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Male and female contributions to heterosis in lifetime performance of mice *

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Summary. Six straightbred lines of mice, some of their F_1 crosses and a synthetic line were used to evaluate male and female contributions to heterosis in lifetime performance measured on females. Females from each straightbred line or F_1 crosses were pair-mated randomly at day 42 with either a male of the corresponding genetic group or from a synthetic line, and pairs were maintained for 155 days (lifetime). Each mother was allowed to rear all young born alive until day 18 when the young were discarded. Data were analyzed using a model in which the group mean of lifetime performance was expressed as the sum of (additive direct) genetic and environmental effects for each of the male and female genetic groups used for mating. Comparison of group means for lifetime performance revealed that estimates of F_1 heterosis due to male and female averaged 10 and 9% for number of parturitions during lifetime, 7 and 28% for total number of young born alive, 6 and 31% for total body weight of young born alive, 8 and 33% for total number of young raised to day 18, 9 and 43% for total body weight of young raised to weaning, and 8 and 8% for days from first mating to last parturition. The male's contribution to heterosis in lifetime performance was smaller than female's contribution for productive traits (total number of young born alive and at day 18, and total body weight of young born alive and at day 18), and was nearly equal in reproductive traits (number of parturitions during lifetime and days from first mating to last parturition).

Key words: Heterosis – Lifetime performance – Mice – Male and female – Mate

Introduction

The performance of the crosses (F_1) of two breeds (lines) often exceeds the average performance of the two parental breeds. This phenomenon, termed heterosis, has been well documented in plants and animals. Various mating systems such as rotational crossbreeding (Gregory and Cundiff 1980) have been devised to capitalize on the heterosis at F_1 generation in subsequent generations of crosses (Dickerson 1973). Estimation of the magnitude of heterosis is important in predicting performance of crosses under these mating systems.

The net reproductive rate of a female is measured by number of young raised by the female during her lifetime (time until death or culling). Although the character is expressed by the female through ovulation rate, uterine environment and postnatal maternal care including lactation, it is affected by the male (mate) both directly (e.g. semen quality, libido) and through progeny (e.g. survival rate before weaning). Therefore, when crossbred males are used as mates, female's performance is affected by heterosis in the male. When crossbred females are used for mating, heterosis in female performance is expected. If crossbred males are cohabited with crossbred females during their lifetime, rather than used for artificial insemination, the effect of the male can be delineated and heterosis in lifetime performance exhibited by the female can be expressed as the sum of male and female components of heterosis.

In the present study with mice, single males and females were cohabited continuously for 155 days after the first mating (hereafter, lifetime). The purpose of the study was to estimate male and female contributions to heterosis in various lifetime performance traits measured on females, using six straightbred lines of mice, some of their F_1 crosses and a synthetic line.

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Materials and methods

Mice

Six randombred lines of mice were used: M_P, W_P, C_P, M_Q, W_Q and C_Q. The breeding history of these lines has been reported by Nagai et al. (1978) and Nagai et al. (1980). Briefly, in two populations (P and Q) of different origin, selection was conducted in the M lines to increase post-natal maternal performance, as measured by 12-day body weight of a cross-fostered first litter, and in the W lines to increase adult weight, as measured by individual body weight at 42 days in the first litter. Control lines (C) were maintained unselected. Inbreeding coefficients of the C lines were approximately 13 percent. Using the selected lines (M_P, W_P, M_Q and W_Q) matings were made as follows: W_P (male)×M_P (female), $M_Q \times M_P$, $W_Q \times M_P$, $M_Q \times W_P$, $W_Q \times W_P$ and $W_Q \times M_Q$. Resulting F_1 progeny were randomly mated to form a synthetic, S. The unselected synthetic line had been randomly bred for four generations before it was used for the present experiment. This would help avoid unfavorable conditions resulting from linkage disequilibrium.

