Genet. Res., Camb. (1960), **1**, *pp.* 39–49
Printed in Great Britain

The birth weight of rabbits born after heterospermic insemination

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(*Received* 4 *May* 1959)

INTRODUCTION

Insemination with mixed semen from two or more sires has been called *heterospermic insemination*. The more usual mode of insemination, using semen from one sire at a time, may be called *homospermic insemination*. During an experiment with the rabbit (Beatty, 1955, 1957*a*), it was noted that when genetically large and genetically small offspring were born in the same litters after heterospermic insemination, the average difference in birth weight between them was greater than when they were conceived in different litters after homospermic insemination. This accentuation of the difference in birth weight was termed the *enhancement effect* in relative birth weight. An approximate test of significance suggested that the effect was real. In a search for supporting evidence, an analogous situation was explored in mammalian twins, where the genetically large and genetically small offspring are the male and female young respectively. Like-sexed twin pairs are analogous to litters born after homospermic insemination. Unlike-sexed twin pairs are analogous to mixed litters born after heterospermic insemination. An enhancement effect was, indeed, apparent in human twins and in those from the sheep (Beatty, 1956). An independent and more detailed study of sheep twins by Donald and Purser (1956) showed the same effect.

The present work is, primarily, an independent confirmation of the reality of the enhancement effect after heterospermic insemination in the rabbit. As in the earlier work with rabbits, it has been possible also to test the claim that heterospermic insemination gives superior practical results in the form of 'heterospermic vigour' among the offspring, evidenced by greater birth weight (see, e.g., Kushner, 1954). However, once again, no real 'heterospermic vigour' could be demonstrated. The sampling structure of the earlier experiment was not well defined, and no formal quantitative integration with the present results has been attempted.

The enhancement effect is of interest in showing that the size of an animal at birth is influenced by the genotype of its litter-mates. Further, it constitutes evidence of competition among offspring *in utero.*

MATERIAL AND METHODS

Two sires were used. ♂L was a Flemish Giant, weighing 4·5 kg., and genetically *AA BB CC DD RR*. ♂S was of indeterminate breed, weighed 2·5 kg., and was genetically *aa B cc^h D rr*. The two males were known to give offspring differing considerably in mature weight, and named Large and Small offspring. The sixty-eight females, from a stock of indeterminate breed averaging about 3·0 kg. in weight, were each used once only, and were of genetic constitution *cc* and/or *rr*. When the female was *cc* (homozygous for the recessive character albino), offspring of ♂L had dark eyes (*Cc*), while those of ♂S were unpigmented (either *cc* or cc^h). When the female was *rr* (homozygous for rex, a recessive hair-waving factor), offspring of ♂L had normal whiskers (*Rr*), whereas offspring of ♂S had waved whiskers (*rr*). At birth, offspring could therefore be traced to their sires by eye-colour and/or the appearance of their whiskers. Artificial insemination was carried out by the method of Walton (1945). In heterospermic insemination, semen of the two sires was mixed in proportions that yielded roughly equal numbers of offspring from each sire. 0·85% NaCl was used as semen diluent. Inseminates were 1 ml. in volume and contained a total of *ca.* 5–30 million spermatozoa. All inseminations were artificial, excepting that eleven additional litters born after natural mating were available and were classed among the homospermic litters. Females, as they became available for the experiment, were allocated to the different classes of insemination so that running totals of roughly equal numbers of litters were obtained from ♂L only, from ♂S only, and from mixed semen.

Hutches were examined for litters from 9 a.m. to 5 p.m. daily. Offspring found were recorded as born on that day. Their birth weight was scored, to the nearest gramme, as their weight at the time they were found. Five damaged offspring, and a miniature still-birth, were dealt with as described in Table 1.

The following classes of litter were obtained. It may be noted that 'heterospermic litters' are all litters born after heterospermic insemination, while 'mixed litters' are the class of 'heterospermic litters' in which offspring by both sires are present in the same litter.

