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Growth, Feed Efficiency and Lifetime Performance of Crosses Between Lines Selected for Nursing Ability and/or Adult Weight in Mice*

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Summary. Two populations of randombred of different origin (P and Q) containing eight lines (M_P, W_P, B_P, C_P, M_Q, W_Q, B_Q and C_Q) were used to evaluate the growth, feed efficiency and lifetime performance of females from eight pure lines and 16 F_1 crosses. Line comparisons within populations (P or Q) revealed that the heaviest line at days 21, 42 and 63 was W, followed by lines B, M and C in both populations, while the highest in feed efficiency between days 21 and 63 was line W, followed by lines B, M and C in population P, and was line B followed by lines W, M and C in population Q. Generally, average body weights and feed efficiencies of crosses within and between populations were similar to those of mid-parents. Selection produced line W superior to the line M in additive direct genetic effects on body weight and feed efficiency in each population, and line W_P superior to line W_Q in additive maternal genetic effects on body weights at days 21, 42 and 63. In lifetime performance tests, total 20-day weight of litters produced by a dam during 200 days averaged from 442.7 g (W_P) to 739.1 g (M_P) for the eight lines. Lines M and W of populations P and Q generally did not differ in additive direct and maternal genetic effects on lifetime performance. Crosses excelled lines in the number of litters raised to weaning (5.44 vs. 5.25) and total 20-day litter weight per dam during 200 days (648.5 vs. 589.3 g). For lifetime 20-day litter weight per group, crosses from unselected lines (C) exceeded crosses from lines selected for nursing ability (M), adult weight (W) and both traits (B). Crosses of lines from different populations showed a higher heterosis in lifetime performance than crosses of lines within populations. Heterosis in the number of litters raised to weaning, and total 20-day litter weight per dam was significant in crosses between lines C_P and C_Q, between lines W_P and W_Q, and between lines W_P and M_Q. Crosses C_PC_Q and C_QC_P had a highly persistent production during lifetime tests.

Key words: Heterosis – Growth – Feed efficiency – lifetime performance – Mouse lines

Introduction

A breeding system based on the development of specialized sire and dam lines for eventual crossing has been investigated theoretically by Smith (1964) and Moav and Hill (1966). Two important questions about this breeding system which require investigation experimentally are whether heterosis in crosses between a sire line and dam line in the same population differs from heterosis in crosses of lines of different populations, and how heterosis in crosses of selected lines differs from heterosis in crosses of unselected lines.

Crosses between lines (breeds) usually exhibit heterosis, particularly for fitness traits. The value of heterosis in farm animals might be substantial for a complex of fitness traits. In dairy cattle, for example, lifetime milk production depends on calving interval, resistance to disease (e.g. mastitis), longevity etc. If these component traits exhibit favorable heterosis, substantial benefit from crossbreeding could be expected for lifetime milk production.

Although research has been conducted on lifetime performance in purebred animals (Gill and Allaire 1976 in dairy cattle; Baker et al. 1978 in sheep; Tomita et al. 1976, Wallinga and Bakker 1978 in mice) the literature dealing with lifetime performance in crosses is scarce. In the only study with mice, Roberts (1961) reported that compared to the better parental strain, crosses weaned three times as many offspring whose total weaning weight was four times as great.

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adult weight and an unselected control line have been developed in each of two populations of different origin (Nagai et al. 1978). The objective of this study was to examine heterosis for growth, feed efficiency and lifetime performance exhibited by F_1 crosses from the eight lines.

Material and Methods

Mice

The mouse lines used were the three selected lines (M, W and B) and one unselected control (C) in each of the two randombred populations (P and Q). The breeding history of these lines has been described by Nagai et al. (1978) and Nagai (1978). Briefly, selection was conducted in M for increased nursing ability, as measured by mean 12-day litter weight in a crossfostering set, in W for increased adult weight (42-day weight), and in B for increased selection index value combining 42-day weight of an individual and the nursing ability of its mother. The C line was maintained as unselected control in each population. After 12 generations (generations 0 to 11) of selection, the six selected lines (M_P, W_P, B_P, M_Q, W_Q, B_Q) were maintained without selection for three generations of random mating, and were then selected again for five generations (generations 15 to 19). Mice used for this experiment were female offspring born to parents at generation 20.

Eight pure lines and 16 F_1 crosses were produced by the mating design shown in Table 1. At birth, litter size was standarized to eight. At weaning, 30 females were randomly chosen in each group (pure line or cross) with the restriction that they represent litters produced by 18 pair-matings. Thirty females were individually caged from days 21 to 63. At day 63, each female was cohabited with a male from an unrelated randombred population (R). When females produced their first litters, litter size was reduced to nine, where possible. Litters of less than nine mice were not augmented. The litter was maintained until day 20 in a cage with its sire and dam. At day 20, the litter was discarded. This procedure was repeated until dams reached 263 days of age. When sires died, new adult males were introduced for pair-mating, while when dams died, no replacement was made. Females that did not produce a first litter by day 93 were mated with a new male, and were destroyed at day 123 if no litter had been produced or pregnancy was not apparent. A similar procedure was applied subsequently. Throughout 200 days of observation, 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 from 40% to 50%, respectively.

