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Crossbreeding effects after long-term selection for purebred performance: a model experiment with mice

2. Performance of three-breed crosses

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Summary. Results are presented from two replicated three-breed cross diallels that were conducted after 20 generations of selection for purebred performance in mice. The selection criteria for the different lines were: litter size at birth (LS), weaning weight at 4 weeks (WW), weight gain from week 4 to week 6 (WG), and body fat content at week 6 (FT). Additionally, a random-mating control line (C) was kept. Significant maternal heterosis was found in litter size and weaning weight. Estimates of maternal heterosis in litter size were very high, ranging from 17 to 50% of the mean of the corresponding single crosses. Maternal heterosis in weaning weight usually was negative and ranged from +9 to −11%. Significant maternal heterosis in feed efficiency and weaning weight could only be found in a few cases. Total performance of three-breed crosses was highly superior to that of single crosses and purebreds. Means of the corresponding purebreds or single crosses were of little use in predicting three-breed cross performance.

Key words: Mice – Diallel cross – Maternal heterosis – Litter size – Growth traits

Introduction

Most crossbreeding programs in animal breeding use a female F_1 cross as a dam of the final product to utilize maternal heterosis. Testing of all possible F_1 females in the initial phase of a crossbreeding program is very expensive. Results of Bell et al. (1955) indicate that the testing of combinations from lines with poor purebred performance is not worthwhile.

In this study, all possibe three-breed crosses from five lines of mice were established after 20 generations of selection for purebred performance within the lines. Results in the literature from beef cattle (Dillard et al. 1980; Alenda and Martin 1981) and mice (Lin and Nagai 1986) were derived from incomplete designs by means of multiple regression models. However, for complete designs, crossbreeding parameters may be estimated directly with a fixed or mixed model. Generally, this estimation leads to lower residual errors than estimation by means of a regression model. This paper gives the results of the parameter estimation with a new model for the description of crossbreeding parameters in three-breed crosses.

Materials and methods

Design

The experiment was carried out from 1976 to 1981 at the Institute of Laboratory Animals, Hannover. From a HAN : NMRI outbred population, five lines were formed by random sampling. These lines were selected for different traits in closed populations for 20 generations. An unselected control line was also kept. The design of the selection experiment has been described in a previous paper (Götz et al. 1991). The selection criteria of the five lines were as follows:

LS: large litter size at birth (number born alive, first parity);
WW: high average weaning weight of young at the age of 4 weeks;
WG: high weight gain from 4 to 6 weeks;
FT: low body fat percentage;
C: unselected control.

After 20 generations of purebred selection, a complete 5 × 5 diallel of testcrosses with 20 matings per crossbred and 30 matings per purebred subcell was set up. The parents in the diallel were taken at random from all litters of the 20th generation. The female offspring from the testcross diallel were then used to

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produce all possible three-breed crosses with ten matings per subcell, including crosses with reciprocal line combinations of the female.

Statistical analysis

For the statistical analysis, data from the first testcross diallel and the three-breed cross diallel were analyzed together. One problem arising from this approach is that seasonal effects could not be accounted for, since there was no overlapping of purebred and single crosses and three-breed crosses, respectively. However, due to the strictly maintained generation interval, litters of the single cross and three-breed cross diallel were born within a period of 15 weeks.

Hörstgen-Schwark et al. (1984) mated females from a testcross diallel to an unrelated tester line. They expanded the model of Eisen et al. (1983) and introduced maternal heterosis (h_{ij}^m), specific reciprocal grandmaternal effects (u_{ij}^*), and average direct grandmaternal effects (v_j).

This model was not suitable for the present data set for two reasons. First, it cannot account for possible interactions between crossbred dams and different sire lines, and second, the definition of the grandmaternal effect (v_j) for all of the subcells leads to inconsistent parameter estimates for purebreds and single crosses, as compared to the model of Eisen et al. (1983). Therefore, the model was modified to fit the present data set.

The following assumptions were made. The expected phenotypic value of a certain cross (P_L) in any trait is determined by the mean genotypic value of the cross for that trait and its maternal environment. Since only the average performance of lines or crosses is examined, one can assume that random environmental effects are normally and independently distributed, with mean zero and variance σ^2. Thus, maternal environment is the expected value of the maternal line or maternal cross for maternal traits. For the present design, maternal environment is the only systematic environmental effect affecting the expected value of the progeny. As in the models of Eisen et al. (1983) and Hörstgen-Schwark et al. (1984), a dominance model is assumed.

