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Mating frequency in male chickens : crosses among selected and unselected lines

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Summary

The mode of inheritance of mating behavior and blood testosterone levels were examined in lines of chickens selected for high and low mating frequency and the randombred population from which the selected lines originated. Comparisons involved purelines and reciprocal crosses among them. Circulating plasma testosterone levels of a random sample of all males appeared to be of a sufficient magnitude to insure a positive effect on the behaviors measured. Males from the line selected for high mating frequency exhibited a significantly larger number of courts, mounts, treads, and completed matings than those from either the control or the low line. The means for the control line were intermediate and significantly different from those of the selected lines. Means for crosses between parental lines were, significantly larger than their pureline midparent means, indicating a heterotic effect. It appears that the threshold for mating activity has been either lowered or overridden by genetic variation for increased mating frequency in the high mating line and crosses of the parental lines.

Key-words : Heterosis, chickens, mating behavior.

Résumé

Croisements entre lignées sélectionnées sur le comportement sexuel des coqs

Le déterminisme génétique du comportement sexuel et du niveau de sécrétion de testostérone ont été étudiés dans des souches de poulet sélectionnées pour leur fréquence haute (HH) et basse (LL) d'accouplement ainsi que dans une souche témoin (CC) fondatrice. L'étude a porté sur la comparaison des lignées pures et des croisements réciproques. Les taux de testostérone étaient assez élevés pour ne pas être susceptibles d'influencer le comportement sexuel. Les mâles de la lignée HH ont manifesté un nombre plus important de sollicitations, de montes, de piétinements et de copulations que ceux de la lignée (LL) ou (CC). Le niveau enregistré dans la lignée CC était intermédiaire mais néanmoins significativement différent de ceux des lignées HH et LL. Les croisés dépassaient largement la moyenne parentale indiquant par là un effet d'hétérosis. Il semble que le seuil relatif à l'activité sexuelle ait été, soit abaissé, soit dépassé du fait de la sélection sur la fréquence d'accouplement dans la lignée haute et les croisements parentaux.

Mots-clés : Hétérosis, poulet, comportement sexuel.

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I. Introduction

Several short-term selection experiments for mating frequency have been conducted with chickens (WOOD-GUSH, 1958, 1960; TINDELL & ARZE, 1965; GALPERN & DUKHNO, 1974). From these experiments and those of SIEGEL (1965, 1972), a model has been developed (COOK & SIEGEL, 1974; VAN KREY *et al.*, 1977) to describe the mode of inheritance of mating behavior in male chickens. Additional insights into the genetic architecture of mating behavior in the male fowl can be obtained from long-term selection for mating frequency and crosses among populations differing in this behavior. The experiment reported here contains the results of reciprocal crosses between lines of chickens that have undergone 20 generations of divergent selection for high and low mating frequency of males, and of reciprocal crosses between the selected lines and the random mating population from which they originated.

II. Materials and methods

A. Stocks and husbandry

F₁ and S₂₁ generation progeny were produced on the same date from reciprocal crosses and pureline matings of S₂₀ generation parents from lines of chickens selected for high (H) and low (L) cumulative number of completed matings (CNCMs) by males and the randombred control (C) which was used as the base population for the selected lines. Mating combinations used in this experiment are designated with the first letter denoting the sire line and the second letter denoting the dam line. Descriptions of these lines were presented by SIEGEL (1972) and DUNNINGTON & SIEGEL (1983). All matings were made via artificial insemination with parental lines produced from pedigree matings and crosses from pooled semen from the same sires. Dams for the parental and cross matings were selected at random with each mating combination consisting of 10 sires and 40 dams that were age contemporaries.

Traits associated with mating behaviors were measured between 28 and 32 weeks of age. They included the frequency of courting, mounting, treading and completed matings as outlined by SIEGEL (1965). Briefly, the procedure for measuring these behaviors consisted of releasing a male that had been maintained in an all-male flock since eight weeks of age singly into a flock of six females for ten minutes and recording the number of courts, mounts, treads and completed matings. A male that mounted was assumed to have courted, one that treaded was assumed to have courted and mounted, and one that completed a mating was assumed to have courted, mounted and treaded. At the completion of each test, the male was returned to his home flock. Males from all mating combinations were tested once each day with the procedure repeated on eight separate days. The cumulative score for the eight observation periods was considered the observation for each male. Assignment of males to female tester flocks was at random.

