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Heterosis among lines of mice selected for body weight

1. Growth

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Summary. To examine the effect of selection on levels of heterosis, crosses were made between three groups of six lines of mice, one group unselected (controls) and the other two selected for high (large lines) and low (small lines) 6-week body weight, respectively. The coefficient of inbreeding of each line was about 0.60. Each line was crossed reciprocally to one line from each of the parental groups, as well as producing purebred progeny. Heterosis for 3-week weight, 6-week weight and 3–6 week gain averaged 0.0%, 2.4% and 4.2%, respectively, and was higher for males than for females. Heterosis was more extensive in crosses involving large or control lines than in crosses with small lines. There was no detectable heterosis in several measures of developmental rate, such as age at vaginal opening. Food conversion efficiency and carcass composition were measured on a sample of the animals. Food consumption, gonadal fat pad weight, and hindquarters weight, each expressed as a proportion of body weight, exhibited −4.0%, 5.6%, and 2.3% heterosis, respectively.

Key words: Heterosis – Mice – Selection – Growth

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Introduction

Heterosis in crosses among breeds, inbred and long isolated strains has been observed in most farm and laboratory animals, the effects typically being largest for reproductive performance, intermediate for growth rate and small for carcass composition (Falconer 1981). It is expected from the dominance model of heterosis that heterosis will increase as lines become more distant genetically, and there are data illustrating this (e.g. Glodek 1974 for pigs). If, however, lines are very distant or locally adapted, the heterosis may become less, presumably due to epistatic interaction (Falconer 1981; Sheridan 1981). There is less information on how the amount of heterosis depends on the selection history of populations of similar genetic distance: for example, is more or less heterosis to be expected between crosses of lines in which animals are of different size than those in which animals are the same size?

Following the replicated selection experiment of Falconer (1973) there were available in the laboratory 18 lines of mice derived from the same base population almost 60 generations previously. Of these, six had been selected for high body weight, six for low body weight and six were unselected controls. This provided the opportunity to study amounts of heterosis between lines of different selection history. In this paper we report the results on purebreds and two-way crosses of traits of the growing animal: body weights at different ages, rates of live weight gain, rates of development, food conversion efficiency and carcass composition. In a subsequent paper we will report results on reproductive performance of purebred dams with purebred and two-way crossbred progeny and of crossbred dams (Bhuvanakumar et al. 1985).

Materials and methods

Animals

The lines used for this experiment derived from the Q strain and were selected either for large 6-week weight (L), or for small 6-week-weight (S) together with unselected controls (C), there being six replicate lines of each (labelled A to F) (Falconer 1973). Selection within litters was practised for 23 generations and subsequently all lines were maintained with random mating within lines, no selection, and as far as possible equal replacement from each litter within lines. During the 23 generations of selection the objective was to use 8 litters per line, and, subsequently, 16 litters. When the experiments described here were carried out, from generation 59 onwards, the coefficient of inbreeding was approximately 0.60, higher than expected for the population size because of infertility and other losses.

Crossing programme

A complete diallel cross was made between the sizes of lines (L, C and S) with a partial diallel cross among lines to limit the number of crosses to what could be managed. The design is shown in Fig. 1. For example, males of the large line of replicate A were mated either to females of their own line or to females of the large, control, or small size lines of replicate B. Because replicate lines of different sizes with the same designation, e.g. B, are not substantially more highly related than those of different designations (Falconer 1973), each line was, in effect, crossed to one random line of each size. There was an average time gap of one week between matings of pairs of replicates (AB, CD and EF), these three pairs being designated as three "blocks". The number of matings per cell ranged from three to ten, partly to equilize numbers of pure and cross matings and partly due to availability of mice.