Table 1. Number of females (pure lines and F_1 crosses) used for the growth and feed efficiency experiment

Sire	Dam M_P	W_P	B_P	C_P	M_Q	W_Q	B_Q	C_Q
M_P	30	30			30	29		
W_P	30	30	30		30	30		
B_P			30					
C_P				30				29
M_Q	30	30			30	30		
W_Q	30	30			29	28	30	
B_Q							30	
C_Q				30				29

Number of females used for the lifetime performance experiment was 30 for each of eight pure lines and 16 F_1 crosses shown above

Measurement

Body weight and feed weight were recorded individually at days 21, 42 and 63. Feed efficiency for each period (days 21 to 42, days 42 to 63 and days 21 to 63) was defined as the ratio (%) of body weight gain (g) to feed intake (g) during the period. In the lifetime performance tests, the number of young within the litter (NY) and body weight of the litter (LW) were recorded at day 20. At the end of the 200-day period, the number of litters raised to weaning (WNU) was counted for each dam. Also, total number young raised (TNY), total litter weight (TLW) and their means (ANY = TNY/WNU and ALW = TLW/WNU) were calculated for each dam. These measurements characterize lifetime performance of a dam. Number of dams weaning a litter (DN) was multiplied by the mean TLW for the lifetime 20-day weight of litters raised by line or cross (LLWG). DN measures the survival of productive dams while WNU and ANY measure their reproductive efficiency. ALW indicates a composite of nursing ability of the mother, growth potential of the young and preweaning survival (ANY) for standardized litters.

Statistical Analysis

Data from 24 groups (8 pure lines and 16 crosses) were analyzed in a one-way analysis of variance (between and within groups). The within group variance was used to conduct t-tests when a priori linear contrasts were mutually orthogonal and Dunn's tests (Kirk 1968) when the contrasts were non-orthogonal. Contrasts involving means from lines M_P, W_P, M_Q, W_Q and their crosses, and those from control lines C_P and C_Q and their crosses were used to estimate additive direct and maternal genetic effects and direct heterosis for lifetime performance. Mean performance of a line or cross was assumed to be completely determined by additive direct and maternal genetic effects and direct heterosis. Dickerson (1969) and Eisen (1973) have given the genetic models for interpreting line-cross data. The contrasts for additive direct genetic effects (g), additive maternal genetic effects (m), and direct heterosis (h) for lines A and B, and their F_1 crosses are as follows:

$$\bar{A} - \bar{B} - \bar{F}_1(B \times A) + \bar{F}_1(A \times B) = g_A - g_B,$$

$$\bar{F}_1(B \times A) - \bar{F}_1(A \times B) = m_A - m_B,$$

$$\bar{F}_1(B \times A) + \bar{F}_1(A \times B) - \bar{A} - \bar{B} = 2h_{AB},$$

where for example, $\bar{A}$ is the group mean of line A females and $\bar{F}_1$ (B × A) is the group mean of F_1 females from the mating of line B sires with line A dams.

Results

Growth and Feed Efficiency

Mean body weights at days 21, 42 and 63 are presented in Table 2. Estimates of mean body weight gains from days 21 to 42 and from days 42 to 63 can be obtained from

Table 2. Mean, standard error (SE) and coefficient of variation (CV) of body weight for female mice of pure lines and their F_1 crosses

Line or cross	No.	Day 21 Mean (g)	SE	CV	Day 42 Mean (g)	SE	CV	Day 63 Mean (g)	SE	CV
M_P	30	14.6	0.29	11	25.3	0.41	9	29.0	0.76	14
W_P	30	16.6	0.36	12	30.1	0.61	11	36.5	1.02	15
B_P	30	15.2	0.33	12	28.9	0.47	9	33.5	0.72	12
C_P	30	12.6	0.28	12	21.7	0.27	7	23.8	0.34	8
M_Q	30	16.2	0.22	8	27.2	0.37	7	30.1	0.53	10
W_Q	28	18.7	0.40	11	35.4	0.90	13	40.7	1.25	16
B_Q	30	17.6	0.33	10	34.1	0.71	11	41.1	1.29	17
C_Q	29	15.2	0.17	6	24.3	0.41	9	26.2	0.50	10
Line mean		15.8	0.30	10	28.4	0.52	10	32.6	0.80	13
M_PW_P	30	16.8	0.20	7	28.4	0.55	11	34.5	0.88	14
W_PM_P	30	16.2	0.30	10	27.4	0.39	8	32.4	0.91	15
W_PB_P	30	16.6	0.42	14	30.9	0.47	8	36.3	1.13	17
M_QW_Q	30	16.9	0.43	14	30.1	0.45	8	33.2	0.65	10
W_QM_Q	29	18.2	0.29	8	31.2	0.42	7	35.3	0.74	11
W_QB_Q	30	17.8	0.44	14	34.0	0.86	14	38.8	1.46	21
M_PM_Q	30	16.0	0.23	8	25.4	0.42	9	28.6	0.74	14
W_PW_Q	30	16.5	0.62	21	31.5	0.73	13	35.8	0.88	13
C_PC_Q	29	14.0	0.31	12	22.7	0.29	7	24.8	0.41	9
M_PW_Q	29	16.2	0.40	13	28.5	0.48	9	33.7	0.77	12
W_PM_Q	30	16.5	0.33	11	27.9	0.42	8	32.6	0.85	14
M_QM_P	30	15.5	0.31	11	25.6	0.46	10	28.4	0.61	12
W_QW_P	30	18.9	0.36	10	33.7	0.71	12	40.4	1.25	17
C_QC_P	30	13.1	0.27	11	22.2	0.41	10	24.6	0.55	12
M_QW_P	30	16.4	0.26	8	28.0	0.39	8	33.0	0.72	12
W_QM_P	30	17.1	0.25	8	29.4	0.51	10	34.7	0.93	15
Cross mean		16.4	0.34	12	28.6	0.50	10	33.0	0.84	14