Type of insemination	Sire of offspring	Convention for naming litter		Number of litters	Number of offspring
Homospermic L	♂L	Homospermic L	Homospermic	18	87
Homospermic S	♂S	Homospermic S		23	116
Heterospermic	♂L	Heterospermic L	Heterospermic	2	7
	♂S	Heterospermic S		3	13
	♂♂L+S	Mixed litter		22	68 by ♂L 76 by ♂S

The object of study was birth weight, in the form of the litter average of the logarithmic birth weights of the class of offspring under consideration, and it was desired to adjust for certain attributes of each litter. The remainder of this section describes the biometrical methods employed.

Table I. *Summary of geometric-mean birth weights of offspring in each litter (in grammes); number in litter; gestation period; classified by sire and by type of insemination*

Homospermic insemination						Heterospermic insemination				
Sire L			Sire S			Sire L		Sire S		
Birth weight	Number in litter	Gestation period (days)	Birth weight	Number in litter	Gestation period (days)	Birth weight	Number in litter	Birth weight	Number in litter	Gestation period (days)
78	4	33	59	2	32	68	4	—	–	32
41	2	28	60	4	33	54	3	—	–	32
71	3	34	50	6	32	—	–	46	5	31
66	2	33	46	8	31	—*	–	46*	7	31
85	1	33	55	3	32	—*	–	63*	1	33
96	2	33	50	5	31	27	2	23	2	28
37	9	31	50	7	31	62	2	56	2	32
60	4	33	58*[c]	3	35	28	6	29	1	27
31[c]	5	30	65*[c]	2	32	58	2	44	7	32
45	9	31	44*	5	32	74	1	60	2	32
55	7	32	50*	5	31	71	1	65	2	32
52	6	32	36*[c]	5	30	62	5	41	4	31
58*	5	32	56*	6	33	63	3	49	6	31
69*	5	32	46*	5	30	69	4	52	1	33
56*[c]	5	35	48*	4	30	60	3	54	4	31
69*	4	33	55*	5	30	52	5	46	2	31
76*	4	32	47*	4	32	60	6	54	1	33
26*[a]	10	30	40*	8	31	58	4	48	5	32
			62*	7	31	59	4	49	3	31
			51*	6	31	62	6	60	1	33
			52*	5	31	45	2	35	3	32
			50*	5	31	38	4	42	5	32
			50*	6	32	46*	1	51*	5	32
						46*	2[d]	36*	6	30
						39*	2	35*[b]	7	31
						66*	1	65*	3	31
						66*	2	55*	4	31

[a, b] If the original mean logarithmic birth weights (to two places of decimals) are to be reconstituted, double rounding-off error is avoided by taking 1·41 as the logarithm at *a* and 1·55 as the logarithm at *b*.

[c] One offspring in each litter damaged and unweighable, and given a substitute birth weight equal to the mean of its litter-mates.

[d] A still-birth weighing 2·5 g. was excluded when computing mean birth weight and proportion of Large offspring in the litter, but is included in the 'number in the litter'.

* Two classes of dam were used, differing in body weight. Litters from the lighter class are marked with an asterisk.

Birth weight was analysed after $\log_{10}$ transformation of the birth weight of each offspring. This was known to improve homogeneity of variance within the litter. It also brought birth weight into nearly linear relationship with an important variable, the number of offspring per litter (Venge, 1950). Further, it was felt that relative birth weight of the two types of offspring, as measured by a difference between logarithms, would be more nearly a constant than the actual difference in grammes. The following averages of the logarithmic birth weights were studied, and formed the dependent variables in the multiple regressions described later: Y_1, mean logarithmic birth weight per litter in homospermic litters (data from homospermic L + homospermic S litters); Y_2, mean logarithmic birth weight per litter in heterospermic litters (data from heterospermic L + heterospermic S + mixed litters); Y_3, mean logarithmic birth weight per litter of Large offspring in heterospermic litters (data from heterospermic L + mixed litters); Y_4, mean logarithmic birth weight per litter of Small offspring in heterospermic litters (data from heterospermic S + mixed litters); Y_5, mean logarithmic birth-weight difference in mixed litters (mean logarithmic birth weight of Small offspring subtracted from mean logarithmic birth weight of Large offspring in the twenty-two mixed litters).