At 34 weeks of age, five ml of blood was obtained by cardiac puncture from a random sample of males from each line and assayed for testosterone. Extraction and assay methods were developed from those described by BENOFF *et al.* (1978) and KATTESH *et al.* (1979). Testosterone levels were determined using a radioimmunoassay with rabbit antibody (obtained from Dr. HAFS H.D., Michigan State University, East Lansing, Michigan).

B. Statistical analysis

The statistical analyses used to compare mating combinations followed those described by COOK *et al.* (1972), which was a modified analysis for testing contrasts (SCHEFFE, 1959, 1970). The nonorthogonal linear contrasts (with unequal group numbers) for each trait are shown in Table 1. Differences among male progeny of reciprocal crosses are attributable to maternal effects and not sex linkage as the homogametic (XX) males have comparable sex chromosomes in reciprocal crosses (EISEN *et al.*, 1966). Contrasts were calculated using (1) all males, regardless of whether or not they mated, and (2) mating males (only those males who completed at least one mating during the eight 10-minute observation periods).

TABLEAU 1

Summary of SCHEFFE's nonorthogonal linear contrasts and genetical inferences.

Liste des contrastes linéaires non orthogonaux de SCHEFFE avec leur interprétation génétique.

Contrast code	Mating comparison	Genetical inference
1	HH - LL	Additivity
2	HH - CC	Additivity
3	LL - CC	Additivity
4	HC - CH	Maternal
5	HL - LH	Maternal
6	CL - LC	Maternal
7	(CH + HC) - (HH + CC)	Nonadditivity
8	(LH + HL) - (HH + LL)	Nonadditivity
9	(LC + CL) - (CC + LL)	Nonadditivity
10	(HL + LH) - 2CC	Nonadditivity
11	(HH + LL) - 2CC	Asymmetry and/or Nonadditivity

Mating efficiency was considered in three ways, the ratio of number of mounts to courts, CNCMs to courts, and CNCMs to mounts. Ratios were adjusted using the Freeman-Tukey arc sine transformation for binomial proportions with less than 50 observations (MOSTELLER & YOUTZ, 1961). The frequencies of courts, mounts, treads and completed matings of each male were transformed to square roots prior to analysis. Analyses of variance were conducted on behavioral and endocrine data for all males and for maters only. The ratio of maters to nonmaters was compared by Chi-square analyses. Since data from a particular mating combination were used more than once in the Chi-square analyses, tau was set as 11 and the 0.05 alpha level was determined from the tables of JENSEN *et al.* (1968).

III. Results and discussion

A. Testosterone

Plasma testosterone levels for each mating combination are presented in Table 2. The levels obtained in this experiment were lower than those reported for the HH, LL and CC lines by BENOFF *et al.* (1978), but within the range of those observed at 24 weeks

of age by DE SANTO *et al.* (1982). Coefficients of variation for plasma testosterone levels were high, with individual values ranging from 0.04 to 12.66 ng/ml. These values bracketed the range of 0.84 to 7.83 ng/ml obtained by liquid gas chromatography procedures for a different population of cockerels by FURR & THOMAS (1970). Although no significant differences among mating combinations were found for testosterone levels, whether or not nonmaters were included in the analyses, crosses had consistently lower values than their midparent values, suggesting a modest negative heterosis for this trait.

Correlations of testosterone with the number of courts and CNCMs were calculated within each mating combination. None was significant except that involving the CH mating combination (Table 2). Correlations were tested and found to be homogeneous (SNEDECOR, 1946). Since nonmaters were included in the correlations, and the radioimmunoassay showed all birds to have circulating testosterone, it appears that the threshold testosterone level (MCCOLLOM *et al.*, 1971) was reached in these populations and that differences in courting and CNCMs were due to other factors.

TABLEAU 2

Means and standard errors of testosterone levels (ng/ml) and correlations of testosterone levels with courting and CNCMs by mating combination.

Moyenne et écart-type des niveaux de testostérone (ng/ml) et corrélations de ceux-ci avec le nombre de sollicitations et le nombre cumulé de copulations selon le type d'accouplement.

Mating	Testosterone		Correlations of testosterone with	
	N° ¹	$\bar{x} \pm se$	Courts	CNCMs
HH	11	2.5 ± 0.7	0.15	0.07
LL	11	2.5 ± 1.1	-0.53	0.00
CC	11	3.1 ± 1.3	-0.09	-0.06
HC	13	2.0 ± 0.7	-0.21	0.05
CH	12	2.5 ± 0.8	0.62*	0.66*
HL	15	1.6 ± 0.3	-0.21	0.14
LH	13	2.2 ± 0.7	-0.24	-0.11
LC	15	2.8 ± 0.1	-0.05	0.07
CL	12	2.1 ± 0.6	-0.25	0.10

¹ Number of observations

* $P \leq 0.05$.

