicular tissue into castrates increased the magnitude of erythrocyte values to that of adult males. They suggested that because of the close relationship between the male hormone and erythrocyte number that the latter could be used as an assay for the former.

Taber *et al*. (1943) studied the red blood cell values in castrates of both sexes of chickens. The number of red blood cells of capons and poulards receiving daily injections of testosterone increased in eleven days from 2.5 x 10^6 to 3.3 x 10^6 per mm^3. After 24 days of injection the level was 3.6 x 10^6 cells per mm^3, a level comparable to that for the adult male. Although three levels of testosterone (1.25, 2.50, and 3.75 mg) were administered, differences among levels in number of red blood cells were not significant.

Finkelstein _et al_. (1944) found that male rats produced new red blood cells faster than females after being subjected to bleeding. They concluded that the male hormone reduces the time for return to normal blood values because the hormone has erythropoietic properties. Injection of testosterone in castrated rats stimulated erythrocyte production and the combination of cobalt plus testosterone caused a greater response than either agent alone.

Stein and Carrier (1945) substantiated the relationship between red blood cell numbers and the secretion of the male hormone. They followed the changes in erythrocyte values in hamsters after castration and subsequent testosterone administration. Castration of males caused a 25 to 35 per cent decrease in red blood cells. Testosterone injected daily for three days restored the erythrocyte values to normal.

Newell and Shaffner (1950) reported that while packed cell volume as a percentage of total blood volume remains essentially constant for female chickens of all ages it increased rapidly in males upon the attainment of sexual maturity. Packed cell volumes of adult males were 50 per cent higher than that for young birds. Comparable results were obtained by Wood-Gush (1960) and Washburn and Siegel (1963).

Androgen and Comb Size

The combs of chickens are considered secondary sex characteristics whose growth and development are under the influence of androgens. Juhn *et al*. (1932) suggested that comb growth would be a good assay for male sex hormones because the comb was external and the action of the hormone could be easily recognized.

Breneman (1937) obtained a positive correlation between comb size, and gonadal weight, however, there was a plateau effect in the response of the comb. Further, Breneman (1938) found that divided dosages of T.P. were more effective in causing comb growth than a single dose. Davis and Domm (1943) used injection levels of 1.25, 2.50, and 3.75 mg of T.P. in poulards and Taber *et al*. (1943) injected levels ranging from 1 to 3.75 mg T.P. daily into castrates of both sexes. Although comb growth was noted, in neither study was a determination made of the threshold dosage. Comb growth was measured at dosages of 0.5 and

1.0 µg of T.P. by Breneman and Mason (1951) who estimated the physiological threshold level of 40-day-old Leghorn cockerels to be under 50 µg. Ortman (1964) injected T.P. in dosages ranging from 0 to 1 mg per bird per day and found that comb growth plateaued at the 0.8 mg level.

Dorfman and Dorfman (1948) demonstrated the precision of the comb unction method of androsterone assay. They found breed differences in chick comb response to T.P. applied directly to the combs. White Leghorn males were 15 times more sensitive than Rhode Island Reds and 20 times more sensitive than Barred Rocks.

Jaap _et_ _al_. (1961) indicated that comb and testes response to hormones was genetically controlled. Later, Nestor and Jaap (1965) selected lines for differences in comb response to T.P. and pregnant mare serum. They concluded that the responses were partly attributable to changes in the sensitivity of the comb to the hormones.

METHODS AND MATERIALS

Chickens used for the investigation presented in this thesis were samples taken from the Athens-Canadian Randombred control population (Hess, 1962) and from two selected lines which originated from the randombred population. The selected lines had undergone mass selection for a high number of completed mating (HML) and a low number of completed mating (LML). Details concerning the selection procedures were given by Siegel (1965). Athough the genes for both rose (R) and pea (P) comb were segregating in these populations, only single comb (rrpp) chicks were used. This was to facilitate comb measurements.

Preliminary Studies with Secondary Sex Characteristics

Comb Size: This trial was conducted to provide a comparison among lines for the response of comb growth to graded levels of T.P.[1] At one day of age 36 F_8 HML, 18 F_8 LML, and 21 unselected control line male chicks were wingbanded and placed in wire-floored batteries. Feed and water were supplied *ad libitum*.