For example, M_PW_Q is the F_1 cross from the line M_P sire mated with the line W_Q dam

the figures shown in Table 2. The four lines (M, W, B and C) of population Q were heavier than the corresponding lines of population P at days 21, 42 and 63. The within population comparison revealed that each of the selected lines (M, W, and B) were significantly ($P < 0.01$) heavier than the control line (C), except line M_Q at day 21. Line ranking for body weights at days 21, 42 and 63 was W > B > M > C in both Populations (P and Q). Coefficients of variation were, on the average, similar for the eight lines and 16 F_1 crosses at days 21, 42 and 63. Cross W_PB_P was significantly heavier than cross W_PM_P and cross W_QB_Q was heavier than cross W_QM_Q for body weights at days 42 ($P < 0.01$) and 63 ($P < 0.05$). Crosses involving the index line (B) selected for both nursing ability and adult weight were heavier than crosses involving the line (M) selected for nursing ability.

Mean feed efficiencies for the periods between days 21 and 42, days 42 and 63, and days 21 and 63 are shown in Table 3. Estimates of mean feed intake during the corresponding periods can be obtained from Table 3. Feed efficiency between days 21 and 42 was more than twice the feed efficiency between days 42 and 63 in lines and F_1 crosses. Among the eight lines, B_Q was the highest in feed efficiency during the period between days 21 and 63 (10.5%), followed by lines W_Q (9.7%), W_P (8.7%), B_P (8.5%) and the remainder (7.8 to 6.4%). Line B_Q was highest in feed efficiency both between days 21 and 42 (14.9%) and between days 42 and 63 (6.44%). In line B_Q, body weight gains were 16.5 and 7.4 g for the periods between days 21 and 42, and between days 42 and 63, respectively, while feed intakes were 110.4 and 111.7 g during the corresponding periods. Comparison within populations revealed that the selected lines (M, W, and B) had significantly larger feed efficiency between days 21

Table 3. Mean, standard error (SE) and coefficient of variation (CV) of feed efficiencies for female mice of pure lines and their F_1 crosses

Line or cross	No.	Between days 21 and 42 Mean (%)	SE	CV	42 and 63 Mean (%)	SE	CV	21 and 63 Mean (%)	SE	CV
M_P	30	13.7	0.30	12	3.90	0.363	51	7.8	0.38	26
W_P	30	12.4	0.36	16	5.27	0.440	46	8.7	0.34	22
B_P	30	13.0	0.34	14	4.15	0.345	46	8.5	0.25	16
C_P	30	10.9	0.35	17	2.27	0.171	41	6.4	0.19	16
M_Q	30	12.0	0.34	16	3.23	0.296	50	7.6	0.23	17
W_Q	28	14.7	0.56	20	4.58	0.385	45	9.7	0.37	20
B_Q	30	14.9	0.29	11	6.44	0.520	44	10.5	0.39	20
C_Q	29	10.7	0.28	14	2.32	0.281	65	6.5	0.23	19
Line mean		12.8	0.35	15	4.02	0.350	49	8.2	0.30	20
M_PW_P	30	11.7	0.35	16	5.67	0.337	33	8.6	0.30	19
W_PM_P	30	11.4	0.31	15	4.76	0.482	55	7.9	0.34	24
W_PB_P	30	13.2	0.48	20	5.46	0.688	69	8.8	0.40	25
M_QW_Q	30	13.3	0.36	15	4.71	0.261	38	8.2	0.23	15
W_QM_Q	29	12.8	0.36	15	4.17	0.344	44	8.5	0.33	21
W_QB_Q	30	14.5	0.40	15	5.38	0.615	63	9.4	0.41	24
M_PM_Q	30	10.8	0.33	17	3.34	0.332	54	7.0	0.27	21
W_PW_Q	30	14.5	0.48	18	4.22	0.361	47	9.3	0.35	21
C_PC_Q	29	10.4	0.36	19	2.35	0.212	49	6.3	0.22	19
M_PW_Q	29	12.5	0.32	14	4.98	0.399	43	8.8	0.29	18
W_PM_Q	30	12.0	0.43	20	4.61	0.450	53	8.3	0.35	23
M_QM_P	30	11.4	0.29	14	3.16	0.303	52	7.4	0.20	15
W_QW_P	30	13.5	0.49	20	6.55	1.031	86	9.7	0.41	23
C_QC_P	30	11.2	0.30	15	2.92	0.316	58	7.1	0.23	18
M_QW_P	30	12.4	0.37	16	4.85	0.399	44	8.5	0.33	21
W_QM_P	30	12.7	0.27	12	5.05	0.459	50	8.8	0.31	19
Cross mean		12.4	0.37	16	4.51	0.437	52	8.3	0.31	20

and 63 than the control (C) in both populations, except for line M_Q. Feed efficiency for the period between days 21 and 63 varied among crosses, ranging from 6.3% (C_PC_Q) to 9.7% (W_QW_P).

Comparison of the control lines (C_P and C_Q) in the two populations provides the basis for the comparison of selection response of two lines in different populations (P and Q). Lines C_P and C_Q differed significantly ($P < 0.01$) for body weights at days 21 and 42 (Table 4). When differences between the two control lines (C_P-C_Q) were taken into consideration, line W_Q was heavier (2.6 g) than line W_P in body weight at day 42, line B_Q was heavier (5.1 g) than line B_P for body weight at day 63, and was more efficient (1.9%) for feed efficiency between days 21 and 63. Lines M_P and M_Q did not differ in any traits examined.