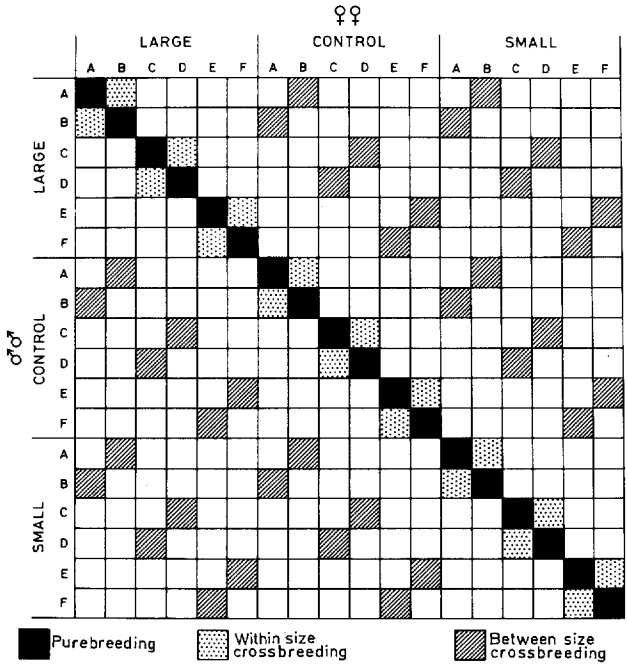

Fig. 1. Experimental design to show the crosses made

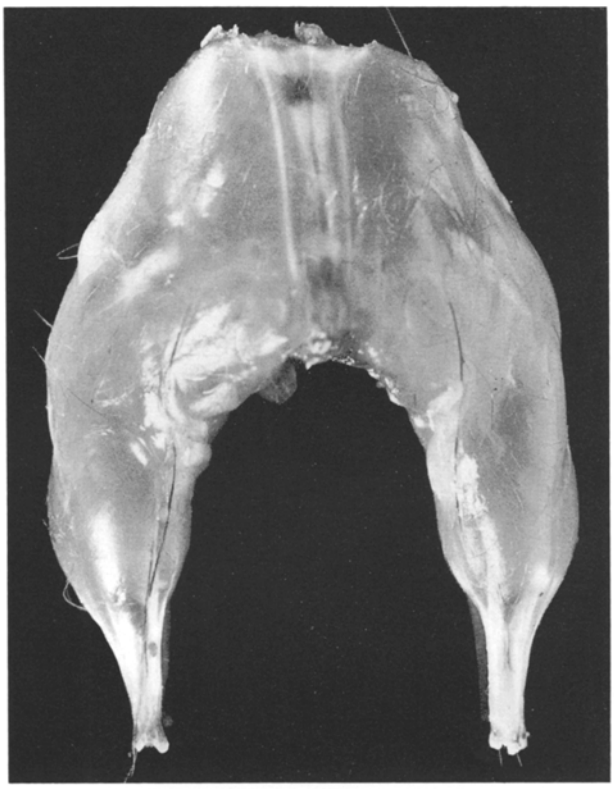

Fig. 2. Hind quarters dissected piece

Matings were made in five separate phases, comprising different generations of the Q lines, with the mice used as parents for phase 1 being from generation 59 of the Q lines and phases 2–5 from generations 61–64, respectively. In each phase individual 3- and 6-week weights were taken, other data being recorded in some of the phases. Mice were maintained as previously for the Q lines, with pair mating, weaning at 21 days, and subsequent group housing, except in phases 3–5 when harem matings, with 2–5 females per male, were made. Records of food consumption were taken on individually housed mice.

Carcass composition

In phases 3 and 4, mice were slaughtered at final (6- or 7-week) weighing and dissected. Gonadal fat pads and a simulated "butcher's cut" of the hind quarters (Fig. 2) were dissected out and weighed. The latter was obtained as follows: animals were put on their stomach, a horizontal skin incision was made at the lumbro-sacral region, the skin from the hind-quarters was pulled back and any subcutaneous fat remaining was removed by a scalpel. The hind quarters were cut off at approximately the lumbo-sacral joint, which was the anterior of the dissected piece, and the posterior mark was the first or second coccygeal vertebra; the feet were removed at the tibio-tarsal joint.

Stages of development

In phase 4, weights of animals were taken every week from 3–8 weeks of age. In phase 5, animals were inspected individually daily from day 2 of age for external ear eruption, from day 7 for eruption of both lower incisors, from day 10 for

corneal visibility in both eyes and after weaning for vaginal opening in females. Animals were weighed when each of these events was observed.

