A GENETIC HYPOTHESIS FOR SEX-MATING SYSTEM INTERACTIONS IN GROWTH OF CATTLE AND POULTRY (1)

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SUMMARY

Heterosis in weaning weight of female Hereford calves was 15% whereas it was 8% in males. Thus 50% of the heterosis in weight is associated with the extra sex chromosome. In turkeys, where the male is the homogametic sex, the heterosis in the male was 10% and 9% for linecrosses vs/inbreds crossbreds vs/purebreds, respectively, and 3% and 1% in the females, or 70% to 80% of the heterosis was associatd with the extra sex chromosome. In broilers, the hetrosis 10-week body weights was 8% for females and 14% for males. This corresponds to the turkey results. Thus, in these species, as well, the greater heterosis is in the homogametic sex. It is suggested that this disproportional contribution to heterosis by the sex chromosomes be called *homogametic heterosis.*

Males were heavier than females in cattle, chickens and turkeys, but the sex differences were small in linecross cattle, whereas they were large in hybrid turkeys and broilers. Maleness, *perse,* combined with homogametic heterosis seem to offer an explanation of these results.

The occurrence of differential levels of heterosis in the sexes ordinarily has not been reported from results of hybridizing experiments. This may be due to non-existence of consistent sex-mating system interactions or due to the fact that many of the highly heterotic traits are sex-limited, such as litter size, egg production and spermatogenesis.

However, in non sex-limited traits, there have been indications of different degrees of heterosis in males and females in the few crossing experiments were the means of sex groups within mating system were presented. (Arakeljan, 1959; Brown and Bell, 1961; Clark, 1960; Cox, 1961; Gerlaugh, Kunkle and Rife, 1951; Glazener and Blow, 1951; Moreng and Thornton, 1958). If there is consistently more heterosis in one sex than the other, the lack of additivity between the degree of hybrid vigor and the sex environment is of special interest to physiologists. If such interactions a e not prevailingly sex-associated but

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rather are characteristics of given species, genera or classes, there may be interesting avenues of exploration for the geneticist as well. Evidence on sex-mating system interactions in beef cattle and poultry and possible genetic explanations for their existence are given in this paper.

Weights at about 5 and 7 months of age were taken on unselected inbred and linecross Hereford Bull and heifer calves. These 1229 calves were born during 1952-60 at the San Juan Basin Branch of the Colorado Agricultural Experiment Station. The inbreds and linecrosses were paternal half-sibs since the sires were concurrently mated to inbred cows from within their lines and to unrelated linecross cows produced by outcrossing inbred sires on unrelated females.

The numbers, ages, inbreeding coefficients, and weights by sex, mating system and year of birth are shown in table(1). Means of inbred and linecross calves definitely indicated a degree of heterosis in weight at about 200 days of age. Five month weights followed a similar pattern. Linecross bull calves weighed 424 lb, whereas their inbred half brothers weighed 394 lb. at 199 days. Linecross bull calves thus exceeded the inbreds by 8%. Linecross heifer calves weighed 403 lb., whereas their inbred half sisters weighed 352. lb. Linecross heifer calves thus exceeded the inbred heifers by 15% or twice that found in the bulls. The sex difference for inbreds was 42 lb. or 12%, whereas that for hybrids was 21 lb. or 5%. The interaction between mating system and sex is highly significant as indicated in table (2).