The following data recorded for each litter formed the independent variables in the multiple regressions described below, the means being the grand experimental means (weighted by number of offspring per litter): X_1, gestation period in days, mean 31·4; X_2, number of offspring in litter, mean 6·29; X_3, maternal weight, entered as a 'dummy variate' with values of 100 for a heavier lot of females and 0 for a lighter lot, mean 58; X_4, percentage of Large offspring per litter, entered as either 100% or 0% for homospermic L and homospermic S litters respectively, and varying from 100% to 0% in the heterospermic litters, mean 44%. These grand means will be referred to as 'standard gestational conditions' to which birth weights could be adjusted before comparison.

Multiple regressions of $Y_1 \dots Y_5$ were then carried out on the four independent variables $X_1 \dots X_4$. The regressions of $Y_1 \dots Y_4$ were weighted by the number of young under consideration per litter. The regression of Y_5 was weighted by $n_1 n_2/(n_1+n_2)$, n_1 and n_2 being respectively the numbers of Large and Small offspring per litter. The multiple regressions of $Y_1 \dots Y_4$ were highly significant and accounted for about half the sum of squares of Y. This was mainly due to the large sums of squares taken out by the partial regressions on X_1 and X_2. The partial regression coefficients on X_3 and X_4 were all small and non-significant. In using these multiple-regression equations for adjusting birth weights, the means of $Y_1 \dots Y_4$ were little affected by setting $X_1 \dots X_4$ to 'standard gestational conditions', but a considerable diminution in the standard errors of predicted Y was achieved. Neither the multiple regression of Y_5 nor any of its partial-regression coefficients even approached significance, and it was therefore concluded that the *relative* birth weight of Large and Small offspring in mixed litters bore little or no relation to the values of $X_1 \dots X_4$. No adjustment of Y_5 to 'standard gestational conditions' was deemed necessary. The mean logarithmic birth-weight difference between Large and Small offspring in mixed litters was therefore taken as the simple weighted mean of the 22 differences.

The relationship between birth weight and number of offspring per litter was nearly linear as a result of the logarithmic transformation of birth weight. Other relationships implicit in the multiple regressions were assumed for the present purposes to be approximately linear.

In any multiple regression, it is implicit that variations in the X may cause changes in the value of Y, but that variations in Y do not affect the X. This one-way direction of cause and effect certainly applies for X_3, whose values were set wholly by the choice of dam, while X_4 was determined largely by the proportions in which semen from each male were arranged to contribute to the final inseminate. Variations in X_1 and X_2 were assumed to be determined mainly by the particular constitution of each dam (see Venge, 1950; Beatty, 1957*a*). Possible effects of Y on X_1, X_2 and X_4 were assumed to be negligible.

The five multiple regressions served the purpose of integrating the information of this experiment in convenient form for computing the various weighted logarithmic means and standard errors described in the Results section. Antilogarithms of the logarithmic means yielded weighted geometric-mean birth weights in grammes. Antilogarithms of mean differences yielded geometric-mean ratios. It has not been felt necessary to repeat in what follows that all data are weighted. Analyses have been conducted only so far as to bring out the main points of the experiment.

RESULTS

A summary of the original data is given in Table 1.

1. *Comparison of birth weight in homospermic and heterospermic litters; absence of 'heterospermic vigour'*

Birth weights in homospermic and heterospermic litters were compared first from the crude data, i.e. from the mean logarithmic birth weights of all homospermic and of all heterospermic offspring. As shown in the right-hand column of Table 2, in the form of geometric means, there is little difference between the homospermic and heterospermic litters, the heterospermic offspring averaging 1·1 g. *less* than the homospermic offspring: this difference was found to be non-significant.

Birth weights were then analysed after adjustment to 'standard gestational conditions'. As shown in Table 2, the difference between the mean logarithmic birth weights of homospermic and heterospermic litters scarcely exceeds its standard error and is obviously non-significant. These logarithmic means have been translated into geometric means in the central column of figures of the Table; heterospermic offspring average 2·3 g. more than homospermic litters.

In the crude data and in the adjusted data, there is therefore no evidence of any real effect of heterospermic insemination on the birth weight of the heterospermic litter as a whole.