The six straightbred lines were used to produce straightbreds, and F_1 males and females for mating, as shown in Table 1. Females in each genetic group were pair-mated at random (but avoiding full sib mating in straightbred matings) with either a male from their own genetic group (group I) or a male from the synthetic line (group II).

Females 42 days old were pair-mated with slightly older males. They were maintained in the same cage continuously for 155 days (lifetime) unless they did not give birth for 50 days after previous parturition or the first mating (day 42). At birth, litter size was not standardized and the young produced were left with their dams until they were discarded at 18 days of age.

Throughout the experiment, a commercial pellet feed (Purina Mouse Chow) and tap water were supplied ad libitum. Temperature and humidity in mouse rooms ranged from 20° to 24 °C and 40% to 50%, respectively.

Measurement

The following traits were recorded for each female: number of parturitions during 155 days, total number of the young born alive and raised to day 18 (number of live young in a litter, summed over litters produced during 155 days), total body weight (in g) of the young born alive and raised to day 18, and number of days from the first mating to the last parturition (reproductive life). All data were recorded for the terminal parturition even if the 155-day period was exceeded.

Table 1. Mating structure

Class	Group I		Group II	
	Males from own line (cross)		Males from S line	
	Male ×	Female	Male ×	Female
1	M_P	M_P	S	M_P
2	W_P	W_P	S	W_P
3	C_P	C_P	S	C_P
4	M_Q	M_Q	S	M_Q
5	W_Q	W_Q	S	W_Q
6	C_Q	C_Q	S	C_Q
7	F_1 ($M_Q M_P$)	F_1 ($M_P M_Q$)	S	F_1 ($M_P M_Q$)[a]
8	F_1 ($M_P M_Q$)	F_1 ($M_Q M_P$)	S	F_1 ($M_Q M_P$)
9	F_1 ($W_P W_Q$)	F_1 ($W_Q W_P$)	S	F_1 ($W_Q W_P$)
10	F_1 ($C_P C_Q$)	F_1 ($C_Q C_P$)	S	F_1 ($C_Q C_P$)
11	F_1 ($M_P W_P$)	F_1 ($W_P M_P$)	S	F_1 ($W_P M_P$)

[a] F_1 females from the mating of M_P sires with M_Q dams

Expected genetic components for lifetime performance

Lifetime performance (for example, number of parturitions during reproductive life) was measured on females, but it is the joint contribution of the male and female under the conditions of the present experiment (continuous cohabiting of a male and a female). If crossbred males (or females) are used for the continuous cohabiting, lifetime performance can be affected by heterosis in the crossbred parent. In this paper, the magnitude of heterosis in lifetime performance was estimated separately for each sex, assuming that the effect of interaction between two sexes on heterosis is negligible.

A model is proposed which is analogous to the one presented by Willham (1963) dealing with maternal effects on the performance of progeny. Performance (P_A) for a given individual female (individual pair) from a hypothetical line A can be partitioned as follows:

$$P_A = {}_{f}g_A + {}_{f}e_A + {}_{m}g_A + {}_{m}e_A$$

where ${}_{f}g_A$ and ${}_{f}e_A$ are the genotypic and environmental values, respectively, of the individual female component (f) for line A, and ${}_{m}g_A$ and ${}_{m}e_A$ are the genotypic and environmental values of the individual male component (m), as measured in P_A. When lifetime performance is considered as the female's trait, the latter two terms are considered as environmental factors to act on the female even they contain genetic and environment effects. In the present study, only additive direct genetic effects (g) were considered, and other genetic effects (e.g. additive maternal genetic effects) were neglected. Reciprocal F_1 crosses were assumed to exhibit the same magnitude of direct heterosis.

