Research Into Sex Linked Control of Bodyweight in Poultry and Rabbits

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SUMMARY

Sixteen weeks bodyweight from one progeny group of rabbits, and six weeks bodyweight from progeny groups of three breeding flocks of poultry were analysed. Variance components and two sets of heritability estimates were calculated for each sex in each group. In both species, the estimated variance components strongly suggested that sex-linkage was operating in bodyweight inheritance. Progeny from a broiler breeding experiment provided further evidence for sex-linked control of bodyweight in poultry.

In two reports in the literature of work with turkeys, it was possible to explain results in terms of sex-linked control of bodyweight. Three reasons are suggested why so many reports ignore sex-linkage in bodyweight inheritance.

It was concluded that sex-linkage was important in the inheritance of bodyweight (or growth rate), in rabbits, poultry, and probably turkeys. It appears reasonable to expect sex-linkage to affect bodyweight inheritance in other species as well.

I. INTRODUCTION

Few reports on inheritance of bodyweight at any particular age consider sex-linked genes. In poultry, reports by Jull (1952), Godfrey (1953) and (1957), Brunson et al (1956), and Jerome et al (1956) indicate that some variation in bodyweight is due to sex-linked genes. On the other hand many reports including in poultry Morris and Skaller (1958), in turkeys Johnson and Asmundson (1957), in mice Falconer (1951) and Chai (1958), and in rabbits Yao and Eaton (1954), make no reference to sex-linkage in bodyweight inheritance.

This paper presents evidence that sex-linkage affects both 16-weeks bodyweight of rabbits and 6-weeks bodyweight of poultry. Further, reports in the literature of work with turkeys are discussed to show that sex-linkage may have operated in bodyweight inheritance.

II. MATERIALS AND METHODS

(a) Rabbits.-Data on 16-weeks bodyweight were obtained from 429 rabbits reared at the C.S.I.R.O. laboratory at Prospect during 1959. The rabbits were the progeny of 25 sires, mated to an average of 3.5 dams each. Mating was at random, with no conscious selection for bodyweight. Examination of pedigrees showed inbreeding to be low.

(b) Poultry.-Data on 6-weeks bodyweight were obtained from the progeny of three breeding flocks of poultry at the Poultry Experiment Station, Seven Hills, during 1959. The flocks were (1) Australorp (AO)—701 progeny; (2) White Leghorn (WL)—610 progeny; and (3) A flock of crossbreds in which the reciprocal crosses between AO and WL were mated in all combinations-759 progeny (F2 generation between AO and WL). These flocks were under selection for egg production and had not been selected for bodyweight. Each flock consisted of 12 sires each mated to 10 dams

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at random with the restriction that full-sib matings were not permitted. The progeny were hatched in six hatches at weekly intervals during August and September.

(c) Broiler Breeding **Experiment.**—5½-week bodyweight data were obtained from the progeny of reciprocal crosses between three commercial broiler strains, A, B and C, mated to White Leghorns (WL). In these matings three males were rotated through the pens of 12 dams to produce each cross. About 60 chickens of each sex were hatched per pen in five hatches. Similar data was obtained from reciprocal crosses between AO and WL, the controls for this breeding programme.

(d) Analysis of data.-Within each progeny group (Section (a) and (b)) sexes were analysed separately. The poultry data (Section (b)) was analysed within hatches following King and Henderson (1954), with degrees of freedom for sires within hatches, and for dams within sires within hatches, pooled over all hatches. The method of these workers was followed also in all analyses for the calculation of the coefficients of the variance components and the variance component estimates.

III. CALCULATION OF HERITABILITY ESTIMATES

Heritability in the narrow sense, i.e. the proportion of variation due to additive genetic variation, is usually calculated as follows, assuming that this variation is not sex-linked:—

$$h^2_S = \frac{4S}{S+D+Q} \qquad \text{or} \qquad h^2_D = \frac{4D}{S+D+Q}$$

where S = estimated variance component due to sires
D = estimated variance component due to dams
Q = estimated variance between full sibs
and $S+D+Q$ = total phenotypic variation.

This is because the additive genetic variation in a, population mating at random is derived as follows :—One fourth from sires, one fourth from dams, and one half from chance at meiosis (Wright 1921). These formulae apply whether the population is of mixed sex or of either sex on its own.

Where additive genetic variation is assumed to be located on the X chromosomes only, the situation in a population of males differs from that in a population of females. Using Wright's approach as before, the following solutions are obtained for completely sex-linked, additive variation in randomly mating populations:- .