Using data from M_P, W_P, M_Q, W_Q and their crosses, and lines C_P and C_Q and their crosses, additive direct and maternal genetic effects and heterosis for body weight and feed efficiency were evaluated (Table 5). Again, the difference between lines C_P and C_Q was taken into account when genetic effects for two lines of different populations were compared. For additive direct genetic effects on body weights at days 21, 42 and 63, the lines selected for adult weight (W_P and W_Q) were greater than the lines selected for nursing ability (M_P and M_Q) with line W_Q being superior to line W_P. Additive maternal genetic effects of lines selected for nursing ability (M_P and M_Q) did not differ from those of lines selected for adult weight (W_P and W_Q), except that line M_Q was superior to line W_Q for body weight at day 21. Line W_P exceeded line W_Q for additive maternal genetic effects on body weight at days 21, 42 and 63. There was no evidence of significant heterosis except for crosses of lines M_P and W_P for body weight at day 21. In fact, negative heterosis was frequently observed for body weights at days 42 and 63.

Analyses of feed efficiency revealed that in general,

Table 4. Differences in body weight and feed effciency between lines of different populations (P and Q)

Trait	$^aM_P-M_Q$	$^aW_P-W_Q$	$^aB_P-B_Q$	C_P-C_Q
Body weight at day 21 (g)	1.1	0.5	0.3	−2.6**
Body weight at day 42 (g)	0.7	−2.6*	−2.5	−2.7**
Body weight at day 63 (g)	1.3	−1.8	−5.1*	−2.4
Feed efficiency, days 21 and 42 (%)	1.5	−2.4	−2.0	0.2
Feed efficiency, days 42 and 63 (%)	0.7	0.7	−2.2	−0.0
Feed efficiency, days 21 and 63 (%)	0.3	−0.9	−1.9*	−0.1

[a] Adjusted for the difference, C_P-C_Q
* Significant $P < 0.05$
** Significant $P < 0.01$

Table 5. Additive direct and maternal genetic effects for body weight and feed efficiency

Genetic effect	Lines	Body weight (g) at Day		
		21	42	63
Direct	M_P-W_P	−1.4	−3.9*	− 5.3*
	M_Q-W_Q	−3.8**	−9.2**	−12.6**
	M_P-M_Q	0.7	−0.0	1.3
	W_P-W_Q	−2.8*	−5.4*	− 6.6
	M_P-W_Q	−5.0**	−11.0**	−12.7**
	W_P-M_Q	2.3	4.8*	8.3**
	C_P-C_Q	−1.7*	− 2.1*	− 2.2
Maternal	M_P-W_P	−0.6	− 0.9	− 2.1
	M_Q-W_Q	1.3**	1.0	2.0
	M_P-M_Q	0.4	0.7	0.0
	W_P-W_Q	3.4**	2.7**	4.8**
	M_P-W_Q	1.0	0.9	1.0
	W_P-M_Q	0.7	0.7	0.5
	C_P-C_Q	−0.9	− 0.5	− 0.2

For genetic effects involving two populations, P and Q, the effects of C_P and C_Q were taken into account
* Significant $P < 0.05$
** Significant $P < 0.01$

the difference in additive direct and maternal genetic effects between lines and direct heterosis were not statistically significant. The exceptions were line M_Q minus line W_Q (−2.3%, $P < 0.01$) and line M_P minus line W_Q (−1.9%, $P < 0.05$) for additive direct genetic effects between days 21 and 63, and the cross from lines M_P and W_P for heterotic effects (−1.5%, $P < 0.01$) between days 21 and 42.

Lifetime Performance

Mean lifetime performance of females and total weight of litters produced by eight lines and 16 F_1 crosses are shown in Tables 6 and 7, where entries in each line or cross are listed in descending order of lifetime litter weight per line or cross (LLWG). The number of dams producing young over the 200-day period (DN) averaged 26 (88% of the initial 30 dams) for the eight lines and 28 (93%) for 16 crosses, indicating a higher reproductive capability for crosses. Crosses showed a higher productivity than pure lines: 5.44 vs. 5.25 for number of litters raised to weaning (WNU), 43.5 vs. 40.7 for number of young raised during the 200-day period (TNY), and 64 9 g vs. 5 89 g for body weight of litters raised during the period (TLW). Consequently, the mean LLWG was 15% heavier in crosses than lines (17,984 g vs. 15,724 g). Crosses between populations (W_QM_P, W_PM_Q, M_QW_P and M_PW_Q) exceeded crosses within populations (W_QM_Q, M_QW_Q, M_PW_P and W_PM_P): 28 vs. 27 for DN, 5.6 vs. 5.0 for WNU, 44.9 vs. 39.5 for TNY, 690 g vs. 594 g for TLW, and 19,079 g vs. 16,211 g for LLWG.

Differences in lifetime performance between lines within populations are shown in Table 8. Lines M_P and M_Q selected for nursing ability exceeded the lines selected for adult weight (W_P, B_P, W_Q and B_Q) in WNU, TLW and TNY, indicating superior reproduction (fertility and nursing) of lines M_P and M_Q. They exceeded the unselected lines (C_P and C_Q) in average litter weight (ALW = TLW/WNY). Lines selected for adult weight were inferior to the unselected lines in WNU but were superior in ALW, indicating that they were poor in reproduction but rapid in growth.