The observation that the greatest heterosis in weight was found in the heifers and that this led to a greater sex difference for inbreds than for hybrids raised the question of the possibility of a sex mating system interaction in a species where the female is the heterogametic sex. Through the courtesy of R.E. Moreng, I found published 24 and 28 week weight data on purebred and crossbred turkeys and inbred and linecross turkeys available in the publications of Clark (1960) and of Moreng and Thornton (1958). In both of these studies the ratios of weights of hybrids to inbreds were greatest for the toms, the homogametic sex. Thus, the toms show greater heterosis or a greater regression of weight on inbreeding than did the turkey hens. In the crossbreeding trial, the ratio of crossbred to purebred weights in the toms was 1.10 (Table 3). These weights were taken over a period of 6 years and included over 1200 purebred and 650 crossbred turkeys. In the Moreng study, inbred lines of turkeys were compared to single cross and 4 - linecross hybrids. In his study, the ratio of hybrid to inbred weights in the males, the homogametic sex, was 1.10 ; whereas in the females it was 1.03 (Table 4). In turkeys, the sex mating system interaction is even more marked than in beef cattle. If it were not for the appreciable heterosis in the toms, there would be little heterosis in body weight in turkeys.

Top cross data on weights of broiler chickens were presented by Glazener and Blow (1951). In their experiment, eight inbred lines of chickens derived from S. C. White Leghorn, Rhode Island Red, Barred Plymouth Rock and New Hampshire foundation stocks were topcrossed to non-inbred tester females from the White Plymouth Rock as well as the four previously mentioned breeds. From Glazener's and Blow's table (1) the 10-week weight data of the males and females were analyzed for the purpose of comparing the relative heterosis in body weights of the males and females.

The weights were as follows : inbred and topcross males, 35.3 and 40.3 oz. respectively ; inbred and topcross females, 30.8 and 33.4 oz. The topcross/inbred ratios are 1.08 for females and 1.14 for males. Thus there was considerably more heterosis in body weight for the males than for the females. This corresponds to the turkey results.

The conclusion from these observations is that heterosis in body weights of these very different species is largely due to the contribution of the sex chromosomes. In beef cattle it appears that about half of the total heterosis found is the contribution of the sex chromosome complex. In turkeys it appears that 70 to 80% of the heterosis found is due to the action of the sex chromosomes, while in broilers this is about 40%.

A genetic model which might be devised as an explanation of this phenomenon must bridge the evidence indicated in the following results.

A.—There is heterosis in body weight in chickens, turkeys and cattle.

B.—Males were heavier than females, regardless of which sex is homogametic.

C.—Regression of weight on inbreeding is greatest in the homogametic sex in cattle, chickens, and turkeys. Thus it appears the heterosis found herein was more consistently associated with the sex chromosomes than with the sex endocrine environment. The results of these few experiments excite interest as to whether there may be a phenomenon such as *homogametic heterosis*, that is, whether a disproportionate amount of total heterosis in animals and birds may be attributable to the sex chromosomes.

D.—Hybrid heifers are almost the same weight as hybrid bulls at weaning ; whereas in turkeys and to a lesser extent chickens the hybrid male is considerable heavier than hybrid female.

Thus in turkeys and broilers it appears that the male has two stimuli for growth not possessed by the female. First, they have the growth impetus associated with the male endocrine system ; second, they have the advantage of the homogametic hybrid.

In contrast, in cattle, it appears that the two sexes in the linecrosses approach each other in body weight because each one possesses a quite different mechanism contributing to weight differences. The bull has the growth stimulus associated with maleness, but the linecross female has the growth advantage of the homogametic hybrid.

The question that persists is how can 50 to 90% of the heterosis be restricted to the special conditions involving perhaps as little as3-4% of the total chromosomal material ?

It may be argued that greater hybridization effects can be achieved in the sex chromosomes than is attainable with the same degree of inbreeding in the autosomes. In polygamous species such as cattle, inbreeding through extended use of a foundation sire can be easily attained. In the cattle lines from which these data were taken, this was a commonly followed mating procedure. Presumably, all daughters then obtain the same X from their sire. With extended use of a sire it may be estimated that inbreeding for X-linked genes would be about twice that achieved in the autosomal genes. But the actual average performance of all hybrids (not the heterosis as measured by the $\frac{F_1}{I}$ where the $\frac{F_1}{I}$ is the mean of all hybrids and I is the mean of all inbreds) would not be expected to become greater at higher inbreeding levels unless there were an appreciable culling of individuals and lines, which did not seem to be the situation for the cattle. However, as Tantawy (1957) has shown, when one measures heterosis as the ratio $\frac{F_1}{I}$ as was done in this paper, the degree of heterosis increases as the inbreeding of the parents increases. His data suggest, however, that there is not actually much shift in the average performance of the hybrids but the widening ratio is more likely attributable to a continued decline of the inbreds. It seems unlikely that this presumably small amount of sex chromosomal material could be ten to twenty fold as efficient as the autosomes in contributing to the heterosis found. Nevertheless, the higher rate of inbreeding in sex chromosomes than autosomes would contribute to an expanded $\frac{F_1}{I}$ (hybrid/inbred) ratio because of the faster rise in inbreeding in the X than other chromosomes in homogametic sexes.