In the following, components that are environmental effects for the progeny are given in capital letters, while genetic components of the progeny are in small letters. Combinations of genetic and/or maternal components (e.g., ll_{ij}, lM_{ij}) denote interactions between these components. Thus, the phenotype of a single cross between lines i and j for a trait L (P_L) may be derived as follows:

Sire line (i)	Dam line (j)
G_L: l_i	G_L: l_j
P_L: l_i+m_i	P_L: l_j+m_j

Offspring (ij)

$$G_L\colon\ \tfrac{1}{2}(l_i+l_j)+ll_{ij}$$

$$P_L\colon\ \tfrac{1}{2}(l_i+l_j)+ll_{ij}+M_j+lM_{ij}\ ,$$

where

$\frac{1}{2}(l_i+l_j)$ = average of the direct genetic effects of lines i and j;
ll_{ij} = interaction between average direct genetic effects of lines i and j;
M_j = maternal phenotype of line j;
lM_{ij} = interaction between average direct genetic effect of line i and maternal phenotype of line j.

This model is equivalent to the one of Eisen et al. (1983) under the restrictions $ll_{ij}=ll_{ji}$ and $lM_{ij}=-lM_{ji}$ and the usual restrictions for l_i and M_j. In this case, ll_{ij} is equal to the direct heterosis of a cross (h_{ij}), and lM_{ij} equals the specific reciprocal effect of cross ij (r_{ij}^*). The effect lM_{ij} includes possible interactions between direct heterosis and maternal environment (llM_{ijj}), which cannot be separated unless a cross-fostering design is used.

In the same way, the phenotype of a cross for maternal performance (P_M) can be derived as:

$$P_M\colon\ \tfrac{1}{2}(m_i+m_j)+mm_{ij}+M_j+mM_{ij}\ .$$

The phenotype of a three-breed cross offspring from sire line t and first-cross dam ij is derived as follows:

Sire line (t)	Crossbred dam (ij)
G_L: l_t	G_L: $\frac{1}{2}(l_i+l_j)+ll_{ij}$
	P_M: $\frac{1}{2}(m_i+m_j)+mm_{ij}+M_j+mM_{ij}$

Offspring (tij)

$$G_L\colon\ \tfrac{1}{4}(2l_t+l_i+l_j)+\tfrac{1}{2}(ll_{ti}+ll_{tj})+\tfrac{1}{2}ll_{ij}$$

$$\begin{aligned}P_L\colon\ &\tfrac{1}{4}(2l_t+l_i+l_j)+\tfrac{1}{2}(ll_{ti}+ll_{tj})+\tfrac{1}{2}ll_{ij}\\&+\tfrac{1}{2}(M_i+M_j)+MM_{ij}+M_j'+MM_{ij}'\\&+\tfrac{1}{2}(lM_{ti}+lM_{tj})+\tfrac{1}{4}(lM_{ij}+lM_{ji})+lM_{tj}'+\tfrac{1}{2}lM_{ij}'\\&+llM_{tij}'+llM_{tjj}'\ ,\end{aligned}$$

where the influence of the dam's dam on the performance of the offspring is marked with a prime (M') in order to distinguish it from the pure maternal effects. There are three new components in the phenotypic value of the progeny, i.e., $\frac{1}{2}ll_{ij}$, lM_{tj}', and llM_{tij}'. The first is an interaction of genes within the maternal gamete and stands for the recombination loss as in Dickerson (1969, 1973). An F_2 individual would suffer from this loss in both of its gametes, therefore the factor is ½. This effect is always confounded with maternal heterosis (MM_{ij}) and cannot be separated from it in this design.

The component lM_{tj}' (and lM_{ij}') denotes the interaction of average direct genetic effects with the grandmaternal influence on the dam's phenotype in maternal traits. The expression llM_{tij}' describes the interaction of individual heterosis and the grandmaternal effect, which is estimable. Because of the above restriction, lM_{ij} and lM_{ji} sum to zero.

Therefore, the statistical model for the analysis of the data was as follows:

$$\begin{aligned}Y_{tijk}=\mu&+\tfrac{1}{4}(2l_t+l_i+l_j)+\tfrac{1}{2}(m_i+m_j)+\delta_1\,[\tfrac{1}{2}(h_{ti}+h_{tj}+r_{ti}^*+r_{tj}^*)]\\&+\delta_2\,[(h_{ij}^m+u_{ij}^*)+v_j+lv_{tj}+\tfrac{1}{2}lv_{ij}+llv_{tij}+llv_{tjj}]+e_{tijk}\end{aligned}$$