Cockerels were randomized within lines into three equal treatment groups for the bioassay of a total of

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[1] Testosterone propionate (T.P.) - Upjohn lot no. 8801

0, 5, and 20 µg of T.P. in a seven day period. Cottonseed oil was used as a carrier according to the procedure of Lerner et al. (1963). Starting when the chicks were two days of age, 0.005 ml, containing one seventh of the total bioassay amount (0, 5, 20 µg), were injected daily at the base of the comb with a Hamilton microsyringe. At ten days of age, 24 hours after the final injection, chicks were individually weighed, sacrificed, and their combs excised and weighed. Data were analyzed by the model:

$$X_{ijk} = \mu + l_i + h_j + lh_{(ij)} + e_{ijk}$$

where l and h represented lines and hormone levels, respectively.

Packed Cell Volume: Microhematocrits were measured in 20 F_7 HML, 14 F_7 LML, and 13 unselected control line males. All birds had been hatched on the same date, and were 43 weeks of age at the time of determination. Duplicate samples of blood were obtained from the right bracheal vein, centrifuged in a Drummond microcentrifuge at 3,000 RPM for three minutes, and read with a Drummond microhematocrit reader. The average value of the duplicate samples was used in the analysis which followed the model:

$$X_{ij} = \mu + l_i + e_{ij}$$

where l represents lines.

Mating and Endocrine Relationships

Chicks from pedigreed matings of F_7 generations HML and LML and the unselected control line were hatched and sexed. The females were discarded and the males were wingbanded and housed in wire-floor batteries with feed and water provided ad libitum.

At three weeks of age the cockerels were transferred to floor pens and maintained in flocks. One week later they were randomly separated on a within line basis into two equal groups. Cockerels within one group were caponized during the following week, while those in the other group served as intact controls. At 23 weeks of age, capons and intact males were randomly assigned, on a within line basis, into injection and non-injection groups. The factorial nature of the experiment is shown in Table 1.

Cockerels in the injected group received daily injections of 0.9 mg T.P. per 0.25 ml cottonseed oil for 14 consecutive days. The injection site was the pectoralis major with the injections being alternated from left to right sides to minimize bruising. Mating trials began on the afternoon following the day of the last injection.
Mating trials followed the method of Siegel (1965) and the frequency of courts, mounts, treads, and completed matings were recorded. Six daily mating periods were afforded each bird and the cumulative values were used in the analyses.

Table 1. Number of birds per treatment group at 23 weeks of age.

Treatment		Lines HML	 LML	 Unselected
Castrate	T.P.	9	9	9
	N.T.P.	5	5	5
Noncastrate	T.P.	10	10	10
	N.T.P.	10	10	10

HML = high mating line

LML = low mating line

Unselected = randombred

T.P. = testosterone propionate injected

N.T.P. = no testosterone propionate injected

At the conclusion of the injection period, measurements were obtained on the length (l) and height (h) of combs. The comb factor, (l x h)/2, of Breneman and Mason (1951) was used in the analysis. Packed cell volumes were obtained at the conclusion of the last mating trial. The statistical model used for analysis was:

$$X_{ijkl} = u + l_i + h_j + c_k + lh_{(ij)} + lc_{(ik)} + hc_{(jk)} + lhc_{(ijk)} + e_{ijkl}$$

where l, h, and c represented lines, hormone levels and castrate versus intact animals, respectively. The square root transformation was used in the analyses because the variances of the mating behavior data were heterogeneous.

RESULTS

Preliminary Studies

No significant differences were found among T.P. dosages and lines for body weight at 10 days of age (Table 2). The line-dosage (L x D) interaction was also not significant. Line effects (L) and the line-dosage interaction were not significant for comb weights at 10 days of age (Table 2), showing the same response for both lines to T.P. However, highly significant differences were found among dosages (D) for the comb weights (Table 2). Cockerels that received 20 µg of T.P. had significantly heavier than those that received no T.P. or 5 µg of T.P. (Table 3). Differences between these latter two levels were not significant.

Means and standard errors for percentage packed cell volumes were 47.3 ± 1.0, 46.2 ± 1.1, and 50.1 ± 0.8 for HML, LML, and control line adult males, respectively. Differences among lines were not significant.

Mating and Endocrine Relationships

Mating trials commenced when the cockerels were 26 weeks of age. The cumulative number of courts, mounts, treads, and completed matings for 6 ten-minute observation periods were used in the analyses shown in Table 4. Means

Table 2. Analyses of variance for body and comb weights of chicks at 10 days of age.