(a) In male rabbits (X—) additive variation is derived as follows :—

None from sires (S) *
½ from dams (D) *
½ from chance

The heritability estimate thus is $h^2_D = \frac{2D}{S+D+Q}$

(b) In female rabbits (XX) additive variation is derived as follows :—

½ from sires (S)
¼ from dams (D)
¼ from chance

Heritability estimates thus are $h^2_S = \frac{2S}{S+D+Q}$ or $h^2_D = \frac{4D}{S+D+Q}$

(c) In male poultry (XX) additive variation is derived as follows:—

¼ from sires (S)
½ from dams (D)
¼ from chance

Heritability estimates thus are $h^2_S = \frac{4S}{S+D+Q}$ or $h^2_D = \frac{2D}{S+D+Q}$

(d) In female poultry (X—) additive variation is derived as follows :-

½ from sires (S)
None from dams (D)
½ from chance

The heritability estimate thus is $h^2_S = \frac{2S}{S+D+Q}$

* Sires' component (S) and dams' component (D) may of course contain variation from non-additive gene action or maternal effects, as in the autosomal case. Also S+D+Q again equals total phenotypic variation.

IV. RESULTS

Table I shows for the four progeny groups analysed, the estimated variance components and heritability estimates, calculated assuming either completely autosomal, or completely sex-linked additive genetic variation. Table II shows average 5½-weeks bodyweights of reciprocal crosses between heavy broiler strains and light WL poultry Figures in brackets are standard errors.

V. DISCUSSION OF RESULTS

The variance components of table I suggests sex-linked inheritance of bodyweight in both species. In rabbits (a) The relative effect of each parent is greater in progeny of opposite sex, and (b) Sires' component in sons is 0. This is expected as rabbit sires do not contribute X chromosomes to sons. With autosomal inheritance sires' components of similar order and value relative to dams' components are expected in both sexes. These results thus depart from completely autosomal inheritance, yet may be satisfactorily explained by sex-linkage.

In each of the poultry flocks (a) The relative effect of each parent is again greater in progeny of opposite sex, and (b) The component for dams in sons' bodyweight is very much greater than any of the other three components Sires' in Sons, and both Sires' and Dams' in daughters. As indicated in Section III (c) the heterogametic dam must give exactly the same X chromosome to all her sons. Dams thus contribute no sex-linked variation between full sibs, all variation due to dams appearing between dams (i.e. in D). These results again depart from autosomal inheritance in which relative values of parents ought to be similar in both sexes. In both pure breeds AO and WL, there is an unexplained departure from both sex-linkage and autosomal inheritance. In these groups sires' components in sons are 0. The reason for this is not known to the author.

Indirect evidence for sex-linkage rather than autosomal inheritance in both species is obtained by comparing the two columns of heritability estimates. Assuming autosomal inheritance, it would be necessary to assume also the presence of much higher maternal effects than under sex-linkage. In both species therefore the evidence is overwhelmingly in favour of sex-linkage in the inheritance of bodyweight.

TABLE 1. Variance Components, Heritability Estimates and Co-efficients of Variation Calculated from One Group of Rabbits and Three Flocks of Poultry.

Description of Data		Source of Variation	d.f.	Estimated Variance Components	Heritability * % Assuming:—		Mean Weight	Coefficient of Variation of Full Sib %
					Autosomal	Sex-linked		
Rabbits: 16 Weeks' Body Weight (gms.)	(F.)	Between sires	23	26,145	80.20	40.10	—	—
		Between dams W. sires	58	35,401	108.59	108.59	—	—
		Between full-sibs	119	68,861	—	—	2196 gms.	11.9
	(M.)	Between sires	24	0 (–2,522)	0	—	—	—
		Between dams W. sires	62	38,516	177.43	88.72	—	—
		Between full-sibs	141	48,316	—	—	2045 gms.	10.7
Poultry: Australorps 6 Weeks' Body Weight (lbs.) Within Hatches	(F.)	Between sires	63	.00309	57.46	28.73	—	—
		Between dams W. sires	215	.00628	116.78	—	—	—
		Between full-sibs	184	.01214	—	—	.797 lb.	13.8
	(M.)	Between sires	46	0 (–.00169)	0	0	—	—
		Between dams W. sires	113	.01129	130.48	65.24	—	—
		Between full-sibs	68	.02332	—	—	.868 lb.	17.6
White Leghorns 6 Weeks' Body Weight (lbs.) Within Hatches	(F.)	Between sires	59	.00281	69.25	34.63	—	—
		Between dams W. sires	182	.00232	57.18	—	—	—
		Between full-sibs	146	.01110	—	—	.655 lb.	16.1
	(M.)	Between sires	50	0 (–.00010)	0	0	—	—
		Between dams W. sires	106	.00939	155.79	77.90	—	—
		Between full-sibs	55	.01472	—	—	.780 lb.	15.6
Crossbreds 6 Weeks' Body Weight (lbs.) Within Hatches	(F.)	Between sires	59	.00161	37.10	18.55	—	—
		Between dams W. sires	226	.00017	3.92	—	—	—
		Between full-sibs	191	.01558	—	—	.757 lb.	16.5
	(M.)	Between sires	41	.00314	41.47	41.47	—	—
		Between dams W. sires	129	.00965	127.43	63.72	—	—
		Between full-sibs	101	.01750	—	—	.871 lb.	15.2

* Calculated from the appropriate variance component, e.g., in AO (F.): $h_S^2 = 57.46\%$ or 28.73%; $h_D^2 = 116.78\%$

The average bodyweights of progeny in the broiler breeding experiment shown in table II provide further evidence for the operation of sex-linkage in poultry. Female progeny from heavy (broiler) sires are heavier than the female progeny of the light (WL) sires. There is no such distinct difference among male offspring. The difference between sexes is much greater in the cross, small sire x large dam, than in the reciprocal cross. These results simply reflect the genetic merit for bodyweight of the various X chromosomes.