where

Y_{tijk} = observed value of the k^{th} litter of a cross from sire line t and dam line combination ij;
μ = mean performance of all purebreds;
l_i = average direct genetic effect of line i;
m_j = average maternal genetic effect of line j;
h_{tj} = direct heterosis of lines t and j ($=ll_{tj}$);
r_{tj}^* = specific reciprocal effect of lines t and j ($=lM_{tj}$);
h_{ij}^m = maternal heterosis of crossbred dam ij ($=mm_{ij}+\frac{1}{2}ll_{ij}$);
u_{ij}^* = specific reciprocal grandmaternal effect of lines i and j ($=MM_{ij}'$);
v_j = average grandmaternal effect of line j ($=M_j'$);
lv_{tj} = interaction of average direct genetic effect of line t and grandmaternal effect of line j ($=lM_{tj}'$);
llv_{tij} = interaction of individual heterosis of lines t and i with grandmaternal effect of line j ($=llM_{tij}'$);
δ_1 = 0, if $t=i=j$, otherwise $\delta_1=1$;
δ_2 = 0, if $i=j$, otherwise $\delta_2=1$;
e_{tijk} = random error.

As far as possible, the notation of Eisen et al. (1983) and Hörstgen-Schwark et al. (1984) was used to allow for a direct comparison. However, grandmaternal effects are only defined for three-breed crosses, whereas Hörstgen-Schwark et al. (1984) defined them for single crosses, too. The definition of the parameters of purebreds and single crosses is exactly the same as in the model of Eisen et al. (1983), and new terms are only introduced for three-breed crosses.

The following restrictions were applied to the parameters:

$$\sum_j l_j = \sum_j m_j = \sum_j v_j = 0$$

$$\sum_i h_{ij} = \sum_j h_{ij} = 0\,, \quad h_{ij} = h_{ji}$$

$$\sum_i r^*_{ij} = \sum_j r^*_{ij} = 0\,, \quad r^*_{ij} = -r^*_{ji}$$

$$\sum_i h^m_{ij} = \sum_j h^m_{ij} = 0\,, \quad h^m_{ij} = h^m_{ji}$$

$$\sum_i u^*_{ij} = \sum_j u^*_{ij} = 0\,, \quad u^*_{ij} = -u^*_{ji}$$

$$\sum_i lv_{ij} = \sum_j lv_{ij} = 0$$

$$\sum_t llv_{tij} = \sum_i llv_{tij} = \sum_j llv_{tij} = 0\,.$$

Because of significant interactions of group means and replications, the two rooms were analyzed separately. Weaning weight, weight gain, and feed efficiency (g feed/g gain) were measured as average performance of the litter, corrected for sex ratio. Litter size was defined as number of pups born alive *per mating*; therefore, it reflects fertility as well as prolificacy. Under the above restrictions the equations for weaning weight, weight gain, and feed efficiency were solved directly using weighted least squares. The weights were given by the reciprocals of the variances of litter means within the purebred and crossbred groups, respectively. A linear regression on litter size was added to the model. The equations for litter size were solved using ordinary least squares.

Direct and maternal heterosis were partitioned as described in Gardner and Eberhart (1966) and Hörstgen-Schwark et al. (1984), respectively:

$$h_{ij} = \bar{h} + h_i + h_j + s_{ij}\,,$$

$$h^m_{ij} = \bar{h}_m + h^m_i + h^m_j + s^m_{ij}\,,$$

where

$\bar{h}$ = average direct heterosis,
h_i = line direct heterosis,
s_{ij} = specific heterosis,

and $\bar{h}_m$, h^m_i, and s^m_{ij} are the components of maternal heterosis, respectively.

Results and discussion

Table 1. Significance of crossbred parameters (F-test)

Trait	LS		WW		WG		FE	
Parameter	Room							
	1	2	1	2	1	2	1	2
l	**	***	*	–	***	***	***	***
m	*	***	***	***	**	–	***	–
v	–	–	–	–	–	–	–	–
$\bar{h}$	–	**	***	–	–	–	–	–
h_i	–	–	*	–	***	**	–	–
s_{ij}	–	–	*	–	**	–	–	–
r^*_{ij}	–	–	–	**	–	–	–	–
$\bar{h}_m$	***	***	***	***	–	*	–	***
h^m_i	–	–	**	–	*	*	**	–
s^m_{ij}	–	–	–	–	–	**	–	**
u^*_{ij}	–	–	–	***	–	–	–	–
lv_{ij}	–	–	*	–	*	–	–	–
llv_{tij}	–	–	–	–	**	*	–	–
b	x	x	***	***	***	***	***	***
n	1,127	1,147	922	913	920	912	915	905