Sources of variation	Df	Mean Square		
			Comb Weight	
		Body Weight[1]	Unadjusted[2]	Adjusted[3]
Among lines (L)	2	57.5	0.23	0.43
Among dosages (D)	2	115.8	10.45**	13.63**
L x D	4	178.6	0.17	0.24
Error	65	129.2	0.56	0.70

[1] weights in gm

[2] weights in mg

[3] weights in mg/100gm body weight

**$P \leq 0.01$

Table 3. Means and standard errors for comb weights of chicks at 10 days of age.

T.P. dosage	Comb weight	
	Unadjusted[1]	Adjusted[2]
0	1.27 ± 0.14^{a}	1.16 ± 0.16^{a}
5 ug	1.27 ± 0.09^{a}	1.64 ± 0.10^{a}
20 ug	2.39 ± 0.19^{b}	2.90 ± 0.21^{b}

Any two means in a column with the same superscript are not significantly different $P \leq 0.05$.

T.P. = testosterone propionate.

[1] weights in mg

[2] weights in mg/100gm body weight

Table 4. Analyses of variance for courts, mounts, treads, and completed matings.

Sources of variation	df	Mean Square			
		Courts	Mounts	Treads	Completed matings
Among lines (L)	2	40.5**	27.8**	20.0**	12.3**
Between hormone levels (H)	1	21.8**	1.6	1.6	1.2
Castrate vs noncastrate (C)	1	332.1**	36.6**	30.2**	20.7**
L x H	2	7.9	1.0	0.6	0.2
L x C	2	26.5**	7.3**	5.8**	3.2**
H x C	1	70.4**	5.0**	4.5**	3.2**
L x H x C	2	69.7**	12.3**	10.0**	5.9**
Error	90	2.2	0.5	0.4	0.4

**$P \leq 0.01$.

Table 5. Means and standard errors of courts, mounts, treads, and completed matings for main treatment effects.

Main treatment variables[1]	Mating behavior			
	Courts	Mounts	Treads	Completed matings
Lines:				
HML	46.3 ± 3.7^{c}	9.7 ± 1.0^{c}	8.5 ± 0.8^{c}	6.0 ± 0.6^{c}
LML	19.3 ± 3.1^{a}	1.8 ± 0.5^{a}	1.6 ± 0.5^{a}	1.2 ± 0.4^{a}
Unselected	29.5 ± 4.3^{b}	3.3 ± 0.6^{b}	3.1 ± 0.5^{b}	2.6 ± 0.5^{b}
Castrates:				
Castrate	10.6 ± 1.9^{a}	1.5 ± 0.3^{a}	1.5 ± 0.3^{a}	1.1 ± 0.2^{a}
Intact	46.5 ± 3.4^{b}	7.3 ± 0.7^{b}	6.4 ± 0.6^{b}	4.8 ± 0.5^{b}
Hormone:				
T.P.	32.4 ± 2.6^{a}	5.0 ± 0.6^{a}	4.5 ± 0.5^{a}	3.4 ± 0.4^{a}
N.T.P.	30.9 ± 3.7^{a}	4.8 ± 0.6^{a}	4.2 ± 3.4^{a}	3.1 ± 0.4^{a}

Any two means in a column within a treatment group with the same superscript are not significantly different $P \leq 0.05$.

T.P. = testosterone propionate injected

N.T.P. = no testosterone propionate injected

[1] within a variable all other main treatments are pooled, eg. HML includes injected and noninjected, castrates and intact males from that line.

and standard errors of main treatment groups are presented in Table 5.

Courts: HML males courted significantly more frequently than the LML and unselected line males with the unselected males courting significantly more than those from the LML. Castration resulted in a significant reduction in the frequency of courting, whereas, injections of T.P. in intact animals had no significant influence on the frequency of courting (Table 5). The line-hormone interaction was not significant indicating that all lines were similarly effected by the hormone.

Means showing the significant first order interactions (line-castrate and hormone-castrate) for courts are presented in Table 6. The mean frequency of courting was similar among castrates from all lines whereas there were significant differences among lines for the intact males. Courting was not observed among castrates that did not receive T.P. injections whereas those which received T.P. injections courted an average of 16.4 times. Among intact males the means were 46.8 courts for those that received injections of T.P. and 46.3 for those that received no T.P. This resulted in a highly significant hormone-castrate interaction.

Mounts: Males from the HML line mounted more than those from other lines. The frequency of mounts for males

Table 6. Means demonstrating the line-castrate and hormone-castrate interactions for courts, mounts, treads, and completed matings.