Statistical analysis

Least squares analyses of variance were conducted using the LSML76 program of Harvey (1977). The main results tabulated are of least squares means fitting a model containing: phase (up to 5 for the complete data set), sex (male or female), sire size-dam size-heterosis combination (12 classes comprising 9 crosses and 3 purebreds), block (1 to 3, corresponding to AB, CD or EF lines and crosses), and individual mouse effects. Sums of squares for the complete analysis of variance were computed in a series of runs in which main effects and interactions were fitted, and variation among individuals was partitioned between and within litters. Each block comprised purebreds and crosses of a different set of lines, so block differences included random effects due to genetic drift. Therefore, main effects, such as size of sire, were tested against the interaction between blocks and those effects. In order to test for the sire size × dam size interaction among the crosses (i.e. free of heterosis estimates from the purebreds), separate analyses were performed on the crossbred data alone.

Data on weights were analysed both raw and after transformation to logarithms to check whether size effects acted additively or multiplicatively, and to reduce heterogeneity of variance. Some traits were measured on few animals and for these traits a full diallel analysis was not undertaken.

Results

Body weights at 3 and 6 weeks

Numbers of animals recorded and least squares means are given in Table 1. Animals for which records were unavailable at either 3 or 6 weeks were eliminated from the data.

The large-small difference in 6-week weight of 13.3 g or a factor of 1.9 in the purebreds (Table 1) contrasts with a difference of almost 19 g or a factor of 2.3 when selection ceased at generation 23 (Falconer 1973). There were substantial reciprocal cross differences in 3-week and 6-week weight with, for example, progeny of S sire × L dam being heavier than progeny of L sire × S dam, but little reciprocal cross differences in 3–6-week gain.

Values of heterosis, estimated as the mean of reciprocal crosses less the mean of the corresponding purebreds, are shown in Table 2. There was no heterosis for 3-week weight and the heterosis was 0.51 g for 6-week weight and 3–6-week gain. This value is 2.4% of the mean 6-week weight, 3.8% of the large-small difference in 6-week weight, and 4.2% of the 3–6-week gain, so the heterosis was not great. For 6-week weight (and gain) there was more heterosis for crosses involving large (0.71 g) or control (0.71 g) lines, much less for crosses of small lines (0.13 g). The SE of the difference between these heterosis estimates, taken from the within cell variance, is 0.12; but a more formal test using block variation was not undertaken. On untransformed data (arithmetic scale) crosses of animals of the same size, e.g. C × C, generally showed more heterosis than crosses of different sizes, e.g. L × S. This effect was removed by transformation to logarithms, suggesting that the appropriate purebred mean for estimating heterosis in the large × small crosses was the geometric rather than arithmetic mean. Average heterosis estimates for crosses within and between size of line are summarized in Table 3. After log transformation there were no significant differences between these types of cross, even when the SE was estimated from the within cell variance.

Extracts from the analysis of variance tables are shown in Table 4. Although many of the important tests lack power because they were against interactions involving blocks, the heterosis effect, for example, was

Table 1. Body weight at 3 and 6 weeks and 3–6-week gain: numbers of animals and least squares means, averaged over sexes

		No. of animals				
		Crossbred				Purebred
Sire	Dam	L	C	S	Total	
L		748	669	572	1,989	603
C		420	790	315	1,525	716
S		545	651	595	1,791	502
Total		1,713	2,110	1,482	5,305	1,821
		Least squares means				
		Crossbred				Purebred
Sire	Dam	L	C	S	Mean	
		3-week weight (g)				
L		11.14	8.86	8.11	9.37	11.23
C		11.03	8.62	7.60	9.08	8.49
S		9.62	8.20	7.16	8.33	7.07
Mean		10.60	8.56	7.62	8.93	8.93
		6-week weight (g)				
L		29.80	24.16	20.72	24.89	28.37
C		26.77	21.61	17.80	22.06	20.77
S		22.34	18.84	15.26	18.81	15.08
Mean		26.30	21.54	17.93	21.91	21.41
		3–6-week weight gain (g)				
L		18.65	15.30	12.62	15.52	17.14
C		15.74	12.99	10.20	12.98	12.28
S		12.71	10.64	8.09	10.48	8.00
Mean		15.70	12.98	10.30	12.99	12.47