x = not part of the model
* = $P<0.05$
** = $P<0.01$
*** = $P<0.001$

Levels of significance for the different parameters are given in Table 1. Average direct genetic effects (l) and average maternal effects (m) were significant for all of the traits, except for weight gain and feed efficiency in room 2. Significant estimates for the components of direct heterosis ($\bar{h}$, h_i, s_{ij}) were found for weaning weight in room 1. For the weight gain line, direct heterosis was significant in both rooms, while specific heterosis was significant only in room 1. In litter size, average direct heterosis was significant in room 2. Average maternal heterosis was of importance for litter size and weaning weight. Weight gain and feed efficiency in room 2 also showed average maternal heterosis. Line maternal heterosis was important for weight gain in room 2. Reciprocal grandmaternal effects (u^*) were significant for weaning weight in room 2.

Direct grandmaternal effects (v) were not significant, but interactions of grandmaternal effects with average direct genetic effects (lv) and with direct heterosis (llv) were significant for weaning weight and weight gain. In the following, results for only the specific parameters of three-breed crosses will be presented, since parameters for single crosses have already been discussed in a previous paper (Götz et al. 1991).

Average maternal and maternal line heterosis

Estimates for average maternal heterosis in *litter size* were high in both rooms, with values of 2.44 and 2.35 pups born alive per mating, respectively (Table 2), giving a superiority of 30.7% (31.4%) relative to the mean of all purebreds. The estimates for both rooms did not differ significantly. Maternal heterosis was mainly caused by a higher percentage of fertile matings. While for crossbred dams on average 90% of the matings were fertile, purebred dams showed only 72% fertile matings. Hörstgen-Schwark et al. (1984) reported a difference of only 3% in the percentage of successful matings between purebred and crossbred dams. However, these authors did not consider infertile matings that were due to the infertility of

Table 2. Parameter estimates for average maternal ($\bar{h}_m$) and line maternal heterosis (h_i^m) in *litter size* and *weaning weight*, standard errors (SE), correlation of the estimates (r), and coefficients of variation (CV); (deviation from control in brackets)

	Litter size				Weaning weight (g)			
	Room 1		Room 2		Room 1		Room 2	
$\bar{h}_m$	2.44		2.35		−1.08		−1.31	
SE	0.31		0.32		0.22		0.20	
h_i^m								
LS	−0.07	(−0.48)	−0.37	(+0.02)	−0.76	(−0.39)	−0.30	(−0.80)
WW	−0.25	(−0.66)	−0.20	(+0.19)	−0.50	(−0.13)	−0.11	(−0.61)
WG	0.77	(+0.36)	0.77	(+1.16)	1.03	(+1.40)	−0.32	(−0.82)
FT	−0.86	(−1.27)	0.19	(+0.58)	0.60	(+0.97)	0.23	(−0.27)
C	0.41		−0.39		−0.37		0.50	
SE	0.54−0.59		0.57−0.62		0.37−0.39		0.31−0.35	
CV	7.9		6.5		3.7		1.6	
r	0.28				−0.08			

Table 3. Parameter estimates for average maternal ($\bar{h}_m$) and line maternal heterosis (h_i^m) in *weight gain* and *feed efficiency*, standard errors (SE), correlation of the estimates (r), and coefficients of variation (CV); (deviation from control in brackets)

	Weight gain (g)				Feed efficiency			
	Room 1		Room 2		Room 1		Room 2	
$\bar{h}_m$	−0.14		0.28		−0.06		−0.36	
SE	0.11		0.12		0.09		0.09	
h_i^m								
LS	0.18	(−0.07)	0.12	(+0.41)	−0.20	(+0.13)	−0.15	(−0.34)
WW	0.02	(−0.23)	−0.33	(−0.04)	−0.13	(+0.20)	0.05	(−0.14)
WG	−0.65	(−0.90)	0.50	(+0.79)	0.51	(+0.84)	−0.10	(−0.29)
FT	0.19	(−0.06)	0.00	(+0.29)	0.14	(+0.47)	0.01	(−0.18)
C	0.25		−0.29		−0.33		0.19	
SE	0.19−0.20		0.18−0.20		0.14−0.16		0.14−0.17	
CV	2.9		2.8		5.1		2.0	
r	−0.76				−0.49			

the male. Since in this experiment the same parental lines were used for the production of all crosses and purebreds, the increase in fertility probably was due to improved fertility in females.

Compared to the effects of average maternal heterosis, line maternal heterosis is of minor importance. Line WG showed a positive deviation from the control line in both rooms. The low correlation of 0.28 between the estimates of both rooms is mainly due to the different estimates for FT and C in the two replications. However, the effect was not significant (Table 1).