If lines A and B are used to produce F_1 males and F_1 females for mating, the mean performance ($F_{AB}:F_{BA}$) of F_1 females (F_{BA}) mated with F_1 males (F_{AB}) is expressed as follows:

$$F_{AB}:F_{BA} = ({}_{f}g_A + {}_{f}g_B)/2 + ({}_{m}g_A + {}_{m}g_B)/2 + {}_{f}h_{AB} + {}_{m}h_{AB} \tag{1}$$

where h_{AB} is direct heterosis in cross of lines A and B. The average performance of lines A and B is:

$$(A:A + B:B)/2 = ({}_{f}g_A + {}_{f}g_B)/2 + ({}_{m}g_A + {}_{m}g_B)/2 \tag{2}$$

The difference between (1) and (2) estimates the absolute amount of the combined heterosis (${}_{f}h_{AB} + {}_{m}h_{AB}$).

If males of a synthetic line, S, that are produced from four lines A, B, C and D, are mated with F_1 females from lines A and B, mean performance ($S:F_{AB}$) is

$$\begin{aligned} S:F_{AB} = {} & ({}_{f}g_A + {}_{f}g_B)/2 \\ & + ({}_{m}g_A + {}_{m}g_B + {}_{m}g_C + {}_{m}g_D)/4 + {}_{f}h_{AB} \\ & + ({}_{m}h_{AB} + {}_{m}h_{AC} + {}_{m}h_{AD} + {}_{m}h_{BC} \\ & + {}_{m}h_{BD} + {}_{m}h_{CD})/(6 \times 2) \end{aligned} \tag{3}$$

assuming that the synthetic (random-bred) line maintains one half of the average heterosis from six combinations of lines A, B, C and D. The last term in (3) is expected to be:

$$(S:A + S:B + S:C + S:D)/4 - (A:A + B:B + C:C + D:D)/4 \tag{4}$$

because by subtraction, all additive direct genetic effects (${}_{f}g_A$, ${}_{f}g_B$, ${}_{f}g_C$, ${}_{f}g_D$, ${}_{m}g_A$, ${}_{m}g_B$, ${}_{m}g_C$, and ${}_{m}g_D$) cancel out, leaving $({}_{m}h_{AB} + {}_{m}h_{AC} + {}_{m}h_{AD} + {}_{m}h_{BC} + {}_{m}h_{BD} + {}_{m}h_{CD})/(6 \times 2)$.

When males from line S are mated with line A females and with line B females, the difference between $S:F_{AB}$ and the average of S : A and S : B means is

$$
\begin{aligned}
&S:F_{AB}-(S:A+S:B)/2\\
&\quad=(({}_{f}g_{A}+{}_{f}g_{B})/2+{}_{f}h_{AB}+({}_{m}g_{A}+{}_{m}g_{B}+{}_{m}g_{C}+{}_{m}g_{D})/4\\
&\qquad+({}_{m}h_{AB}+{}_{m}h_{AC}+{}_{m}h_{AD}+{}_{m}h_{BC}+{}_{m}h_{BD}+{}_{m}h_{CD})/12)\\
&\qquad-(({}_{f}g_{A}+{}_{f}g_{B})/2+({}_{m}g_{A}+{}_{m}g_{B}+{}_{m}g_{C}+{}_{m}g_{D})/4\\
&\qquad+({}_{m}h_{AB}+{}_{m}h_{AC}+{}_{m}h_{AD}+{}_{m}h_{BC}+{}_{m}h_{BD}+{}_{m}h_{CD})/12)\\
&\quad={}_{f}h_{AB} \qquad (5)
\end{aligned}
$$

Thus ${}_{f}h_{AB}$ is estimable from formula (5), and ${}_{m}h_{AB}$ is estimable by subtracting ${}_{f}h_{AB}$ from ${}_{f}h_{AB}+{}_{m}h_{AB}$ (formulae 1 and 2).