Table 2. Body weight at 3 and 6 weeks and 3–6-week gain: heterosis on arithmetic and on a logarithmic scale averaged over reciprocal crosses. Also heterosis is averaged over the crosses of size of parent and over all crosses (mean)

	Untransformed data				Log transformed data			
	L	C	S	Mean	L	C	S	Mean
				3-week body weight (g)				
L	−0.09	0.09	−0.29	−0.10	−0.003	0.000	−0.007	−0.003
C		0.13	0.12	0.11		0.003	0.007	0.003
S			0.09	−0.03			0.003	0.001
Mean (SE)[a]				0.00 (0.06)				0.000 (0.003)
				6-week body weight (g)				
L	1.43	0.90	−0.19	0.71	0.023	0.021	0.017	0.020
C		0.84	0.40	0.71		0.018	0.013	0.017
S			0.18	0.13			0.003	0.011
Mean (SE)[a]				0.51 (0.09)				0.016 (0.002)
				3–6-week body weight gain (g)				
L	1.51	0.81	0.10	0.81				
C		0.71	0.28	0.60	(Log transformation not used)			
S			0.09	0.16				
Mean (SE)[a]				0.52 (0.07)				

[a] Approximate SE computed from within-cell variance

Table 3. Heterosis estimates averaged according to whether the cross was between or within size of parent class, and mean heterosis

	Type of cross		Mean[a]	(SE)[b]
	Between	Within		
Body weights in main trial (Table 1)				
3-week wt (g)	−0.03	0.04	0.00	(0.06)
6-week wt (g)	0.37	0.82	0.51	(0.09)
3–6-week gain (g)	0.39	0.77	0.52	(0.07)
log 3-week wt	0.000	0.001	0.000	(0.003)
log 6-week wt	0.017	0.015	0.016	(0.002)
Food consumption and body composition trial (Table 7)				
Food cons. 6–7 weeks (g)	−0.26	0.61	0.03	(0.36)
Food cons./body wt	−0.18	−0.026	−0.021	(0.015)
Gonadal fat wt/body wt	0.24	0.89	0.46	(0.26)
Hind quarter wt/body wt	0.0035	0.0015	0.0028	(0.0010)

[a] Note: mean over all crosses, six between and three within
[b] Approximate SE computed from within-cell variance

highly significant for 6-week weight on the logarithmic scale and for 3–6 week gain, but not for 3-week weight. There was also a significant sex × heterosis interaction for 6-week weight and gain, the heterosis being approximately 0.7 g greater in males than in females compared to an average heterosis of a little over 0.5 g (Table 2). This interaction was not removed by the logarithmic transformation.

Body weights at weekly intervals from 3–8 weeks

Results, pooled over crossbreds and purebreds, for those mice weighed weekly are given in Table 5. The numbers of mice (crossbreds plus purebreds) ranged from 1,312 at 3 weeks to 487 at 8 weeks. Means were computed as means of family means, with each type of cross and purebred weighted equally, there being 105

Table 4. Body weight at 3 and 6 weeks and 3–6-week gain: extract from analysis of variance[a]

Source	df	3-week wt	6-week wt	3–6-week gain	log 3-week wt	log 6-week wt	Test vs[c]
Heterosis (Het)	1	9.6	470.5	345.6*	0.0357	0.3195*	Het × Bl
Het × Sex	1	2.3	175.6**	217.73**	0.0110*	0.0381**	Remainder
Het × Block (Bl)	2	26.5	37.4	9.9	0.0316	0.0151	Litters
SS × DS[b]	4	38.3	221.5	93.0	0.638	0.0258	SS × DS × Bl
SS × DS × Bl[b]	8	77.8**	78.5	40.1*	0.1288*	0.0332*	Litters
Litters	800	27.1**	40.7**	20.1**	0.0564**	0.0161**	Remainder
Remainder	6,149	0.761	4.420	3.451	0.00201	0.00193	