Table 2. *Birth weights of offspring in homospermic and heterospermic litters*

Type of litter	Birth weight adjusted to 'standard gestational conditions': Logarithmic mean ± standard error	Birth weight adjusted to 'standard gestational conditions': Geometric mean (g.)	Unadjusted geometric mean birth weight (g.)
a. Heterospermic	$1{\cdot}703 \pm 0{\cdot}0158$ (22 d.f.)	50·4	48·7
b. Homospermic	$1{\cdot}682 \pm 0{\cdot}0124$ (36 d.f.)	48·1	49·8
Difference, $a-b$	$+0{\cdot}021 \pm 0{\cdot}0200$ (58 d.f.)		

The column of logarithmic means and standard errors is derived from the multiple regressions of Y_1 and Y_2, with $X_1 \ldots X_4$ set at the grand experimental means. The antilogarithm of the logarithmic mean gives the geometric mean. The unadjusted geometric means are derived from logarithmic means of the crude data without use of multiple regression.

2. *Difference between birth weights of Large and Small offspring in homospermic versus heterospermic litters; confirmation of the enhancement effect*

From the crude data (geometric means of all offspring in the classes of offspring under consideration, not adjusted by multiple regression), it was found that the difference in birth weight between Large and Small offspring (Large − Small) was −0·09 g. in homospermic litters, but +7·65 g. in heterospermic litters. The difference between these differences (+7·74 g.) represents a positive enhancement effect, as was also found in the more detailed analysis given below.

The mean logarithmic difference in birth weight between Large and Small offspring (Large − Small) in homospermic litters, independent of gestation period, number of offspring per litter, and maternal weight, was given by the partial regression coefficient of Y_1 on X_4. Its value was $-0{\cdot}008 \pm 0{\cdot}0260$ (36 d.f.). This indicates a slight estimated inferiority in the weight of Large offspring, but the difference is clearly non-significant in comparison with its large standard error, and could be consistent with a real difference that was either positive or negative.

The mean logarithmic difference in birth weight between Large and Small offspring (Large − Small) in mixed heterospermic litters was obtained directly from the 22 logarithmic differences, as outlined on p. 42, use of the non-significant multiple regression having been considered unnecessary. Its value of $+0{\cdot}068 \pm 0{\cdot}0124$ (21 d.f.) was highly significant ($P \ll 0{\cdot}001$). The reality of this difference was quite obvious even in the raw data (see Table 1). From the antilogarithm of this mean, it was seen that Large offspring averaged 16·9% heavier than Small offspring at birth, confidence limits being 24·0% and 10·1% at the 0·05 probability level.

The difference between the two mean logarithmic differences measures the enhancement effect. Its value of +0·076 is significantly different from zero, the Behrens-Fisher test (Fisher and Yates, 1948) and the Cochran-Snedecor test (Snedecor, 1956) each yielding a significance level of $P = 0{\cdot}05$–$0{\cdot}01$, and probably nearer to 0·01 than 0·05. The enhancement effect may therefore be considered a real phenomenon.

3. *Effect of heterospermic insemination on the relative birth weights of Large and Small offspring*

The difference in birth weight between Large and Small offspring is enhanced in mixed litters. Is this due to increased weight of Large offspring, or to decreased weight of Small offspring, or to both factors? The question was investigated after adjustment of birth weights to 'standard gestational conditions' of gestation period, number of offspring per litter, and maternal weight. As shown in Table 3,

Table 3. *Mean geometric birth weights of Large and Small offspring in homospermic and heterospermic litters, as at 'standard gestational conditions' of gestation period, number of offspring per litter, and maternal weight*

Type of offspring	Type of litter: Homospermic	Heterospermic	Difference
Large	47·6 g.	54·6 g.	+7·0 g.
Small	48·4 g.	48·1 g.	−0·3 g.

Means for homospermic litters are derived from the multiple regression of Y_1, with $X_1 \ldots X_3$ set at the grand experimental means, and X_4 set at 100 (for Large offspring) or at 0 (for Small offspring). Means for heterospermic litters are derived from the multiple regressions of Y_3 and Y_4, with $X_1 \ldots X_4$ set at the grand experimental means. Tests carried out on the logarithmic figures showed that the difference of +7·0 g. was nearly significant at the $P = 0{\cdot}05$ level, while the difference of −0·3 g. was not significant.

heterospermic insemination brought about little estimated change in the birth weight of Small offspring, the decrease of 0·3 g. being found non-significant. The estimated effect on Large offspring was, however, a considerable increase in birth weight (7·0 g.) whose significance was found to lie close to the conventional limit of $P = 0{\cdot}05$.