B. Behavioral traits

Maters vs nonmaters

The percentage of males that completed matings were 100, 82 and 16 for the HH, CC and LL parental lines, respectively (Table 3), with the differences being significant for each parental line comparison. Differences between reciprocal crosses for percentage maters were not significant (contrasts 4, 5 and 6), suggesting that maternal effects were unimportant. Nonadditivity was apparent since values for the reciprocal crosses of the lines were larger than the midparent frequency in all comparisons with the effect being significant in contrasts 8 and 9 (Table 4). The magnitude of the nonadditivity suggests considerable heterosis for this measure. The significant difference with the higher value for CC males to that of the average for the HH and LL parental lines (contrast 11),

TABLE 3
Means and standard errors of number of courts, mounts, treads and CNCMs plus the percentage of maters and mating efficiency by mating combinations.
Moyenne et écart-type des nombres de sollicitations, montes, piétements et copulations, pourcentage de mâles ayant copulé (« maters ») et indices d'efficacité de l'accouplement selon la combinaison testée.

Mating	No. males	% mater	Number of				Mating Effic. ⁽¹⁾		
			Cts	Mts	Treads	CNCMs	Mts /Cts	CNCMs /Cts	CNCMs /Mts
HH	44	100	96 ± 3	31.2 ± 1.9	25.5 ± 1.5	24.4 ± 1.4	32	25	78
LL	77	16	29 ± 2	0.5 ± 0.1	0.5 ± 0.1	0.3 ± 0.1	2	1	60
CC	63	82	69 ± 4	7.2 ± 0.8	5.8 ± 0.6	5.2 ± 0.6	10	8	72
HC	15	100	112 ± 9	32.3 ± 3.9	25.5 ± 3.6	23.1 ± 3.2	29	21	72
CH	13	100	113 ± 8	32.7 ± 5.7	26.6 ± 3.5	24.5 ± 3.3	29	22	75
HL	17	100	106 ± 5	24.0 ± 2.8	20.4 ± 2.3	18.9 ± 2.2	23	18	79
LH	14	93	75 ± 8	18.1 ± 3.8	15.4 ± 3.1	15.0 ± 3.0	24	20	83
LC	15	87	65 ± 7	7.4 ± 1.3	6.5 ± 1.2	5.8 ± 1.2	11	9	74
CL	15	93	83 ± 10	10.3 ± 2.3	8.7 ± 2.0	8.1 ± 1.8	12	10	79

Cts = courts; Mts = mounts.

(1) Ratio × 100.

TABLE 4
Percentage heterosis (1) and asymmetry for various traits.
Effets d'hétérosis et d'asymétrie sur diverses caractéristiques.

Contrast code	% Maters	Number of				Mating efficiency		
		Cts	Mts	Treads	CNCMs	Mts /Cts	CNCMs /Cts	CNCMs /Mts
7 (nonadditivity)	10	36(*)	69(*)	66(*)	61(*)	38	30	- 2
8 (nonadditivity)	66(*)	45(*)	33(*)	38(*)	37(*)	38(*)	46(*)	17
9 (nonadditivity)	84(*)	51(*)	130(*)	141(*)	153(*)	75(*)	111(*)	16
10 (nonadditivity)	18	39(*)	192(*)	209(*)	226(*)	135(*)	138(*)	13
11 (asymmetry and/or nonadditivity)	-29(*)	- 9(*)	120(*)	124(*)	138(*)	70(*)	66(*)	- 4

Cts = courts; Mts = mounts.

(1) Estimated as percentage deviation of the first from the second combination in the contrast.

(*) Contrast was significant ($P \leq 0.05$) based on SCHEFFE's analysis.

may be attributed to the asymmetrical effect on the midline value of the large number of nonmating LL males. This effect was not observed in contrast 10, which involved a comparison of the control line to the reciprocal crosses of the selected lines and is consistent with the heterotic effect noted in contrasts 7, 8 and 9.

Courts, mounts, treads and CNCMs

Means and standard errors for number of courts, mounts, treads and CNCMs are presented by mating combinations in Table 3. Males from the HH line completed significantly more of these behaviors than those from the LL and CC lines, an observation consistent with that of DUNNINGTON & SIEGEL (1983). This pattern existed regardless of whether or not nonmaters were included in the analyses. CC males completed significantly more courts, mounts, treads and CNCMs than LL males when all males were included in the analysis. When nonmaters were excluded from the analysis, however, the difference existed for courts only. The significant differences among lines for these behaviors is evidence of additive genetic variation since the selected lines had undergone individual phenotypic selection for CNCMs, with the CC line serving as the base population for the selection experiment (SIEGEL, 1972; DUNNINGTON & SIEGEL, 1983).