Treatment variables[1]	Courts		Mounts		Treads		Completed matings	
	Castrate	Non-castrate	Castrate	Non-castrate	Castrate	Non-castrate	Castrate	Non-castrate
Lines:								
HML	10.1^{a}	71.6^{c}	2.6^{c}	14.6^{c}	2.5^{c}	12.7^{c}	1.9^{c}	8.9^{c}
LML	10.8^{a}	25.3^{a}	0.9^{a}	2.5^{a}	0.7^{a}	2.2^{a}	0.5^{a}	1.8^{a}
Unselected	10.1^{a}	42.6^{b}	1.1^{b}	4.9^{b}	1.1^{b}	4.5^{b}	1.1^{b}	3.7^{b}
Hormone:								
T.P.	16.4^{a}	46.8^{a}	2.4^{a}	7.4^{a}	2.3^{a}	6.5^{a}	1.8^{a}	4.8^{a}
N.T.P.	0^{b}	46.3^{a}	0^{b}	7.3^{a}	0^{b}	6.3^{a}	0^{b}	4.7^{a}

Any two means in a column within a group with the same superscript are not significantly different $P \leq 0.05$.

[1] Within any given variable all other treatments were pooled.

in the control line was intermediate to that for the selected lines with the differences between any two lines being significant (Tables 5 and 6). The mean number of mounts for castrated males was 1.5 whereas the mean for intact males was 7.3 with the difference between means being highly significant. No significant difference in number of mounts was found between T.P. injected males and those that did not receive the hormone.

First-order interactions for number of mounts followed the same pattern as that noted for courts. The line-hormone interaction was not significant while the line-castrate and hormone-castrate interactions were highly significant. Although castration reduced the frequency of mounting among males from all lines, the degree of reduction was not consistent, resulting in the highly significant line-castrate interaction. The reduction was 6, 4, and 3 fold in the HML, control line, and LML respectively. The hormone-castrate interaction was highly significant because injections of T.P. had no effect on the frequency of mounting of intact males while it increased the frequency in castrated males.

<u>Treads</u>: There were highly significant differences among lines for number of treads (Table 4). Males in the HML treaded more frequently than males from the other lines and the control males treaded more frequently than those in

the LML (Table 5). Although there was no difference between hormone levels for number of treads, the mean number of treads for intact males was greater than that for capons with the difference being highly significant.

Interactions among main variables for frequency of treads followed the same pattern observed for courts and mounts (Tables 4 and 6).

Completed Matings: The successful completion of the mating act involves very complex behavior patterns. As shown by Guhl (1961) courtship, mounting, and treading include a series of stimuli and responses that precede the final completion of the mating.

There were highly significant differences among lines for number of completed matings (Table 4). All lines differed significantly from each other with the controls being intermediate to the HML and LML (Table 5). There were highly significant differences between castrated and intact males with the former completing fewer matings than the latter. Injections of T.P. did not have a significant influence on the number of completed matings (Table 5).

No matings were completed by capons not injected with T.P. while those receiving T.P. completed an average of 1.8 matings (Table 6). Among intact males the mean number of completed matings was 4.8 for T.P. injected and 4.7 for males not receiving T.P. This response resulted in a highly significant hormone-castrate interaction. Although castration resulted in the reduction of the number of completed matings in all lines the reduction was not proportional resulting in the line-castrate interaction. The reduction was 5, 4, and 3-fold for the HML, LML, and control lines, respectively. There was no significant line-hormone interaction for completed matings indicating a similar response among the lines to the hormone.

<u>General</u>: Differences among lines were found within intact and castrated males for number of mounts, treads, and completed matings. Among intact males there was also a highly significant difference among lines for courts whereas among castrates the line difference was not present (Table 6). This table also shows that the castrated birds exhibited a significant increase in mating behavior in response to the T.P. injections whereas the intact animals showed no increased response, leading to the highly significant hormone-castrate interactions.

The relationships among lines for phases of the mating act leading to completion of mating were consistent throughout (Table 7) and may be considered a measure of mating efficiency. The percentage of courts resulting in completed matings was 12, 7, and 3 for the HML, control line, and LML respectively. Differences among lines were highly significant.