Differences in lifetime performance between corresponding lines of the two populations (e.g. M_P-M_Q) are shown in Table 9, where the difference between selected lines was adjusted again for the C_P-C_Q difference. The unselected line, C_Q, was significantly heavier than the counterpart, C_P, for ALW. However, this difference tended to decrease by selection applied to M, W or B lines. for WNU, selection caused nearly twice as large differences in lines M, W or B as in line C. Selection in line W_P produced a greater response for ALW than in line W_Q but not for ANY and TNY.

Differences between lines in additive direct and maternal genetic effects for lifetime performance were not sta-

Table 6. Mean, standard error (SE) and coefficient of variation (CV) for lifetime performance of females and total body weight of litters produced by pure lines

Line	No. of producing dams	No. of litters raised to weaning (WNU)			No. of young raised (TNY)			Body wt. of litters raised (TLW)			Total litter wt. per line
	(DN)	Mean	SE	CV	Mean	SE	CV	Mean (g)	SE	CV	(LLWG = DN x TLW) (g)
M_P	29	6.6	0.24	19	52.1	1.94	20	739	27.0	20	21,431
C_P	28	6.2	0.41	35	47.3	3.41	38	600	43.9	39	16,800
B_P	27	5.1	0.44	45	39.5	3.80	50	542	54.6	52	14,634
W_P	24	3.9	0.40	50	30.2	3.26	53	443	43.4	48	10,632
M_Q	28	5.6	0.32	30	44.4	2.77	33	706	45.5	34	19,768
C_Q	28	5.9	0.27	24	43.6	2.43	29	640	35.7	29	17,920
B_Q	28	4.3	0.37	46	34.0	3.37	53	530	49.8	50	14,840
W_Q	19	4.4	0.46	46	34.3	3.61	46	514	53.8	46	9,766
Line Mean	26	5.25	0.36	37	40.7	3.07	40	589	43.0	40	15,724

Table 7. Mean, Standard error (SE) and coefficient of variation (CV) for lifetime performance of F_1 females and total body weight of litters produced by F_1 crosses

Cross	No. of producing dams	No. of litters raised to weaning (WNU)			No. of young raised (TNY)			Body wt. of litters raised (TLW)			Total litter wt. per cross
	(DN)	Mean	SE	CV	Mean	SE	CV	Mean (g)	SE	CV	(LLWG = DN x TLW)
C_PC_Q	28	7.2	0.21	16	59.7	2.18	19	824	31.6	20	23,072
C_QC_P	30	7.0	0.26	20	57.3	2.32	22	772	28.4	20	21,660
M_PM_Q	30	5.9	0.41	38	49.0	3.36	38	757	53.5	39	22,710
M_QM_P	29	6.1	0.32	28	49.9	2.81	30	741	41.3	30	21,489
W_QM_P	30	5.8	0.38	35	47.1	2.96	34	711	43.5	34	21,330
W_PM_Q	25	6.3	0.43	34	52.4	3.53	34	808	57.6	36	20,200
M_QW_P	29	5.4	0.35	35	42.3	2.86	36	666	41.8	34	19,314
W_PW_Q	28	5.6	0.39	36	44.2	3.13	37	675	46.6	37	18,900
W_QM_Q	27	5.4	0.29	28	44.4	2.47	29	697	39.2	29	18,819
M_QW_Q	29	4.9	0.35	38	37.9	2.88	41	588	46.4	43	17,052
M_PW_P	28	5.1	0.42	43	38.8	3.33	45	558	46.5	44	15,624
M_PW_Q	27	4.7	0.39	43	37.8	3.48	48	573	50.8	46	15,471
W_QW_P	26	4.7	0.42	46	36.4	3.60	50	551	52.8	49	14,326
W_PM_P	25	4.7	0.42	44	36.7	3.38	46	534	47.0	44	13,350
W_QB_Q	27	4.2	0.37	45	32.4	3.05	49	486	44.8	48	13,122
W_PB_P	26	4.0	0.37	48	30.3	3.02	51	435	40.3	47	11,310
Cross mean	28	5.4	0.38	36	43.5	3.02	38	649	44.5	38	17,984

tistically significant except for line M_P minus line W_P in additive direct genetic effects on WNU (3.1, $P < 0.01$) which led to the differences in TLW (321 g, $P < 0.01$) and TNY (23.9, $P < 0.01$). In general, selection for nursing ability (lines M) or adult weight (lines W and B) did not produce lines different in additive direct and maternal genetic effects for lifetime performance.

Heterosis for lifetime performance in F_1 crosses is shown in Table 10. Effects of heterosis on WNU, TLW and TNY were significant in crosses between W_P and W_Q, between W_P and M_Q, and between C_P and C_Q. It should be noted that F_1 crosses from unselected control lines (C_P and C_Q) showed significant heterosis in all traits examined but some crosses from selected lines showed negative heterosis, though not significant.