Average maternal heterosis for *weaning weight* was negative (Table 2). This could be expected because of the close relationship of litter size and weaning weight if litters are not standardized (Eisen et al. 1984). However, the amount of average maternal heterosis was lower than for litter size (5.2 and 6.1% of the mean of purebreds). This led to a higher litter weight for three-breed crosses, even if the individual weights were lower. Line maternal heterosis was significant only for the first room. Here, lines WG and FT were superior to the control, while LS and WW could be found on the same level.

For *weight gain*, average maternal heterosis was significant in the second room, but was only 2.3% of the purebred mean (Table 3). Line maternal heterosis was significant in both rooms, but no common trend in the two replications could be observed (r of the estimates = −0.76). Line WG especially showed different behavior in both rooms. Estimates for line LS were similar, but the deviations from C were significantly different in both rooms.

The estimates for *feed efficiency* reflect the close relation between this trait and weight gain (Table 3). The correlation between the estimates of both rooms is low, which again may be attributed to the differences of lines WG and C. For both traits, the deviations of maternal line heterosis estimates from C are in the undesired direction in the first, and in the desired direction in the second room.

The relatively high, negative estimates for line WG in these two traits in the first room indicate that recombination loss and, therefore, epistasis may have been of importance. Kinghorn (1983) and Aumann (1986) reported significant influences of epistatic effects on 7- and 5-week body weight, respectively. In the second room, estimates for average maternal and specific maternal heterosis were high, indicating that there was a high variance of gene frequencies at loci exhibiting dominance affecting this trait, which might compensate for recombination losses. On the other hand, it is also possible that fewer favorable epistatic gene combinations were fixed by selection in the second room, resulting in a poorer purebred performance of line WG in the second room, which actually was observed.

Specific maternal heterosis

Specific maternal heterosis was significant for weight gain and feed efficiency in the second room (Table 1). WG × C and LS × FT showed the best estimates for *feed efficiency*, while FT × C and LS × WG had the worst estimates for this same trait (Table 4). The same was true for weight gain. The coefficient of variation for *weight gain* in room 2 was 3.9%, and thus higher than average maternal and line maternal heterosis for this trait. In feed efficiency, the coefficient of variation reached 5%, which was equal in size to the average maternal heterosis for feed efficiency. For the best two combinations, the benefit from specific maternal heterosis was 8.3 and 6.3%, respectively.

Although specific maternal heterosis was not significant in the first room, the estimates for both rooms were in agreement with correlations of 0.45 for weight gain and 0.63 for feed efficiency.

Reciprocal grandmaternal effects

Reciprocal grand maternal effects were significant in *weaning weight* in the second room (Table 5). Very large effects were found for combinations LS × FT and for WW × FT. The estimates were 1.23 and −1.8 g, which is equivalent to 5.7 and 8.4% of the purebred mean, respectively. Since the difference between reciprocal F_1 females is twice the estimate, this effect is of major importance for the absolute performance of these two crosses.

The interactions of average grandmaternal effects with average direct genetic effects (*lv*) and with individual heterosis (*Ilv*) had only very few significant estimates, even if they were a significant source of variation. Therefore, they will not be discussed.

Table 4. Specific maternal heterosis (s_{ij}^m), standard errors (SE), and coefficients of variation (CV) for *weight gain* and *feed efficiency* ($s_{ij}^m = s_{ji}^m$)

Combination	Weight gain (g)		Feed efficiency	
	Room 1	Room 2	Room 1	Room 2
LS × WW	−0.43	−0.14	0.26	0.12
LS × WG	0.26	−0.50	−0.01	0.39
LS × FT	0.10	0.56	−0.15	−0.43
LS × C	0.07	0.09	−0.09	−0.09
WW × WG	−0.01	0.05	−0.15	−0.02
WW × FT	0.44	0.41	−0.23	−0.26
WW × C	0.00	−0.32	0.13	0.16
WG × FT	−0.35	−0.37	0.29	0.19
WG × C	0.11	0.83	−0.13	−0.57
FT × C	−0.19	−0.60	0.09	0.49
SE	0.22–0.25	0.22–0.24	0.17–0.19	0.16–0.20
CV	2.1	3.9	2.8	5.0
r	0.45		0.63	

Table 5. Reciprocal grandmaternal effects (u_{ij}^*), standard errors (SE), and coefficients of variation (CV) in *weaning weight* ($u_{ij}^* = -u_{ji}^*$)