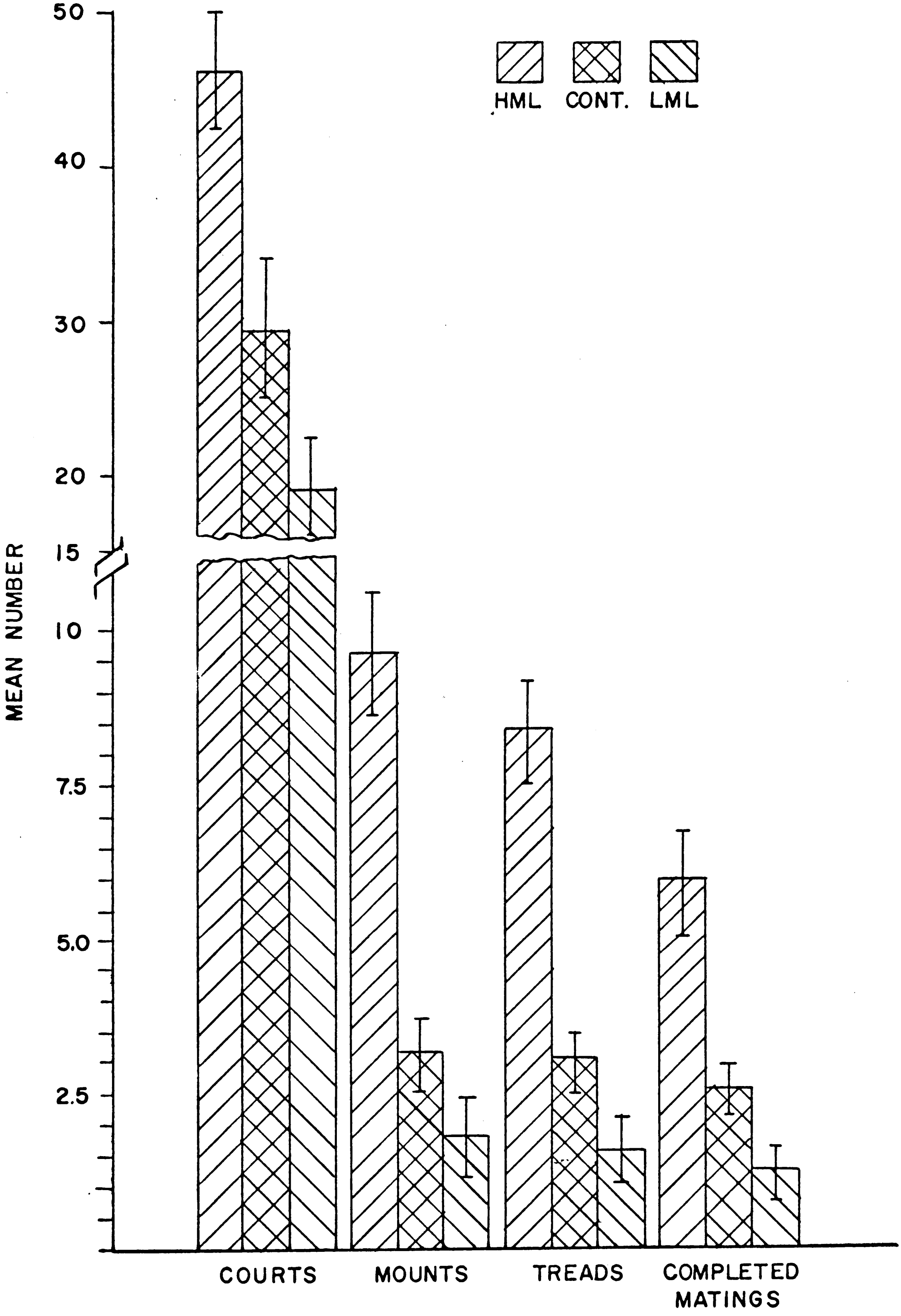
Table 7. Mean percentage of courts, mounts, and treads resulting in completed matings.

Main treatment variables[1]	Percentages		
	Courts:CM	Mounts:CM	Treads:CM
Lines:			
HML	12.0^c	53.0^b	58.1^b
LML	2.9^a	22.3^a	24.3^a
Unselected	7.0^b	48.9^b	51.5^b
Castrates:			
Castrate	6.4^a	29.9^a	30.3^a
Intact	8.0^b	49.4^b	54.7^b
Hormone:			
T.P.	9.7^a	51.9^a	55.4^a
N.T.P.	4.3^b	28.1^b	31.1^b

Any two means in a column within a group with the same superscript are not significantly different $P \leq 0.05$.