Calculation of percent heterosis

Percent heterosis was defined as the ratio of the absolute amount of heterosis to the mean of two parental values (in %). For example, the female contribution to percent heterosis in the cross of lines M_P and M_Q was calculated as follows:

$$\frac{(C7.GII+C8.GII)/2-(C1.GII+C4.GII)/2}{(C1.GI+C4.GI)/2}\times 100$$

where C7.GII, for example, represents the mean for Class 7 and Group II (Table 1). When no reciprocal F_1 was produced, as for other Classes (Classes 9, 10, and 11), the single group mean was used as F_1's performance.

The combined percent heterosis for male and female components was calculated from the difference between formula (1) and (2), multiplied by 100 divided by formula (2). Percent heterosis due to male was calculated by subtracting the percent heterosis due to female from the combined percent heterosis.

Results

The performance of the females of the six straightbred lines when mated with a male from their own line (group I) or a synthetic line (group II) is shown in Table 2. Means for group II exceeded the means for group I in all cases except for reproductive life in M_Q line. This indicates that lifetime performance exhibited by the female is affected by the male and that males from the synthetic line appear to be superior to males from the straightbred lines. Variation within group, as measured by coefficient of variation, was smaller in group II (using males from the synthetic line) than in group I (using straightbred males) in most cases. These observations suggest that the increased heterozygosity of males from the synthetic line was beneficial to female lifetime performance.

In general, productive traits (i.e. number and body weight of the young produced by a female) were positively associated with number of parturitions during 155 days or reproductive life. A separate study revealed that variation in the mean of parturition interval among the six lines was relatively small: means for groups I and II were 24.4 and 24.0 days (M_P), 26.6 and 25.7 days (W_P), 28.7 and 26.3 days (M_Q), 26.9 and 28.6 days (W_P), 24.3 and 24.1 days (C_P) and 25.9 and 24.2 days (C_Q) respectively. Since parturition interval was similar among the six lines, number of parturitions could be considered as a similar measure to days in reproductive life.

Table 2. Mean performance during lifetime (155 days of cohabiting) in six lines of mice

Line-of-female		M_P		W_P		M_Q		W_Q		C_P		C_Q	
Trait	Mating group*	Mean	C.V. (%)**	Mean	C.V. (%)	Mean	C.V. (%)	Mean	C.V. (%)	Mean	C.V. (%)	Mean	C.V. (%)
No. of parturitions	I	4.79^{a}	34	$4.13^{a,b,c}$	41	$3.75^{b,c}$	38	3.50^{c}	52	5.00^{a}	35	$4.60^{a,b}$	32
during 155 days	II	5.50^{a}	26	$4.30^{b,c}$	44	3.90^{c}	42	$4.28^{b,c}$	32	5.55^{a}	26	$5.00^{a,b}$	32
Total no. of young	I	$43.1^{a,b}$	40	34.5^{b}	40	35.2^{b}	42	$38.2^{a,b}$	52	$43.1^{a,b}$	42	47.5^{a}	44
born (day 0)	II	$53.8^{a,b}$	30	40.4^{c}	42	$41.9^{b,c}$	55	$43.3^{a,b,c}$	32	$48.9^{a,b,c}$	26	55.4^{a}	35
Total wt of young	I	$68.3^{a,b}$	37	61.6^{b}	38	61.5^{b}	41	$66.9^{a,b}$	53	$68.1^{a,b}$	39	80.4^{a}	42
born (g)	II	87.9^{a}	27	73.0^{a}	43	72.6^{a}	53	76.0^{a}	33	81.3^{a}	26	91.5^{a}	35
Total no. of young	I	$39.9^{a,b}$	42	31.5^{b}	40	33.9^{b}	43	32.9^{b}	63	$36.4^{a,b}$	51	45.2^{a}	47
at day 18	II	49.7^{a}	31	36.7^{b}	41	$39.2^{a,b}$	61	$41.4^{a,b}$	35	$43.0^{a,b}$	28	49.8^{a}	40
Total wt of young	I	$413.3^{a,b}$	37	346.9^{b}	37	$404.3^{a,b}$	40	333.5^{b}	64	350.5^{b}	49	472.6^{a}	43
at day 18 (g)	II	507.5^{a}	26	380.9^{b}	38	$437.6^{a,b}$	53	$479.6^{a,b}$	36	$439.0^{a,b}$	28	$496.2^{a,b}$	39
Reproductive life	I	$114.0^{a,b}$	28	$108.6^{a,b}$	39	$108.3^{a,b}$	39	$93.3^{a,b}$	48	120.3^{a}	33	118.1^{a}	32
(days)	II	$128.9^{a,b}$	21	$109.0^{a,b}$	41	103.3^{b}	42	$122.6^{a,b}$	32	130.6^{a}	22	$120.5^{a,b}$	31
No. of pairs	I	29		30		28		30		30		30	
	II	20		20		20		18		20		20	