Phenotypic correlations pooled within groups are shown in Table 11. ALW was positively associated with ANY (0.81) while TNY and TLW were associated with WNU (0.94 and 0.93). As expected, TLW was associated with TNY (0.97). In determining litter weights (ALW and

Table 8. Differences in the mean lifetime performance of females between lines within populations

Line	Trait	M	W	B	C
M	WNU		2.6 **	1.5 *	0.4
	ALW		−2.9	9.3	16.4 *
	ANY		0.23	0.38	0.34
	TLW		296 **	197 **	139
	TNY		21.9 **	12.5 *	4.7
W	WNU	1.2 *		−1.2	−2.3 **
	ALW	7.4		12.2	19.3 **
	ANY	0.16		0.14	0.11
	TLW	192 **		−100	−157
	TNY	10.1 *		−9.3	−17.1 *
B	WNU	1.4	0.1		−1.1
	ALW	3.0	−4.4		7.2
	ANY	0.21	0.05		−0.03
	TLW	176	−16		−58
	TNY	10.4	0.3		−7.8
C	WNU	−0.3	−1.6 *	−1.7 *	
	ALW	18.5 **	11.1	15.5 *	
	ANY	0.67	0.50	0.45	
	TLW	66	−125	−110	
	TNY	0.8	−9.3	−9.6	

Above diagonal: line in column minus line in row for population P; below diagonal: line in row minus line in column for population Q;
* $P < 0.05$
** $P < 0.01$

WNU: number of litters raised to weaning, TLW: total litter weight over 200 days, TNY: total number of young raised over 200 days, ALW = TLW/WNU, ANY = TNY/WNU

Table 9. Differences in the mean lifetime performance of females between lines of different populations

Trait	[a]$M_P - M_Q$	[a]$W_P - W_Q$	[a]$B_P - B_Q$	$C_P - C_Q$
No. of litters raised to weaning (WNU)	0.7	0.7	0.6	0.3
Average litter wt. (ALW)	−2.1	8.2	−8.3	−11.1*
Average no. of young per litter (ANY)	−0.3	−0.4	−0.5	0.3
Total litter wt. over 200-days (TLW)	73.1	−31.8	52.0	−39.9
Total no. of young raised over 200 days (TNY)	3.9	−7.9	1.8	3.7

[a] Adjusted for the difference, $C_P - C_Q$
* $P < 0.05$

Table 10. Heterosis for lifetime performance in F_1 cross

Lines	No. of litters raised to weaning (WNU)	Average litter wt. (ALW = TLW/WNU)	Average No. of young per litter (ANY = TNY/WNU)	Total litter wt. over 200 days (TLW)	Total No. of young raised over 200 days (TNY)
M_P,W_P	–0.3	–0.9	–0.08	–45	–3.4
M_Q,W_Q	0.2	3.0	0.09	32	1.8
M_P,M_Q	–0.1	–1.3	–0.18	27	1.2
W_P,W_Q	1.0**	–1.5	–0.03	135*	8.1*
M_P,W_Q	–0.3	7.9*	0.24	15	–1.5
W_P,M_Q	1.1**	5.2	0.24	163**	10.0**
C_P,C_Q	1.1**	9.9**	0.73**	178**	13.0**

* $P < 0.05$
** $P < 0.01$

Table 11. Within-group[a] phenotypic correlations between traits

Trait	ALW	ANY	TLW	TNY
Number of litters raised to weaning (WNU)	–.06	0.01	0.93	0.94
Average 20-day litter weight (ALW)		0.81	0.25	0.18
Average number of young per litter at day 20 (ANY)			0.26	0.30
Total 20-day weight of litters over 200 days (TLW)				0.97

[a] Group is a pure line or cross

TLW) the number of young (ANY and TNY, respectively) was more important than the mean body weight of individuals.

Number of litters weaned and mean 20-day litter weight classified by line and parity are shown in Table 12. Selected lines (M, W and B) generally had heavier 20-day litter weight than unselected line (C) at each parity. The number of dams weaning litters decreased as the parity number increased. Total 20-day litter weight per line and parity (LW times No.) decreased rapidly after the fifth parity when the total 20-day litter weight ranged from 1,391 g (W_Q) to 3,341 g (M_P).

The total 20-day litter weight for each group (line or

Table 12. Number of litters weaned (No.) and mean 20-day litter weight (LW)[a] classified by line and parity

Parity	1		2		3		4		5		6		7		8		9	
Line	No.	LW	No.	LW	No.	LW	No.	LW	No.	LW	No.	LW	No.	LW	No.	LW	No.	LW
M_P	28	117.4	28	121.1	27	119.4	26	112.1	29	115.1	24	112.8	19	94.7	7	115.3	2	76.9
		8.8[b]		8.8		8.6		7.7		7.7		7.8		5.9		7.7	(4)[c]	5.5
W_P	21	117.3	20	128.5	16	104.6	12	101.7	13	108.4	7	102.4	3	121.5	1	89.1	1	118.2
		8.0		8.2		7.1		7.3		7.8		7.4		8.3		8.0	(14)	7.0
B_P	26	109.3	23	115.0	22	105.0	19	99.1	17	108.6	14	105.1	8	104.3	5	99.2	3	104.2
		8.2		8.6		8.2		7.1		7.4		7.6		6.8		6.8	(9)	7.3
C_P	26	97.3	25	93.0	24	105.7	24	104.0	24	95.6	19	98.9	17	96.6	11	78.0	3	77.6
		7.8		7.6		8.3		8.1		7.6		7.6		7.5		6.0	(8)	6.3
M_Q	26	128.8	25	127.8	26	132.0	24	121.7	22	122.4	19	127.9	12	124.4	2	112.7	1	29.3
		8.8		8.5		8.1		7.4		7.5		7.7		7.3		6.5	(5)	2.0
W_Q	17	119.6	15	125.5	13	117.7	13	128.0	12	115.9	7	88.6	4	123.1	1	85.9	1	74.7
		7.8		8.7		7.5		8.4		7.4		6.4		9.0		7.0	(18)	5.0
B_Q	20	119.4	26	112.9	22	131.4	19	133.5	12	135.4	13	127.3	7	116.2	0	–	0	–
		7.9		7.2		8.1		8.6		8.6		8.1		8.0			(13)	
C_Q	20	107.2	28	109.8	25	108.5	26	113.2	26	107.2	21	106.8	14	94.9	6	113.5	0	–
		8.3		7.7		7.3		7.5		7.0		7.1		6.5		7.0	(6)	