No significant differences were noted between reciprocal crosses (contrasts 4, 5 and 6), regardless of whether or not nonmaters were included in the analyses, demonstrating a lack of maternal effects for these behaviors. The percentage of heterosis for courts, mounts, treads and CNCMs was significant in all comparisons (contrasts 7, 8, 9 and 10). This large effect (Table 4) shows that nonadditive genetic variation is important in the frequency of mating behavior.

When the midparent value of the selected lines was compared to that of the randombred base population (CC) by contrast 11, the CC line was significantly greater for courts and very much less for mounts, treads and CNCMs. This pattern existed whether or not nonmaters were included and supported the thesis that the response to selection for CNCMs is asymmetrical, perhaps due to unequal initial gene frequencies.

The results presented in this paper differ from those obtained in the S_{11} generation of this selection experiment (COOK *et al.*, 1973), where the means of mating traits from crosses between the HH and LL lines were lower than their respective midparent values. Now, after an additional ten generations of selection, the progeny from crosses of the high and low lines and these parental lines with the control line exhibited frequencies of mating behavior that were significantly larger than their midparent means. This change may be the effect of modifications in the threshold for mating behavior in the selected lines. The larger values for the crosses is consistent with that observed in swine (NEELY & ROBISON, 1982), and suggest that a high threshold in the low line was overridden in the crosses by heterotic effects which allowed the expression of increased mating behavior. The evidence of a nonadditive genetic variation for increased mating frequency allows for speculation that genes for a low mating threshold are recessive to those for a higher threshold.

The completion of the mating act is based on a sequence of behaviors, and mating efficiency may be considered as the ratio of a behavior to those preceding it. Mating efficiency (Table 3) was significantly greater for males from the HH line than for those from LL and unselected control line (contrasts 1 and 2). This occurred whether or not nonmaters were included in the analysis. Only when nonmaters were included in the comparison was the mating efficiency of CC males significantly greater than that for LL males (contrast 3). There were no differences between reciprocal crosses (contrasts 4, 5 and 6), showing that maternal effects were unimportant for mating

efficiency. Considerable heterosis was noted for mounts to courts and CNCMs to courts in all contrasts measuring nonadditivity (Table 4), with all being significant except those involving contrast 7.

The significant positive differences in contrast 1 (HH-LL) and contrast 2 (HH-CC) and the significant negative difference in contrast 3 (LL-CC) indicate that the HH males carried courtship through to a completed mating more often than either LL or CC males. Furthermore, courting behavior resulted in a completed mating more often in CC than in LL males. When nonmaters were excluded from the calculations, however, no significant differences existed between CC and LL males indicating that some LL males did carry through on the complete mating sequence. It appears that once a mount occurs there is a high probability that the mating will be completed, regardless of the population. This would explain the lack of heterosis for the ratio of CNCMs to mounts (Table 4) and the significant difference in ratios where courts were the denominator. Since courting initially occurs as an aggressive act and then switches to a sexual one (SIEGEL, 1959; KRUIJT, 1966), one would expect genetic differences among populations for the incidence of this switching.

The results presented here indicate that the threshold for low mating frequency has been lowered or overridden by genes for high mating frequency in the high mating line. A possible mechanism for this is an increase in the heterotic expression of genes affecting high mating frequency after the neural threshold has been attained. If these genes result in an increase in the proportion of courts that turn from aggressive to sexual behavior, the increase of CNCMs which occurred in the crosses would be expected.

Whereas behavioral differences were found between the selected lines and crosses, there were no significant differences in plasma testosterone levels. Also, correlations between circulating testosterone and the behaviors were low. This implies that the behavioral differences noted here were due to differences in brain activity control that occur at normal physiological levels of testosterone or its metabolites.

IV. Conclusion

The results of this experiment demonstrate heritable effects on the sexual behavior of male chickens. These effects include additive genetic variation as evidenced by the large differences among populations that had undergone individual phenotypic selection for frequency of completed matings. The importance of nonadditive genetic variation was shown by the large heterotic effects when crossline progeny were compared to their parental populations. No evidence was obtained to suggest that any of the traits measured were influenced by maternal effects.

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