* Males from their own line were used in group I while males from line S were used in group II

** Coefficient of variation. The mean values not sharing a common superscript in the same row are different significantly ($P<0.05$)

Reproductive life averaged 119.2, 111.2 and 100.5 days for lines C, M and W (group I). Lines selected for adult weight (W) showed the shortest reproductive life, lines selected for body weight at weaning (M) showed an intermediate length, and unselected lines (C) had the longest reproductive life. Selection for increased body weight caused a shorter reproductive life.

Duncan's multiple range test applied to data from group I (Table 2) revealed that the six lines were classified into two different classes in size except for number of parturitions during 155 days where three different classes existed. The tests revealed that the six lines were classified differently in group I and II (Table 2). This confirms that lifetime performance exhibited by the female is affected by the male.

The mean performance of the F_1 females mated with either F_1 males (group I in Table 1) or males from the synthetic line (group II) are shown in Table 3. In general, lifetime performance of F_1 females was greater when mated with F_1 males than when mated with males from the synthetic line. Within-group variation, as measured by coefficient of variation, was smaller among F_1 males than among males of the synthetic line. These observations suggest that heterotic effects are larger for F_1 males than for males from the synthetic line.

F_1 females produced from M_Q sires and M_P dams, F_1 (M_QM_P), had the longest reproductive life (138.5 days) when they were cohabited with F_1 (M_PM_Q) males (group I, Table 3). Accordingly, they showed a high productivity (e.g. 688.8 g for total weight of young at day 18). Comparison of F_1 (M_QM_P) with F_1 (M_PM_Q) females in group II (Table 3) revealed that F_1 (M_PM_Q) females exceeded F_1 (M_QM_P) females in the observed lifetime performance. This indicates that F_1 (M_PM_Q) males are superior to F_1 (M_QM_P) males in lifetime performance.

Male and female components of heterosis in lifetime performance when F_1 males and females were pair-mated is shown in Table 4. If F_1 males and straightbred females were pair-mated, the male component (m) of heterosis in Table 4 should apply whereas if straightbred males and F_1 females were pair-mated, the female component (f) is applicable. Heterosis due to the male or female was relatively large in crosses of M_P and M_Q (16 to 46%), and W_P and W_Q (18 to 47%) except for number of parturitions and reproductive life (6 to 18%). Heterosis for productive traits (i.e. total number and weight of the young) was larger in the female component (28 to 47%) than in the male component (16 to 30%). This was particularly true in crosses of M_P and W_P for productive traits where the male component had a negative value (−18 to −13%).

Discussion

A number of papers dealing with heterosis in animals reported that heterosis is exhibited in many traits including reproductive traits (Dickerson 1973; Turton 1981). Noting that most reports have dealt with heterosis in female's reproductive traits, Neely et al. (1980)

Table 3. Mean performance during lifetime (155 days of cohabiting) in five crosses