Combination	Room 1	Room 2
LS × WW	−0.71	−0.68
LS × WG	−0.25	0.31
LS × FT	0.65	1.23
LS × C	0.31	−0.86
WW × WG	−0.94	0.89
WW × FT	−0.06	−1.80
WW × C	0.28	0.22
WG × FT	−1.27	0.42
WG × C	0.08	0.78
FT × C	−0.68	−0.14
SE	0.48–0.70	0.43–0.65
CV	3.0	4.3
r	0.01	

Total maternal heterosis

Estimates of total maternal heterosis (h_{ij}^m) are given in Table 6 for litter size and weaning weight. In *litter size*, total maternal heterosis ranged from 1.35 to 3.76 pups born alive per mating. The highest estimates were 3.76 and 3.19 in the two rooms. Again, the scale of these estimates is mainly due to a significant increase in the number of fertile matings for crossbred dams.

Estimates of maternal heterosis in the two replications are similar. This could be expected because only average maternal heterosis was significant, and the estimates for this same parameter in the two replications are similar. In both rooms, combinations LS × WG,

Table 6. Total maternal heterosis (h_{ij}^m) in *litter size* and *weaning weight* ($h_{ij}^m = h_{ji}^m$) (percentage of mean of the corresponding single crosses in brackets)

Combination	Litter size		Weaning weight (g)	
	Room 1	Room 2	Room 1	Room 2
LS × WW	1.63 (17.2)*	1.34 (13.6)	−1.32 (−5.7)*	−1.96 (−8.3)**
LS × WG	3.14 (35.1)**	3.19 (31.9)**	−1.20 (−5.6)*	−1.07 (−5.1)*
LS × FT	1.64 (16.7)*	2.40 (25.9)**	−1.55 (−7.3)**	−1.90 (−8.9)**
LS × C	3.13 (34.0)**	1.35 (15.4)	−2.52 (−10.9)**	−1.20 (−5.4)*
WW × WG	3.76 (49.3)**	2.91 (30.3)**	−1.43 (−6.3)**	−1.59 (−6.9)**
WW × FT	1.73 (22.2)*	2.70 (32.6)**	−1.57 (−7.1)**	−1.29 (−5.6)**
WW × C	1.88 (23.5)*	1.87 (23.9)*	−1.48 (−6.2)**	−0.71 (−3.0)
WG × FT	1.48 (17.9)	2.72 (31.0)**	1.73 (+8.9)**	−1.52 (−7.2)**
WG × C	3.69 (50.0)**	2.89 (33.8)**	−0.32 (−1.4)	−1.99 (−9.2)**
FT × C	2.31 (28.1)**	2.14 (30.2)**	−1.11 (−5.2)*	0.17 (0.8)
SE	0.98−1.0	1.02−1.05	0.63−0.71	0.57−0.63

*, ** See footnote Table 1

Table 7. Total maternal heterosis (h_{ij}^m) in *weight gain* and *feed efficiency* ($h_{ij}^m = h_{ji}^m$) (percentage of mean of the corresponding single crosses in brackets)

Combination	Weight gain (g)		Feed efficiency	
	Room 1	Room 2	Room 1	Room 2
LS × WW	−0.36 (−2.9)	−0.07 (−0.6)	−0.13 (−1.8)	−0.35 (−4.8)
LS × WG	−0.35 (−2.7)	0.40 (3.2)	0.24 (3.7)	−0.22 (−3.3)
LS × FT	0.33 (2.7)	0.96 (8.4)**	−0.27 (−4.0)	−0.94 (−13.1)**
LS × C	0.37 (3.0)	0.20 (1.7)	−0.68 (−9.6)**	−0.41 (−5.9)
WW × WG	−0.79 (−6.0)*	0.50 (4.1)	0.17 (2.5)	−0.43 (−6.2)
WW × FT	0.51 (4.3)	0.37 (3.2)	−0.28 (−4.1)	−0.57 (−7.7)**
WW × C	0.14 (1.1)	−0.65 (−5.4)*	−0.38 (−5.3)	0.04 (0.5)
WG × FT	−0.96 (−7.1)*	0.41 (3.4)	0.88 (14.8)**	−0.26 (−3.8)
WG × C	−0.43 (3.3)	1.32 (10.8)**	−0.01 (−0.1)	−0.83 (−12.2)**
FT × C	0.11 (0.9)	−0.60 (−5.1)*	−0.15 (−2.3)	0.33 (4.8)
SE	0.33−0.36	0.33−0.36	0.27−0.29	0.26−0.30

*, ** See footnote Table 1

WW × WG, and WG × C were above, and combinations LS × WW and WW × C were below, average.