The experiment was evidently on too small a scale to permit any firm general conclusions in this section. There is suggestive evidence that Large offspring increase in weight after heterospermic insemination. If we accept the implication of the results on p. 43, i.e. that there is no real increase in the birth weight in the heterospermic litter as a whole, it would follow that any increase in the weight of Large offspring must be compensated for by a decrease in the weight of Small offspring. But the reality of this decrease has not been established by a direct test.

DISCUSSION

The enhancement effect seems now to be fairly well established. It may be described as follows. When genetically large and genetically small offspring are born in the same litter, the average difference in birth weight between them is greater than when they are conceived in litters all of one genetic type. This generalization applies to all the existing data, i.e. to the previous experiment with heterospermic insemination in the rabbit (Beatty, 1957*a*), to the present confirmatory experiment with the rabbit, and also to the analogous 'natural experiments' of human and sheep twins mentioned in the Introduction. These effects on development reflect a complex genotype-environment interaction. An offspring develops under the influence of (*a*) its own gene complement, (*b*) the gene complement of the dam, mediated by maternal and possibly by cytoplasmic effects, and (*c*) the various gene complements of its uterine litter-mates, mediated by what appears to be intra-uterine competition. The litter-mates may be regarded as a part of the prenatal environment determined by gene complements that are not the same as those determining the maternal soma.

In the present experiment and in the previous one (Beatty, 1957*a*) it was known that homospermic offspring of the larger sire had a greater *mature* weight than those of the smaller sire. But it has not yet been proved in homospermic litters that the offspring of the larger sire have a significantly greater *birth* weight than those of the smaller sire. The reason for this is, perhaps, that the comparison is difficult to make because it is involved with the high variance between dams. In heterospermic mixed litters, on the other hand, a much more efficient comparison can be made, within the litter. Any accurate comparison of birth weights in homospermic litters demands either larger numbers of observations, or else a more efficient sampling design. Correction for the covariance of the weight of the dam might also be made more efficiently than in the present work. In the meantime, it will be assumed that the larger sires have the larger offspring at birth in homospermic litters. Demonstration of the enhancement effect does not depend on the validity of this assumption.

By contrast with homospermic litters, it has proved quite easy to show in mixed litters born after heterospermic insemination that offspring of a genetically and phenotypically larger sire have a significantly greater birth weight than those of a genetically and phenotypically smaller sire. This was found in the present work and in the previous investigation (Beatty, 1957*a*), and can be computed even in the three mixed litters described by Kopeć (1923). Genomes affecting body weight in a given sense must begin to exert their effect in the embryo or foetus. Further, since the offspring of a heterospermic litter are conceived at the same time and born at the same time, the genetic effect on birth weight must mean a genetically determined prenatal effect on growth rate.

The enhancement effect can be explained in terms of embryonic competition, with the larger type of embryo gaining an undue advantage at the expense of the smaller type. In the earlier data, however (Beatty, 1957*a*, and the references to work on mammalian twins given in the Introduction), it is not possible to eliminate an alternative explanation (see Donald and Purser, 1956) concerned with the gestation period. This begins with the null hypothesis that Large and Small offspring each have their typical average growth rate, irrespective of whether they are born in homospermic or heterospermic litters. In heterospermic litters, the time of birth is necessarily the same for both kinds of offspring in a litter, and the difference in their growth-rates would be immediately revealed as a difference in birth weight. In homospermic litters, the Large offspring, although growing fast, might for some reason be born earlier, and/or the slow-growing Small offspring might be born late. Thus, in homospermic litters, the potential difference in birth weight between Large and Small offspring might be largely annulled by changes in the gestation period. This explanation is, however, eliminated by the present work, in which comparisons of birth weight have been made *as at a constant gestation period* for the whole experiment, and an enhancement effect nevertheless resulted. There seems therefore no remaining obstacle to interpreting the enhancement effect as an example of competition among embryos *in utero*, and indeed as evidence of such competition. The question of exactly what substance or substances are being competed for is outside the scope of this paper.