If the Y is genetically active then females potentially can have more total genes homozygous than males, but again because of the small amount of chromosomal material this would not provide a good explanation for the sex associated heterosis.

On the other hand, within a closed population, in the heterogametic sex there would be selection pressure for genes on the X and the Y which would lead to greater sex fitness and improved combining ability within the sex-linked complex with which they coexist but do not pair. The specific combining ability between the X and Y genomes

would be in a more specifically and intensely selected path than in the autosomal complex. There is a mechanism for selection for combining ability in the X and Y that can be preserved through the forced heterozygosity of the heterogametic sex. The extra fitness accomplished through this special type of interaction should not be diminished in the heterogametic sex through inbreeding. In fact, it might well be enhanced by inbreeding, for effects of selecting out special X- and Y-linked genes that consistently combine well with each other would be preserved more effectually than with continous out-crossing. Over an evolutionary period, selection pressure on X- and Y-linked genes would have to be for combining ability as well as for fitness for the special functions of the heterogametic sex.

The alternating haploid and diploid conditions of some of the X-chromosomes in subsequent generations suggest a degree of parallelism with polyploidy. If the Y isrelatively inert this could be construed as causing homogametic heterosis because of the extra gene dosage. The reasoning does not apply here because the case for homogamatic heterosis rests upon a comparison of inbreds and crosses within the homogametic sex ; thus genic dosages of the compared groups should be equal.

Should the Y-chromosome be relatively inert genetically or missing, as indicated by some researchers, then the fate of X-linked genes is subject to their performance in the heterogametic as well as in the homogametic sex . It seems very likely in this situation that overdominat genes would be selected against within the inbred lines. It would be expected that desirable genes expressing themselves with dominance or additiveness would be favoured in selection over those genes acting with overdominance. This would modify the genic combinations which might contribute to extra heterosis in the homogametic sex. This would make it appear that since restrictions on genes because of mode of expression are clearer cut, there might be less heterosis actually emanating from the X chromosomes than from autosomes.

Another model requiring an inert Y would be sex-linked overdominance with the heterogametic sex as a phenotypic intermediate. The descending order of fitness of genotypes would be $A_x a_x$, A_x-$_Y$, a_x-$_Y$ and $A_x A_x$, $a_x a_x$. The requirement would be that the genic action is such that the heterozygous homogametic sex is superior and the homozygous homogametic sex is inferior to the hemizygous heterogametic sex.

The three major possibilities for explaining this hetrosis which seems to have prevailed in the homogametic sexes of these species are:

(1) In the presence of a gnetically active Y, there is an exceptional selection for combining abilities between the X and Y genomes within inbred lines. Thus the specific combinations are developed and

maintained which, when coupled with the extra homozysgosity inbreeding achieves, provide extra genetic divergence between inbred lines for X-and Y-linked genes. When hybrids are formed the X-linked genes are more dissimilar than the genes in the autosomal chromosomes. Thus we have a greater opportunity for heterosis due to conditions producing greater overdominance and dominance in sex linked genes than in autosomal genes.