VI. GENERAL DISCUSSION

(a) Shaklee et al (1952) investigated the inheritance of sex difference in bodyweight in Beltsville small white turkeys. They analysed the differences in 24 weeks weight between a male and the mean of his sisters, and vice versa. The variance analysis showed a significant effect of dams, and no further effect of sires, on the sex-difference as defined, whether measured as male minus mean female, or mean male minus female. They concluded that full-sib families differed significantly in the amount by which males outweighed females. In terms of sex-linkage these results may be explained as follows. A sire contributes an X chromosome to both sons and daughters. Both sexes thus tend to be influenced equally and difference between sexes is unaffected. Dams supply an X chromosome to sons only. This may improve or depress the mean bodyweight of sons relative to daughters depending on the genetic merit of the X chromosomes.

(b) McCartney (1955) studied heritability of bodyweight of White Holland turkeys at 16 and 24 weeks of age. He used variance component analysis and offspring dam regressions. Table III is condensed from McCartney's table IV. The relatively greater effect of each parent on progeny of opposite sex, suggests that sex-linkage was operating in bodyweight inheritance.

TABLE III.

Heritability Estimates of Body Weight of White Holland Turkeys from Data of McCartney, 1955.

	MALES		FEMALES	
	16 Weeks	24 Weeks	16 Weeks	24 Weeks
h^2_S	.234	.326	.589	.612
h^2_D	.617	.683	.415	.596

These two reports show that sex-linked inheritance of bodyweight may also occur in turkeys. It is probable that mature bodyweight will reflect the trends shown by immature bodyweight (Godfrey 1953 and 1957). Further as sex-linkage of bodyweight appears to operate in three different species it may be expected to occur more generally.

In mammals there are several reports of important maternal influence in bodyweight determination, in which the progeny have not been separated into sexes (Chai 1956, Bailey 1953, Becker 1955, Yao and Eaton 1954). In these reports it is impossible to separate genetic sex-linkage from non-sex-linked maternal effects.

Similarly in birds there are reports where, because sexes have not been separated, or only one sex weighed, differences in non-additive gene effects between reciprocal crosses cannot be analysed into sex-linkage or other gene interactions (Kan et al 1959, Morley and Smith 1954).

TABLE II.

5½ Weeks' Body Weights of Progeny of Reciprocal Crosses Between Heavy and Light Poultry (lbs.)

Sire	A	B	C	AO	WL	WL	WL	WL
Dam	WL	WL	WL	WL	A	B	C	AO
M.	.782	.843	.780	.772	.797	.873	.869	.717
	(.017)	(.018)	(.022)	(.028)	(.020)	(.021)	(.019)	(.031)
F.	.719	.741	.734	.713	.629	.712	.683	.605
	(.016)	(.020)	(.016)	(.027)	(.017)	(.022)	(.018)	(.021)
M.—F.	.063	.102	.046	.059	.168	.161	.186	.112
	(.023)	(.027)	(.027)	(.039)	(.026)	(.031)	(.026)	(.037)

In the many other reports of bodyweight inheritance, which show no evidence for sex-linkage one or more of the following reasons may apply.

(1) Sex-linkage is not detectible due to the nature of the data, e.g. unsexed progeny.

(2) X chromosomes of a breeding population may be uniform for bodyweight determining factors.

(3) Genotype-environment interactions may obscure sex-linked genes affecting bodyweight, e.g. McDonald (1957 a and b) showed that dietary cysteine determined whether a particular sex-linked genetic difference in growth rate was observed in poultry.

VII. CONCLUSIONS AND PRACTICAL CONSIDERATIONS

Sex-linkage plays a significant part in the inheritance of growth rate, or bodyweight, in rabbits, poultry and probably in turkeys. As this mechanism is important in such different species it is likely to be present in other species as well.

Where sex-linkage operates, rate of genetic progress under selection should be highest when the most intense selection can be practised in the homogametic sex. The heterogametic progeny reflect completely the genetic constitution of the homogametic parents, while the homogametic progeny are the average of both parents (Li 1955).

In poultry, the male is homogametic. Sex-linkage may thus be responsible for some of the rapid progress made in bodyweight selection of meat chickens in recent years. Of more short term practical importance to broiler growers is the fact that highly selected cockerels should produce good pullet offspring, leading to a more even progeny of unsexed broilers, as indicated in table II.

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