[1] Within any given variable all other main treatments were pooled.

FIGURE 1: MEANS AND STANDARD ERRORS OF MATING BEHAVIOR TRAITS FOR THE HML, LML, AND CONTROL LINE



The bidirectional nature of the response of the selected lines from the unselected control line is demonstrated in Figure 1. In all cases means for the control line were intermediate to those for the selected lines.

Comb Size and Packed Cell Volume

The secondary sex characteristics, comb size and PCV, were measured on the males used in the mating trials. There was a highly significant difference among all lines for comb size. Males in the LML had significantly larger combs than males from the other lines and the control line males had combs larger than those in the HML (Tables 8 and 9). Combs size was decreased by castration whereas T.P. injections increased the comb size (Table 9). Although castration resulted in a reduction of comb size, the reduction was not proportional among lines resulting in a highly significant line-castrate (L x C) interaction.

T.P. significantly increased the size of the combs of castrates but had no effect on the size of combs of intact animals (Table 10). This resulted in a highly significant hormone-castrate interaction. The line-hormone interaction (Table 8) was not significant indicating that injections of T.P. had a similar influence on all lines.

Significant differences were found for PCV between the HML and LML, but there were no differences between the

Table 8. Analyses of variance for comb size and packed cell volume of chickens at 26 weeks.

Sources of variation	df	Mean Square Comb size[1] ($x10^6$)	PCV[2]
Among lines (L)	2	5.357**	105.7*
Between hormone levels (H)	1	3.957**	437.8**
Castrate vs Noncastrate (C)	1	102.184**	1243.3**
L x H	2	0.101	13.4
L x C	2	1.839**	5.0
H x C	1	6.752**	162.3*
L x C x H	2	15.443**	20.3
Error	63	0.233	27.9

[1] Analysis performed on comb factor which is $\frac{\text{Length x Height}}{2}$ measured in mm.

[2] PCV = packed cell volume.

*$P \leq 0.05$

**$P \leq 0.01$

Table 9. Means and standard errors of comb size and PCV values for main treatment effects of chickens at 26 weeks of age.

Main treatment variables[1]	Comb size[2]	PCV
Lines:		
HML	1547.3 ± 82.6^{a}	41.24 ± 1.0^{a}
LML	2476.3 ± 100.7^{c}	45.10 ± 1.3^{b}
Unselected	2170.3 ± 134.9^{b}	44.43 ± 1.0^{ab}
Castrates:		
Castrate	995.2 ± 37.7^{a}	38.59 ± 0.7^{a}
Intact	2990.2 ± 110.0^{b}	46.75 ± 0.9^{b}
Hormones:		
T.P.	2220.7 ± 71.5^{a}	45.75 ± 1.0^{a}
N.T.P.	1844.8 ± 99.6^{b}	40.81 ± 0.6^{b}

Any two means in a column within a treatment group with the same superscript are not significantly different $P \leq 0.05$.

[1] Within any given variable all other treatments were pooled.

[2] Expressed as comb factor which is $\frac{\text{Length x Height}}{2}$ measured in mm.

Table 10. Means demonstrating the line-castrate and hormone-castrate interactions for comb factors of chickens at 26 weeks of age.

Treatment variables[1]	Comb size	
	Castrate	Noncastrate
Lines:		
HML	739.5^{a}	2312.6^{a}
LML	1173.9^{b}	3436.0^{b}
Unselected	1126.5^{b}	3283.8^{b}
Hormone:		
T.P.	1437.7^{a}	2974.6^{a}
N.T.P.	472.2^{b}	3006.3^{a}

Any two means in a column within a group with the same superscript are not significantly different $P \leq 0.05$.

[1] Within any given variable all other treatments were pooled.

unselected line and each of the selected lines (Table 9). Castration and T.P. injections had a highly significant effect on PCV. The PCV for intact males were higher than those of the castrates and the males receiving T.P. had higher PCV than those males not receiving the hormone (Tables 8 and 9). Administration of T.P. significantly increased the PCV of castrates but had no significant effect on noncastrates resulting in a significant hormone-castrate interaction.

DISCUSSION

Mating Behavior: The primary purpose of this thesis was to investigate the influence of androgens on males from lines of chickens known to differ in mating behavior.

The behavior of the samples of the lines used was consistent to the descriptions given for them by Siegel (1965). Sexual activity was greater in the HML than the LML with the control line being intermediate to the selected lines.