[a] Source, df and mean squares not shown for effects of secondary interest (total df = 168)
[b] Analysis of sire size (SS) × dam size (DS) interation from ANOVA of crosses only, not independent of other effects shown
[c] Error line used unless smaller than Remainder (if effect included sex) or Litters (otherwise) when Remainder or Litters, respectively, was used
* $P < 0.05$; ** $P < 0.01$

Table 5. Body weights at weekly intervals from 3 to 8 weeks (data on 105 crossbred families, 37 purebred families)

Age (weeks)	3	4	5	6	7	8
	Body weight (g)					
Crossbred	6.93	12.32	17.56	21.02	20.90	22.01
Purebred	7.05	11.87	16.38	20.38	20.73	21.82
Heterosis (SE)[a]	−0.12 (0.20)	0.45 (0.32)	1.18 (0.32)	0.64 (0.31)	0.17 (0.26)	0.19 (0.30)
Heterosis (%)	−1.7	3.8	7.2	3.1	0.8	0.9

[a] Approximate SE of the heterosis computed from within-cell variance

Table 6. Ages and weights at various developmental events (data on 77 crossbred families, 20 purebred families)

	Mean age (d)			Mean wt (g)		
	Crossbred	Purebred	Heterosis (SE)[a]	Crossbred	Purebred	Heterosis (SE)[a]
External ear eruption	3.51	3.53	−0.02 (0.15)	2.39	2.34	0.05 (0.09)
Lower incisor teeth eruption	10.82	11.04	−0.12 (0.38)	4.87	4.88	−0.01 (0.26)
Cornea visible in both eyes	14.90	15.14	−0.24 (0.23)	5.74	5.88	−0.14 (0.31)
Vaginal opening	33.23	34.00	−0.77 (1.61)	15.40	15.11	0.29 (1.08)

[a] Approximate SE of difference from between family variance

Table 7. Food consumption from 6–7 weeks, gonadal fat pad weights and hind quarter weights at 7 weeks, relative to 7-week body weight: number of animals, least squares means and heterosis estimates[a]

No. of animals

Sire	Dam	Crossbred L	Crossbred C	Crossbred S	Crossbred Total	Purebred
L		68	51	69	188	98
C		26	73	36	135	82
S		36	71	116	223	64
Total		130	195	221	546	244

		Least squares means: Crossbred				Least squares means: Purebred	Heterosis			
Sire	Dam	L	C	S	Mean		L	C	S	Mean
					Food consumption (g)					
L		43.83	36.71	34.06	28.20	42.13	1.70	−0.76	−0.80	0.05
C		39.07	33.99	32.28	35.11	35.17		−1.18	0.78	−0.39
S		33.26	31.25	28.11	30.87	26.80			1.31	0.43
Mean		38.72	33.98	31.48	34.73	34.70			Mean (SE)[b]	0.03 (0.36)
					Food consumption/7 week body wt (g/g)					
L		1.346	1.450	1.523	1.440	1.394	−0.048	−0.010	−0.025	−0.028
C		1.529	1.526	1.610	1.555	1.605		−0.079	−0.020	−0.036
S		1.488	1.623	1.716	1.609	1.668			0.048	0.001
Mean		1.454	1.533	1.616	1.534	1.556			Mean (SE)	−0.021 (0.015)
					Gonadal fat pad wt/body wt (mg/g)					
L		11.53	9.87	7.57	9.66	10.17	1.36	−0.01	0.06	0.47
C		9.09	9.90	8.54	9.18	8.81		1.09	0.67	0.58
S		8.48	7.36	5.97	7.27	5.75			0.22	0.32
Mean		9.70	9.04	7.36	8.70	8.24			Mean (SE)	0.46 (0.26)
					Hindquarter wt/body wt (g/g)					
L		0.1265	0.1265	0.1273	0.1268	0.1249	0.0016	0.0040	0.0046	0.0031
C		0.1304	0.1286	0.1282	0.1291	0.1239		0.0047	0.0019	0.0035
S		0.1324	0.1251	0.1239	0.1271	0.1256			−0.0017	0.0016
Mean		0.1298	0.1267	0.1265	0.1277	0.1248			Mean (SE)	0.0028 (0.0010)