(2) In the presence of a relatively inert Y there is extra selection pressure for favoured dominant and additive genes as compared with the selection for similarly acting genes on the autosomes. The degree of genetic diversity between lines would not be expected to be so great as in the previously described model. The importance of overdominance would be minimized except for the possible condition described in item 3 and homogametic heterosis would be the result of more intensive selection of favorable dominant genes, of which an increased dosage would occur in the hybrid. This theory would be strengthened if it can be definitely established that hens are XO rather than ZW, or if species could be studied in which XO types are typical.

(3) Sex-linked overdominance with the homozygous homogametic sex being inferior to the hemizygous heterogametic sex.

I do not wish to suggest that the results reported here cannot be coincidental, even though they are well beyond the limits of commonly accepted probability statements. There are other indications in the literature that sex-mating system interactions are appreciable, but not all support the conclusions reached in this paper. Arakeljan (1959) noted in rabbits and pigs a large decrease in numbers of females born relative to males with increased inbreeding. Brown and Bell (1961) found indications that inbreeding resulted in a greater decrease in viability in female than male Drosophila. In the cattle crossbreeding data of Gerlaugh, Kunkle and Rife (1951) there was a slightly greater heterosis in wearing weight for females than males. In contrast to this, Cox (1960) compared purebred and crossbred swine and found less heterosis in viability of females than males. Harvey (1962) reports significant interaction effects in growth rates of lambs to weaning but there was greater heterosis for males than females.

Regressions of yearling body weights on inbreeding of Rambouillet rams were steeper in the 1948 paper by Terrill, Sidwell and Hazel (1948) than reported by Hazel and Terrill in 1946 for yearling Rambouillet.

There is obviously confounding with other factors in some of these papers. Intra-litter competition and year differences appear to exist in some of the sheep and swine reports. The direction of results are contradictory but there is agreement that significant interactions frequently are occurring. It is a subject of sufficient biological interest to encourage further analyses and classification of reasons for the effect of mating system on sex differences.

TABLE 1.—Weaning Weights of Hereford Calves 1952-1960

Year	No.		Calf age days		Dam age, years		Calf inbreeding		Dam inbreading		Actual weight, pounds		Sex difference lb	Sex difference ratio
	M	F	M	F	M	F	M	F	M	F	M	F	M–F	M/F
Inbreds														
1952	18	23	228	220	4.4	3.7	0.31	0.29	0.21	0.19	395	339	56	1.17
1953	30	27	205	196	4.0	4.0	0.31	0.29	0.22	0.19	394	370	24	1.06
1954	39	36	194	193	4.0	4.5	0.31	0.31	0.20	0.22	397	358	39	1.11
1955	25	20	192	192	4.2	4.0	0.32	0.32	0.22	0.22	398	336	62	1.18
1956	27	25	191	186	4.8	4.7	0.35	0.33	0.26	0.23	363	330	33	1.10
1957	22	21	201	200	5.7	5.6	0.33	0.35	0.22	0.23	415	377	38	1.10
1958	29	29	195	192	6.1	5.9	0.32	0.32	0.24	0.23	393	350	43	1.12
1959	25	27	194	184	6.0	5.7	0.35	0.36	0.26	0.26	418	361	57	1.16
1960	28	26	187	193	6.6	5.8	0.37	0.34	0.29	0.28	369	351	18	1.05
Mean	243	234	199	195	5.1	5.0	0 33	0.32	0.24	0.23	394	352	42	1.12
Linecrosses														
1952	36	29	224	229	4.5	4.3	0.05	0.05	0.05	0.05	405	395	10	1.03
1953	30	20	208	196	3.6	4.4	0.05	0.05	0.05	0.05	447	420	27	1.06
1954	35	44	199	195	3.9	3.7	0.05	0.05	0.05	0.05	427	377	50	1.13
1955	27	35	191	195	4.1	4.2	0.05	0.05	0.05	0.05	443	412	31	1.08
1956	39	34	194	196	4.6	4.4	0.05	0.05	0.05	0.05	403	378	25	1.07
1957	34	41	203	205	5.1	5.2	0.05	0.05	0.05	0.05	430	414	16	1.04
1958	37	48	197	196	5.8	5.3	0.05	0.05	0.05	0.05	417	398	19	1.05
1959	39	42	189	198	6.2	6.5	0.05	0.05	0.05	0.05	445	426	19	1.04
1960	35	28	186	193	5.4	5.6	0.05	0.05	0.05	0.05	400	403	— 3	0.99
Average	312	321	199	200	4.8	4.8	0.05	0.05	0.05	0.05	424	403	21	1.05
Ratio = Linecross / Inbreds			1.00	1.03	0.94	0.96	0.15	0.16	0.21	0.22	1.08	1.15	0.50	0.94