Trait	Female cross	F_1 (M_PM_Q)		F_1 (M_QM_P)		F_1 (W_QW_P)		F_1 (C_QC_P)		F_1 (W_PM_P)	
	Mating group*	Mean	CV** (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
No. of parturitions during 155 days	I	5.37^{a}	25	5.87^{a}	18	4.83^{a}	30	5.52^{a}	21	4.69^{b}	39
	II	5.08^{a}	38	4.68^{a}	29	4.36^{a}	41	5.21^{a}	29	4.48^{a}	44
Total no. of young born born (day 0)	I	59.2^{a}	27	60.8^{a}	27	53.2^{a}	35	59.5^{a}	29	41.7^{b}	45
	II	54.5^{a}	42	52.5^{a}	31	46.6^{a}	49	57.2^{a}	33	46.5^{a}	47
Total wt of young born (g)	I	101.0^{a}	26	104.9^{a}	27	96.7^{a}	35	96.8^{a}	29	69.0^{b}	43
	II	94.5^{a}	43	88.8^{a}	29	82.5^{a}	46	96.1^{a}	33	80.6^{a}	45
Total no. of young at day 18	I	57.4^{a}	29	59.5^{a}	27	50.6^{a}	34	56.5^{a}	31	38.2^{b}	38
	II	52.8^{a}	44	50.3^{a}	34	43.2^{a}	49	54.4^{a}	34	43.9^{a}	45
Total wt of young at day 18 (g)	I	663.9^{a}	27	688.8^{a}	23	601.3^{a}	32	621.8^{a}	28	436.8^{b}	44
	II	611.1^{a}	44	587.2^{a}	33	500.9^{a}	42	602.0^{a}	28	501.8^{a}	42
Reproductive life (days)	I	$127.2^{a,b}$	24	138.5^{a}	11	$123.3^{a,b}$	29	135.2^{a}	16	$117.2^{a,b}$	34
	II	127.4^{a}	33	125.2^{a}	28	111.5^{a}	35	127.2^{a}	24	109.0^{a}	41
No. of pairs	I	30		29		29		29		29	
	II	24		25		25		24		25	

* For definition, see Table 1 and text

** Coefficient of variation. The mean values not sharing a common superscript in the same row are different significantly ($P < 0.05$)

Table 4. Percent heterosis in lifetime performance exhibited when F_1 females (f) and F_1 males (m) were pair-mated, cohabiting continuously throughout 155 days of reproduction

Trait	Sex	Lines involved			
		M_P and M_Q (%)	W_P and W_Q (%)	C_P and C_Q (%)	M_P and W_P (%)
No. of parturitions	f	14	14	9	0
	m	18	12	6	5
Total no. of young born	f	37	28	26	20
	m	16	18	5	−13
Total wt of young born (g)	f	41	28	29	24
	m	18	22	1	−18
Total no. of young at day 18	f	40	34	33	23
	m	19	23	5	−16
Total wt of young at day 18 (g)	f	46	47	45	32
	m	19	30	5	−17
Reproductive life (days)	f	14	11	7	− 2
	m	6	11	6	7

studied heterosis in reproductive traits for crossbred boars. Quintana (1980) was concerned with the heterosis of the male and female in swine productivity. The papers published so far have described the magnitude of heterosis measured in one sex but not of heterosis contributed by two sexes. We attempted in the present study to measure heterosis in lifetime performance where heterosis was contributed by male and/or female, and lifetime performance achieved jointly by the male and female included reproductive traits (e.g. days for reproductive life) and productive traits (e.g. litter weight of the young at weaning).

The contribution to heterosis was larger for the female than the male in four of the traits examined: total number of young born alive and at day 18, and total body weight of young born alive and at day 18. The number of young per litter is important both genetically and phenotypically in litter weight (Nagai 1971; Eisen 1981). The number of ova shed from the ovary of a female mouse is the upper limit of the number of young born alive which in turn, controls the number of young at day 18. The observed high heterosis due to the female in the present study could be associated with a high level of heterosis in the ovulation rate and/or embryo survival. McCarthy (1967) showed evidence of heterosis in ovulation rate in mice while Bradford and Nott (1969) suggested that genes affecting pre-implantation survival exhibit a high degree of dominance in mice. Contrary to the four productive traits, the contribution of each sex to heterosis was nearly equal for reproductive traits; number of parturitions during lifetime and days of reproductive life (Table 3).