In *weaning weight*, total maternal heterosis was on average negative or close to zero. Since litters were not standardized, this could be expected. However, total maternal heterosis for weaning weight is not completely determinated by maternal heterosis for litter size. The correlations of the estimates for maternal heterosis in weaning weight and litter size are only −0.24 in room 1 and −0.12 in room 2. Differences between rooms appeared for combinations WG × FT and WG × C.

In *weight gain* and *feed efficiency*, again similar effects could be observed (Table 7). In room 2, more values were significantly different from zero. Taking into account the different significance of average and line maternal versus specific maternal heterosis and the higher absolute performance in weight gain in the first room, it may be concluded that a variable amount of recombination loss is the reason for the different behavior of both rooms.

The range of estimates for maternal heterosis is larger than reported in other studies. Hörstgen-Schwark et al. (1984) found maternal heterosis between 0.5 and 1.7 young born alive. However, it must be taken into account that the level of fertility in that study was higher than in the present one. Van den Nieuwenhuizen et al. (1982) reported maternal heterosis of 1.7 young born alive. In weaning weight, the estimates are comparable to those found by Eisen et al. (1984).

Absolute performance of crosses

Variation in purebred means and maternal heterosis raises the question of what could be gained from crossing under "practical" conditions. Table 8 gives the values of

Table 8. Best purebreds, single crosses, and three-breed crosses for traits *litter size* (LS), *weaning weight* [WW (g)], *weight gain* [WG (g)], and *feed efficiency* (FE)

Trait	Group	Room 1		Room 2	
LS	Purebred	LS	12.73^{a}	LS	9.37^{a}
	Single cross	C × LS	12.55^{a}	C × LS	10.70^{b}
	Three-breed cross	WW × (LS × C)	14.80^{b}	FT × (WW × LS)	14.40^{c}
WW	Purebred	WW	24.94^{a}	WW	26.15^{a}
	Single cross	C × WW	25.26^{a}	FT × WW	26.38^{a}
	Three-breed cross	WG × (WW × LS)	25.17^{a}	LS × (WW × C)	23.71^{b}
WG	Purebred	WG	18.47^{a}	WG	17.60^{a}
	Single cross	WW × WG	16.63^{b}	C × WG	14.57^{b}
	Three-breed cross	WG × (WW × LS)	16.41^{b}	WG × (C × LS)	14.54^{b,1}
FE	Purebred	WG	4.02^{a}	WG	4.74^{a}
	Single cross	LS × WG	5.21^{b}	C × WG	5.79^{b}
	Three-breed cross	LS × (C × WG)	5.61^{b}	FT × (C × WG)	5.37^{ab}

[1] WG × (C × WW) = 14.54

Values marked with the same letter within one trait and room are not significantly different

Table 9. Relative gain for purebreds (PB), single crosses (SC), and three-breed crosses (TC) (mean of all groups = 100)

Group	Room 1		Room 2	
		Average gains		
Purebred		71.44^{a}		68.45^{a}
Single cross		80.05^{a}		80.08^{b}
Three-breed cross		109.03^{b}		105.93^{c}
		Best groups		
Purebred	LS	113.78^{a}	C	90.52^{a}
Single cross	WG × LS	139.15^{ab}	LS × WG	118.70^{b}
Three-breed cross	C × (LS × WG)	154.09^{b}	C × (WG × LS)	156.07^{c}
		Worst groups		
Purebred	WW	52.65^{a}	FT	41.03^{a}
Single cross	WW × WG	46.54^{a}	WG × FT	49.64^{a}
Three-breed cross	FT × (LS × C)	64.76^{a}	WG × (C × FT)	55.63^{a}

Values marked with the same letter within one group are not significantly different

the best absolute performances of purebreds, single crosses, and three-breed crosses in the four traits. It is evident that only for litter size can a clear differentiation between the three groups be made. In weaning weight, three-breed crosses were inferior in the second room. For weight gain and feed efficiency, one purebred line (WG) was superior to all crosses.

However, under "practical" conditions not only the average performances in weaning weight and weight gain are of interest, but also the total performance of a litter. Therefore, an economic index was constructed to evaluate the absolute performance of all breeding groups.

$$G = (c_1 \cdot n \cdot 6\,\mathrm{W}) - (c_2 \cdot n \cdot \mathrm{FE} \cdot 6\,\mathrm{W}),$$

where

G = economic gain,
c_1 = price per g live weight (3 DM/kg),
c_2 = price per g feed (0.25 DM/kg),
n = litter size,
6 W = 6-week body weight of pups,
FE = feed efficiency.