[a] In g
[b] Mean litter size at day 20 (litter size was standardized to nine at birth)
[c] Number of dams that were destroyed because of no production of a litter for 60 days

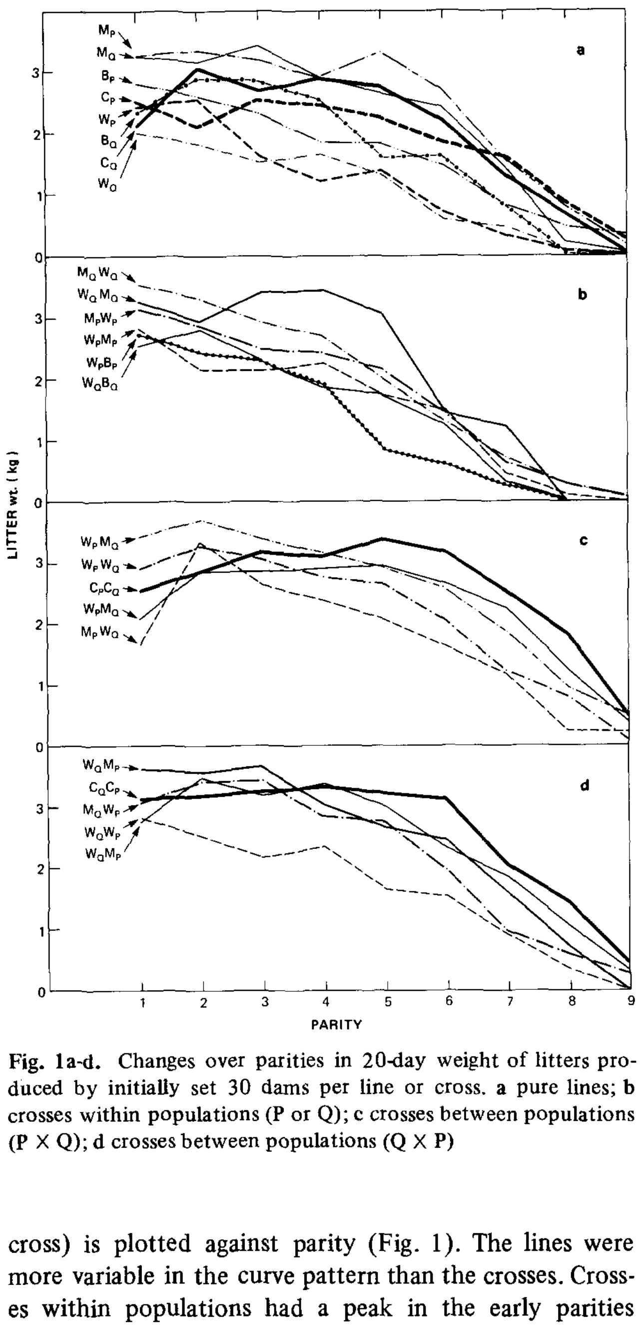

Fig. 1a-d. Changes over parities in 20-day weight of litters produced by initially set 30 dams per line or cross. a pure lines; b crosses within populations (P or Q); c crosses between populations (P X Q); d crosses between populations (Q X P)

cross) is plotted against parity (Fig. 1). The lines were more variable in the curve pattern than the crosses. Crosses within populations had a peak in the early parities while the crosses between populations peaked between the second and fifth parity. Litter weight per parity by group averaged 1,308 g and 522 g for crosses between populations and crosses within populations, respectively between the sixth and ninth parities.

Discussion

Selection had been conducted, based on the records of first litters, for increased nursing ability as measured by '12-day litter weight' and/or adult weight as measured by '42-day weight' (Nagai et al. 1978; Nagai 1978). Thus, 20-day litter weight measured in the present study should reflect the effect of selection, at least, for the first parity. Analyses revealed (Table 12) that 20-day litter weight for the first parity was heavier in selected lines (M, W, and B) than the unselected line (C). The 20-day litter weight of different parities were similar within lines. This indicates the presence of a high genetic correlation between 20-day litter weights of different parities.

Body weight of young before weaning is influenced by both postnatal maternal performance and intrinsic growth potential of the young (Willham 1963). The portion of variance of individual 21-day weight due to postnatal maternal performance and intrinsic growth potential was 52 to 61% and 6 to 19%, respectively (Cox et al. 1959; Young et al. 1965; El Oksh et al. 1967; Rutledge et al. 1972). Thus, litter weight at 21 days provides a measure of postnatal maternal performance. Nagai and Sarkar (1978) have demonstrated that selection for nursing ability which reflects mainly postnatal maternal performance (Nagai et al. 1978) resulted in increased milk production.

Since each cage contained a dam, her litter and the sire, paternal effects were also involved with the measurements of lifetime performance. However, these effects can be neglected for comparison of 20-day litter weight among groups because sires from the same population (R) were used in each group and the contribution of growth potential of the young to 20-day litter weight is small. The observed difference in 20-day litter weight among groups, therefore, reflects mainly the difference in postnatal maternal performance including milk yield.