Comparison of Group I (using males from own genetic groups) with group II (using males from the synthetic line) revealed that F_1 males excelled males from the synthetic line (Table 3) which generally exceeded males of straightbred lines for the six traits examined (Table 2). The observed heterosis due to the male would be through male's sexual performance (e.g. semen quality, libido), survival rate of fetuses and/or growth rate of the young. Studying reproductive traits in crossbred boars, Neely et al. (1980) reported that the magnitude of heterosis was 8.5, 25.4, 33.7, 23.3 and 10.4% for length, weight, total sperm, sperm per gram of right testis and combined width of testes. Sexual behavior and other performance of F_1 males are worth studying.

Regarding heterosis associated with the male, crosses of lines between the two populations (P and Q) different from crosses of lines within the population (P): in the latter (Table 4), the total number of young and the total body weight of the young at birth and at day 18 showed a negative heterosis. On the other hand, the heterosis due to the male (Table 3) was larger in crosses of selected lines (M_P and M_Q, and W_P and W_Q) than in crosses of unselected lines (C_P and C_Q). Selection for increased postnatal maternal performance in M lines or increased adult body weight in W lines, and possibly a higher inbreeding in M and W lines than in C lines, have enhanced the magnitude of heterosis associated with the male. Since both selections resulted in increased adult weight for male, particularly in lines W (Nagai et al. 1978) genes responsible for the increased adult weight in males appear to have caused the higher heterosis associated with the male when lines are crossed between populations, but not within population.

In the present study, heterosis associated with the female was estimated, and the heterosis associated with the male was estimated by subtracting the female components from the male and female components combined. Of course, we can estimate the male component by mating females from the synthetic line with males of different lines. If this approach had also been taken in the present study, the effect of interaction between the male and female could have been evaluated. Since the synthetic line was produced from the selected lines (M_P, W_P, M_Q and W_Q), omitting unselected lines C_P and C_Q, the males from the synthetic line may have acted differently when cohabited with females from the selected lines and when cohabited with those from the unselected lines. It should be noted that the estimates for the male's component given in Table 4 are confounded with the interaction between males and females. Finn (1964) demonstrated that the male effect on litter size was a characteristic of the male rather than a male-female interaction in an experiment using males and females of the same strain. The interaction between males and females of the straightbred and F_1 cross warrants future study.

Sheridan (1981), proposing a hypothesis of an epistatic pathway, demonstrated theoretically that F_2 should show 12.5% (rather than 50%) of F_1 heterosis when two genes are considered. Kinghorn (1982) found that significant epistasis existed for fertility and other traits in mice. On the other hand, McGloughlin (1980) demonstrated with mice that a significant positive linear relationship exists between heterozygosity and heterosis, substantiating dominance as the primary factor for heterosis. Gregory and Cundiff (1980) reported that the relationship between loss of heterosis and loss of heterozygosity approaches linearity. Genetic mechanisms underlying heterosis need to be explored further to accurately predict the performance of a crossbred population under special mating systems. Male and female contributions to heterosis in lifetime performance observed at F_1 generations in the present study should be evaluated at subsequent generations of crossbreeding.

The present study demonstrated that when F_1 males and females were cohabited, lifetime performance reached up to 77% (for total weight of the young raised to day 18 with F_1 crosses of W_P and W_Q) more than the average performance of the straightbred lines (W_P and W_Q). In swine husbandry, and perhaps for polytocus species such as rabbits, the conditions imposed in this experiment are not realistic. Further research is needed to partition the male contribution to heterosis into its biological components (e.g. libido). Nevertheless, the real advantage of using male and female crossbred parents (including F_1 parents) needs to be examined both theoretically and experimentally for livestock production.

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