M = Male, F = Female

TABLE 2.—Estimated Mean Square of 200-Day Weights of Inbred and Linecross Bull and Heifer Calves

Source		M. S.
Total	1229	
Mating system	1	473,560**
Sex	1	223,313**
Mating system x sex	1	44,982**
Remainder	1226	5,011[a]

** Probobility = .01
a = Weaning weight variance taken from Burgess *et al.* (1954).

TABLE 3.—Heterosis in 28-week weights of purebred and crossbred male and female turkeys, Clark, (1960)

Item	Males, M	Females, F
	Mean weight	
Purebreds (P)	19.16 lb.	12.44 lb
Crossbreds (C)	20.87 lb.	12.58 lb
	Ratio of weights	
	$\frac{CM}{PM} = \frac{20.87}{19.16} = 1.09$	$\frac{CF}{PF} = \frac{12.58}{12.44} = 1.01$
	$\frac{PM}{PF} = \frac{19.16}{12.44} = 1.54$	$\frac{CM}{CF} = \frac{20.87}{12.58} = 1.65$

TABLE 4.—**Heterosis in 24-week weights of inbred and hybrid male and female turkeys, Moreng and Thornton (1958)**

Item	Males, M	Females, F
	Mean weight	
Inbred (I)	15.6 lb	11.7 lb.
Hybrid (H)	17.2 lb.	12.0 lb.
	Ratio of weights	
	$\frac{HM}{IM} = \frac{17.2}{15.6} = 1.10$	$\frac{HF}{IF} = \frac{12.0}{11.7} = 1.03$
	$\frac{IM}{IF} = \frac{15.6}{11.7} = 1.33$	$\frac{HM}{HF} = \frac{17.2}{12.0} = 1.43$

(Printed in 1966)

نظرية وراثية لنظام التزاوج الجنسى وعلاقته بالنمو فى المـاشية والدواجن

هوارد ستوناكر

الملخص

تبين من هذا البحث أن قوة الخليط فى العجول الهرفورد الأناث ١٥٪ مقابل ٨٪ فى الذكور وعليه فيمـكن القول أن ٥٠٪ من قوة الخليط فى الوزن تصاحب زيادة مستوى الهرمونات الجنسية . أما فى الدجاج الرومى حيث تكون الذكور متجانسة الكروموزومات فان قوة الخليط فى الذكر تكون ١٠٪ و٩٪ و ٣٪ و ١٪ فى الخليط بين السلالات والمربى تربية أقارب والمربى تربية اباعد والسلالات النقيـة على التوالى . أى أن ٧٠ ــ ٨٠٪ من قـوة الخليط تصاحب العـدد الزائد من الكروموزومات الجنسية . وفى دجاج اللحم سن عشرة أسابيع تكون نسبة قوة الخليط فى وزن الجسم ٨٪ للاناث و ١٤٪ للذكور وهى تنتمى لنتائج الرومى . وفى مثل هذه الأنواع تكون أكبر قوة للخليط فى الجنس المتجانس . واقترح تسمية ذلك بالتجانس الجاميطى لقوة الخليط .

والذكور تكون أكبر فى الوزن فى المـاشية والدجاج والرومى ولكن ينخفض هذا الفرق فى خليط السلالات فى المـاشية .