Selection for adult (42-day) weight produced the heaviest line (W) at day 42 in both populations, P and Q (Table 2). This selection caused positive correlated responses in body weights three weeks before and after 42 days (days 21 and 63) and feed efficiencies involving the three ages (days 21, 42 and 63). Thus, line W was greater than line C for body weights and also feed efficiencies in both populations, P and Q. These findings agree with the previous reports (Sutherland et al. 1974; Bakker et al. 1977; Eisen et al. 1977) that selection for body weight (growth rate) was effective in producing direct and correlated responses in body weight and feed efficiency in mice. Line B was superior to line W for some feed efficiencies (e.g. feed efficiency between days 21 and 42 in population P, and the three feed efficiencies examined in population Q). Mechanisms responsible for this finding are not clear. Line M was larger than line C for body weights and feed efficiencies in both populations. This is likely due to the positive genetic correlation (0.70 and 0.73 in populations P and Q, respectively) between nursing ability and adult weight (Nagai et al. 1978).

Heterosis did not occur generally in the growth and feed efficiency examined (Tables 2, 3). Crosses from lines within populations as well as crosses from lines between populations did not differ in performance from their parental lines. The presence of genes for dominance was not indicated. In contrast, heterosis was evidenced in lifetime performance. On the average, crosses were higher than lines in number of producing dams (5% in DN), number of litters raised to weaning (4% in WNU), total number of young raised (7% in TNY), total 20-day litter weight over 200 days per dam (10% in TLW) and lifetime 20-day litter weight over 200 days per line or cross (15% in LLWG). The presence of gene effects for dominance was indicated for lifetime performance which involves reproductive fitness traits. It should be noted that crosses from lines between populations (W_QM_P, W_PM_Q, M_QW_P and M_PW_Q) exceeded crosses from lines within populations (W_QM_Q, M_QW_Q, M_PW_P and W_PM_P): 4% in DN, 12% in WNU, 14% in TNY, 16% in TLW and 28% in LLWG. The results suggest that crosses between genetically diverse lines exhibit a larger heterosis than crosses between less diverse lines. The importance of the gene frequency difference between lines in heterosis has been well recognized theorectically (Falconer 1960).

Unexpectedly, crosses between the unselected lines, C_PC_Q and C_QC_P, were large in DN, WNU, TNY and TLW, relative to other crosses between selected lines, and had the largest LLWG (Table 7). Selection for adult weight and/or nursing ability involves selection for direct genetic effects on growth (Nagai et al. 1978). Roberts (1961) studying a lifetime performance in mice concluded that selection for a rapid early growth had an adverse effect on reproductive fitness. The present study revealed that selection for adult weight resulted in a smaller number of litters raised to weaning (WNU). The apparently negative genetic correlation between rapid growth and reproductive fitness would have narrowed, among M, W and B, the frequency of genes responsible for lifetime performance, and thus, crosses from the selected lines (M, W and B) exhibited a smaller heterosis in lifetime 20-day litter weight (LLWG) than crosses from lines C_P and C_Q.

Unselected line (C) was larger in DN and WNU than lines selected for adult weight (W and B) and consequently, line C exceeded lines W and B in TLW and LLWG (Table 6). The results indicate that in pure lines, WNU and DN were important in determining TLW and LLWG. For genetic improvement of TLW and LLWG, the value of breeding for reproductive fitness, DN and WNU, cannot be over-emphasized. Although a high genetic correlation between 20-day litter weights of different parities was suggested, prediction of lifetime performance based on 20-day litter weight at first parity would not be accurate unless DN and WNU are well predicted.

In non-inbred mice, 'lifetime' reproduction was examined for the entire lifetime (until death) by Roberts (1961), for 308 days by Wallinga and Bakker (1978), and for 263 days in the present study. For the total number of litters produced by a group (line) of dams, these three periods are similar because at later stages of life, only a small portion of dams continues to reproduce. A common finding of all three studies was that as dams get older, their productivity (total 20-day litter weight of a group per parity) decreases. In actual husbandry, the length of maintaining laboratory animals varies among institutions. If the cost of maintaining aged but still producing dams is considered as in the case of livestock, time at which animals are culled requires an overall evaluation. Genetic and economic aspects of maintaining laboratory animals for multiple parities should be studied further.

The implications of the results from the present lifetime performance study to applied animal breeding are disturbing since it is expected that similar phenomena occur in different mammalian species. In dairy cattle, for example, selection for increased milk yield per lactation would not be expected to increase long-term milk yield unless number of calving also receives selection attention. Phenotypic and genetic correlations of number of calving were 0.95 and 0.95 with lifetime milk yield, and 0.95 and 0.94 with lifetime milk fat (Gill and Allaire 1976). Genetic correlations between different lactations ranged from 0.83 to 0.92, suggesting that production traits of different lactations are essentially the same trait genetically (Tong et al. 1979). However, combining all lactation records as a single trait in sire and cow evaluation for lifetime performance would not be appropriate if calving interval differs among cows. In beef cattle (Hereford, Angus and Shorthorn), heterosis significantly reduced the interval from parturition to first estrus and the average date of conception (Cundiff et al. 1974). This heterosis would be useful in increasing long-term productivity. However, a question arises: how much does the long-term productivity of these crosses differ from that of crosses of less improved breeds? The results from the present study (e.g. lifetime performance of C_PC_Q and C_QC_P) have implications to these matters. Nevertheless, extrapolation of the results from mouse studies to other species cannot be done without reservation. Serious investigations should be conducted in other species to clarify the role of the reproduction in long-term productivity.

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