Because this experiment was intended to be a model for pig breeding, the economic values c_1 and c_2 were chosen to achieve a similar relation of income and feed costs as for pig production under German conditions. Table 9 summarizes the results, where the absolute values are expressed in percent of the mean of all 85 groups. The means for purebreds, single, and three-breed crosses show little differences between the two replications. Three-breed crosses were significantly superior to single crosses and purebreds. In the first room, the best three-breed cross was better than the best purebred, but not significantly better than the best single cross. In the second room, all three groups were significantly different from each other. The best single cross in the first room was the reciprocal of that in the second room and, within rooms, the best crossbred dam was the reciprocal of the best single cross.

Due to the high amount of maternal heterosis for litter size and weaning weight, it was not possible to predict the value of three-breed crosses from purebreds or single crosses. Table 10 gives the correlations between the performance of three-breed crosses and the average performance of the corresponding purebreds or single crosses, respectively. Weaning weight, and especially total performance (G), cannot be predicted from purebreds or single crosses, which fact is confirmed by the composition of the best three-breed crosses. The single cross LS × WG in the first room ranks only on position 55 and WG × LS

Table 10. Correlations between the absolute performance of three-breed crosses and the performance estimated as average of the three purebreds (TC from PB) or as average of the two single crosses of the sire line and one of the dam's lines (TC from SC)

Trait	Room	TC from PB	TC from SC
LS	1	0.51	0.45
	2	0.38	0.65
WW	1	0.04	0.45
	2	0.22	0.59
WG	1	0.84	0.84
	2	0.81	0.77
FE	1	0.50	0.57
	2	0.57	0.46
G	1	0.35	0.29
	2	0.17	0.24

Table 11. Average performances of purebred lines

Line	Room	Litter size	Weaning weight (g)	Weight gain (g)	Feed efficiency
LS	1	12.73	22.09	11.91	7.03
LS	2	9.37	22.15	9.99	7.95
WW	1	5.53	25.44	12.25	7.64
WW	2	8.87	26.31	10.74	7.97
WG	1	4.44	17.63	18.25	4.31
WG	2	5.70	18.94	17.51	4.91
FT	1	8.20	18.05	10.51	6.58
FT	2	4.77	20.01	9.68	7.48
C	1	8.87	22.15	10.10	7.73
C	2	8.67	20.94	12.25	6.66
$\bar{x}$	1	7.95	21.07	12.60	6.66
$\bar{x}$	2	7.47	21.67	12.03	6.99
SE	1	0.86	0.69–1.11	0.27–0.43	0.21–0.48
SE	2	0.91	0.74–1.12	0.34–0.60	0.30–0.53

in room 2 on position 56 of 85. The control line (sire of the best cross) ranks on position 70 in the first and 52 in the second room.

This is contrary to the results of Bell et al. (1955) from their work with inbred lines of *Drosophila*. They found that high performance of crossbred progeny could only be achieved if at least one of the parental lines showed good purebred performance. The authors concluded that it would not be necessary to include lines with poor purebred performance in testcross diallels.

Conclusions

The present study has shown that after 20 generations of selection for purebred performance within lines, a considerable amount of maternal heterosis could be found. For litter size the estimates were in agreement, while in weaning weight, weight gain, and feed efficiency different estimates occurred, mainly due to the differences of two combinations (WG × FT and WG × C).

For the other parameters (average direct and maternal genetic, individual heterosis, and interactions) and the single components of maternal heterosis, the differences between rooms were larger. These differences may be due to several factors. Because of the different fertility of the purebred lines (Table 11), selection differentials in the two rooms were different. Furthermore, the model used in the analysis assumes epistasis to be zero, but varying degrees of heterosis may be due to epistatic interaction, as can be seen from the results for weight gain and feed efficiency. Bell et al. (1955) also found that two or three of their nine inbred lines of *Drosophila* showed different combining abilities in consecutive testcrosses. Therefore, the combining ability of lines or individuals should be regarded in crossbreeding programs where nonadditive genetic effects are to be exploited, which can also be seen from results of reciprocal recurrent selection experiments in the pig (Bell 1982; Sellier 1982; Rempel 1986).

An important influence of maternal heterosis on the absolute performance could only be detected for litter size and weaning weight. Since these two traits influence the total performance of a cross, the performance index also depended on maternal heterosis. None of the several components of the individual phenotype dominated the others. The best crosses showed only moderate heterosis, but in all of the traits. This result leads to the conclusion that testcross diallels are inevitable for the selection of the best crosses form a set of lines.

From this data set, it must also be concluded that testcross diallels should be complete to detect the optimal combination. Since the results of Bell et al. (1955) are in contrast to these findings, further investigation is needed, especially for commercial species.

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