In the previous experiment (Beatty, 1957*a*), the enhancement effect was attributable primarily to decreased weight of Small offspring—but average birth weight in the heterospermic litter as a whole was slightly low. In the present work, the enhancement effect was attributable primarily to increased weight of Large offspring—but average birth weight in the heterospermic litter as a whole was slightly high. These data suggest that the enhancement effect in mixed heterospermic litters is due both to an increase in the birth weight of Large offspring and decrease in the birth weight of Small offspring. This conclusion is provisional. If correct, it would agree with an analogous trend mentioned by Donald and Purser (1956) in their work on sheep twins.

We may now consider the 'heterospermic vigour' said to be evidenced by an increased average birth weight in litters born after heterospermic insemination (e.g. Kopeć, 1923; and a large body of evidence, mainly Russian, summarized by Kushner, 1954). In my first test experiment (Beatty, 1957*a*), average birth weight after heterospermic insemination was slightly *less* than after homospermic insemination from either sire. In the present work, with data adjusted to 'standard gestational conditions', the average birth weight in heterospermic litters was slightly but non-significantly greater than the average birth weights in the two kinds of homospermic litter. Thus, there has been no confirmation of the reality of 'heterospermic vigour' in the average birth weight of the litter as a whole. However, when the enhancement effect is considered, it could be said in a special sense that 'heterospermic vigour' has occurred, because one type of offspring (Large offspring) was, apparently, unduly large in heterospermic litters. But this appeared to be compensated for by a negative 'heterospermic vigour' among the Small type offspring, so that the litter as a whole did not have an unusual average birth weight. It is not clear whether the Russian workers would, in fact, use the term 'heterospermic vigour' in this special sense.

Studies of competition among organisms are at a much more advanced stage in plants, where the type of interaction is well known to alter with the particular genetical and environmental conditions. Further, Sakai (1955) points out as an additional complication that competitive ability in plants is not necessarily a function of size or yield. In mammals, it would be an over-simplification of the situation to expect, under all circumstances, only one kind of interaction between organisms grown under competitive conditions in a microcosm such as the uterus. In pursuing the type of work suggested by the Russian experiments on mammals, the question should be 'What are the different effects of heterospermic insemination under various circumstances?' rather than 'What is the effect of heterospermic insemination?' Offspring in heterospermic litters seem to interact co-operatively in the Russian experiments, but competitively in mine; neither finding is necessarily a disproof of the other. I must admit, however, that I have not been encouraged in a general sense by the results of my three attempts to confirm claims made by the Michurinist school of biology—i.e. in the present work and in the earlier work with heterospermic insemination (Beatty, 1957*a*), and in a search for somatic inconstancy in the chromosome number of mice (Beatty, 1957*b*). Other aspects of 'heterospermic vigour' have also failed to receive general confirmation in the West (see, e.g., Campbell and Jaffe, 1958). But, although the reality of 'heterospermic vigour' may well be viewed with reserve, the proposition that all the Russian work on this subject is always wrong may be viewed with even greater reserve.

SUMMARY

1. Two rabbit sires were used for insemination of sixty-eight females. Insemination was either homospermic (one sire at a time) or heterospermic (mixed semen from the two sires). Each offspring could be traced to its sire by genetic marks. The sires differed in weight and were known to give offspring differing in mature weight and named Large and Small offspring. The object of study was the birth weight of these offspring in logarithmic transformation.

2. After heterospermic insemination, there was no evidence of any real 'heterospermic vigour' in the average birth weight of the litter as a whole.

3. After heterospermic insemination, the difference in birth weight between the two kinds of offspring was accentuated (enhancement effect). This confirms a previous experiment.

4. The enhancement effect is ascribed to competition among embryos. It is not attributable to postulated changes in the gestation period. It appears to arise from an increase in the birth weight of Large offspring, together with a possible decrease in the birth weight of Small offspring. These changes in birth weight are attributable to changes in prenatal growth rate.

5. The bearing of this work on Russian experiments with heterospermic insemination is discussed.

I am grateful to Prof. C. H. Waddington for helpful interest and facilities. Dr D. J. Finney explained some difficult statistical points, and Dr D. S. Falconer was kind enough to criticize the manuscript. The work was carried out with technical assistance from Mr A. M. Dalrymple, and with further assistance from Miss A. G. Stenhouse and Mrs M. Lawson.

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