Capons exhibited no mating behavior, a result consistent with that obtained with mice (McGill and Tucker, 1964), quail (Beach and Inman, 1965), and guinea pigs (Grunt and Young, 1952). This demonstrated the need for testicular tissue for normal mating behavior of male birds and mammals. Although administration of T.P. to castrates elicited mating behavior, the mating level was lower than that observed for intact males. This finding was consistent with that reported for mice (Champlin *et al.*, 1963) and guinea pigs (Grunt and Young, 1953), and showed that androgens, rather than testicular tissue *per se*, was necessary for the elicitation of male sexual behavior. The amount of T.P. injected may have been the reason why the mating behavior of the T.P. injected capons was less than that of intact males. This suggestion is based on the findings of Grunt and Young (1953) who restored normal mating behavior in castrated guinea pigs with T.P. injections.

Administration of T.P. into intact LML males did not stimulate mating behavior. This result was consistent with the observations of Riss and Young (1954), who failed to stimulate low sex drive guinea pigs with injections of T.P. and suggests that the endogeneous androgen levels within the LML were above the threshold levels for mating behavior.

Differences among the lines for courts, mounts, treads, and completed matings were, with one exception, consistent for all treatment combinations. The exception was for the courts in the castrated group where there was no significant differences among lines. This suggests that although the threshold for eliciting courting behavior was low, it rose as the cumulative requirements for mounting, treading, and subsequent completion of the mating were brought into play.

The failure of administration of T.P. to intact males and of castration with hormone replacement to modify differences among lines for mating behavior was consistent with Etkin (1964). He suggested that differences in behavior were due to differences in target sensitivity and not hormone levels. Davidson (1966) and Davidson and Bloch (1967) showed that implantation of androgens and anti-androgens into the hypothalamus of male rats had a direct effect on the reproductive system. This leads to the hypothesis that neural tissues may be important in mediating sexual behavior. This hypothesis is supported further by the results of Vaughn and Fisher (1962) who increased the sexual activity of male rats by electrical stimulation of the hypothalamus. Further, MacLean (1965) has shown, via electrical stimulation of the brains of monkeys, an integral relationship between the brain and sexual responses and displays. Young (1965) concluded that the nature of sexual behavior brought about by gonadal hormones was largely dependent upon the substrate acted upon and that the substrate was probably neural. Caggiula and Hoebel (1966) found that male rats could be made to copulate by electrical discharges through platinum electrodes implanted in the hypothalamus and that systemic introduction of testosterone caused an increase of self-stimulation by these rats.

Comb Size and Packed Cell Volume

There were no differences among lines to administration of T.P. as measured by comb weight at 10 days of age. This indicated a similar response of diverse genetic material to the hormone at an early age. At 26 weeks of age, however, the HML and LML differed significantly for comb size with the combs of the former being smaller than those of the latter. Combs of the unselected line were of intermediate size. Ortman (1964) found no difference in comb size between lines selected for aggressiveness. Siegel (1965) however, has shown that the genetic correlation between sex drive and relative aggressiveness is low; therefore, the discrepency between experiments may not be surprising. If comb size and mating behavior are influenced by androgen, the smaller combs in the HML is difficult to explain from existing biological knowledge. A hypothesis however, may be offered. If circulating levels of androgens were different for the selected lines, they may have been high enough to elicit the thresholds for normal mating behavior of the particular lines and yet have been insufficient to cause comparable comb growth. Equally disparing results have been reported by Buchner et al. (1932) and Lamoreux (1943) who observed that males kept in confinement with limited light grew larger combs than those allowed direct sunlight. Buchner et al. (1932) also noted that the males with the smaller combs had the larger testes. Lamoreux (1943) found that birds kept at 85° F. had larger combs than those maintained at 36° F. Since chickens lack sweat glands they must rely on respiration and radiation for cooling. The primary organs for radiation are the comb and wattles. It is possible that birds maintained in limited light grew larger combs in a gradual response to heat that was not dissipated by panting. The birds maintained in sunlight had the sensory response of direct heat to induce rapid panting and therefore the combs need not grow as large.

Accentuating the fact that comb growth is not a simple phenomenon, Nestor and Jaap (1966) found that selection for chick comb response was associated with increased age of maturity and lowered egg production. It is evident that additional research is necessary to determine further the mechanisms involved in comb growth.

There were no differences among lines for PCV in the randomly selected adult males of the preliminary studies. The PCV values of the chickens used in the mating trials were significantly different for the HML and LML with the control line being intermediate to the selected lines. The significant differences among the lines for PCV may have been a chance occurrence as a subsequent trial on a random sample from these lines revealed no significant differences among the lines. The mean percentage PCV were 47.2, 45.9, and 49.0 for the HML, LML and unselected line, respectively. This was consistent with the results of Wood-Gush (1960) who found no differences in PCV among males selected for high and low sex drive.

These investigations demonstrate the need of androgen for the eliciting of sexual behavior. They have also, however, shown that relative androgen titers were not the causes of differences in the mating ability of the lines used in the investigation presented in this thesis. Androgen when present in above threshold amounts, appears to act upon some mechanism, presumably neural, and the sensitivity of this mechanism to the androgen, or a hormonal metabolite, may be the determinant of differences in sexual behavior.

SUMMARY AND CONCLUSIONS

The primary purpose of this thesis was to investigate the role of androgens in the elicitation of mating behavior of lines selected in divergent directions for cumulative number of completed matings.

The response of chick comb growth to testosterone propionate (T.P.) injections was measured on different samples of the lines at 10 days and 26 weeks of age. Although, in young chicks, there were no differences among lines for comb growth in response to T.P. administration, combs of low mating lines (LML) stags were larger than those contemporaries from the high mating line (HML). Combs of control birds were intermediate to that of the selected lines. This suggests that although the comb growth response to T.P. was similar among the lines in young chicks, other factors in addition to androgens, influence the comb size of adults.

Packed cell volumes (PCV) were measured by the microhematocrit method in two different random samples of adult birds from these lines and in the birds used in the main experiment. Administration of T.P. increased PCV in all lines. No differences were found among lines for PCV based on the values from the random samples, however, a difference among lines was found in the main experiment.

Further study appears necessary to ascertain definitely if the latter result was a chance occurrence.

For the main phase of this thesis males from the HML, LML, and the Randombred unselected control line were saved at hatching. When at five weeks of age one half of the males within each line was caponized and the other half served as intact controls. Then at 23 weeks of age the groups were again subdivided in half. At this time administration of 0.9 mg T.P. to half of the castrated and intact birds commenced and continued for 14 consecutive days. Beginning the day after the final injection all birds were released singly into pens of females for ten minutes per day for six days, and the number of courts, mounts, treads, and completed matings recorded.

Sexual activity was greater in the HML than the LML with the control line being intermediate to the selected lines. These relationships among lines existed within all main treatment groups with one exception. That exception was for number of courts of castrates where there was no difference among the lines. Castrates did not display mating behavior. When injected with T.P. they exhibited mating behavior, but at a level lower than that observed for intact males. Administration of T.P. did not influence the behavior of intact males. These results suggest that the circulating levels of androgens were sufficient for the elicitation of normal mating behavior for these lines. Therefore, differences between these lines selected for mating behavior were not due to differences in androgen levels.

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GENETICS OF BEHAVIOR:
ENDOCRINE RESPONSES IN LINES SELECTED FOR MATING ABILITY

by

Richard Eugene McCollom

ABSTRACT

The role of androgens on mating behavior, packed cell volume (PCV), and comb size was studied in lines selected bidirectionally for mating ability.

Combs of adult low-mating-line (LML) males were larger than those of the high-mating-line (HML) males while those of controls were intermediate. Chick comb response to androgen however, showed no line difference.

Random samples of adults showed no differences among lines for PCV. However, for an unexplainable reason, there was a difference among lines for birds used in the mating trials.

Males were hatched from F_7 matings of the selected and the control line. Half were caponized at five weeks of age and half served as intact controls. Fourteen daily injections of testosterone propionate (T.P.) were given to half of the castrates and half the intact birds commencing at 23 weeks of age. After the final injection, all males were released singly into pens of females for 10

minutes daily. The number of courts, mounts, treads, and completed matings were recorded.

Sexual activity was greatest for the HML and least for the LML with the controls being intermediate. Castrates displayed no mating behavior. Administration of T.P. to castrates elicited sexual behavior but to a lesser degree than observed in intact males. No change in behavior was noted for intact males injected with T.P., suggesting that sufficient endogeneous androgens were present for normal mating behavior. It was concluded, therefore, that the differences among lines for mating behavior were not due to unequal androgen titers.