[a] Heterosis averages as in Table 2
[b] Approximate SE from within cell variance

crossbred and 37 purebred full-sib families at each age. Although numbers are small, there is some indication that the heterosis reached a maximum at around 5 weeks of age, and the weekly weight gains showed most heterosis from 3–5 weeks (gains of 10.63 g in crossbreds and 9.33 g in purebreds). To investigate whether this early heterosis in gain was because the crosses showed more rapid development the following trial was undertaken.

Stages of development

The ages and weights at ear and teeth eruption and opening of the eye and vagina, averaged over all crossbreds and purebreds, are shown in Table 6. There is a small, non-significant, but consistent tendency for the events to occur earlier in the crosses, but there is no such consistency in terms of weight, suggesting the events occur at similar weights. Data on individual

Table 8. Food consumption and food conversion efficiency from 3 to 6 weeks of age

	Crossbreds	Purebreds
No. of animals	134	59
Food consumption, 3–6 weeks (g)	92.4	86.8
3-week wt (g)	8.4	8.3
6-week wt (g)	22.0	21.1
3–6-week gain (g)	13.6	12.8
Efficiency (gain/food)	0.147	0.147
Food/mean wt 3–6 weeks[a]	6.00	5.91

[a] Assuming linear gain

purebreds and crosses (not shown) suggest that the developmental events in the large lines of mice occur slightly earlier (except for ear eruption) but at much heavier weights than in the small mice.

Food consumption and body composition

For the main study on 790 mice, with food recorded from 6–7 weeks and animals dissected at 7 weeks of age, results and heterosis estimates are given in Table 7. Results of a smaller study, comprising 193 mice, on food intake from 3–6 weeks of age, are summarized in Table 8.

Between 6 and 7 weeks of age growth rates are small, so presumably most food is used as "maintenance". Over this period there was almost no difference between purebreds and crossbreds in food intake; but, because their body weight was higher, the crosses consumed slightly less per unit body weight and per unit metabolic body weight, $W^{0.75}$, usually proportional to food intake (Kleiber 1947). Between 3 and 6 weeks of age, the crosses consumed more than the purebreds, but gained more and maintained a higher mean weight over the period.

The dissections at 7 weeks showed very little difference among any purebred or crossbred groups in the ratio of hindquarter to total body weight, but with some indication of a higher ratio in the crossbreds. The ratio of gonadal fat pad weight to body weight was rather higher in the crossbreds. These heterosis effects were not significant ($P > 0.05$), however, when tested against the heterosis × block interaction (analysis of variance not shown).

Discussion

Design

The statistical analysis of these data was complicated by what was, in hindsight (and even moderate foresight), a poor experimental design.

In terms of mouse management with a system of continuous mating, it was very convenient to divide up the replicate lines into three non-contemporaneous blocks A and B, C and D, E and F. This meant, however, that each large line, for example, was crossed to only one other large line, and that there was no connection among the blocks. Thus the proper test for heterosis, of the heterosis mean square against that for heterosis × blocks (which is the variation in heterosis between blocks), was conducted with only 2 d.f. in the denominator, and badly lacked power. There are alternative ways in which the data could have been analyzed, for example by estimating variance components for sire and dam lines (Bhuvanakumar 1980) but these did not give orthogonal estimates because of the confounding of sire and dam lines and did not make interpretation any easier. Providing we are not too concerned by statistical significance per se, interpretation of the results is straightforward from the results shown in, for example, Tables 1 and 2. The formal statistical analysis (e.g. Table 4) is more complicated and less enlightening.

The design could have been improved by crossing each line with more than one other line of each size, with an appropriate connected partial diallel design. There would then have been many more samples of crosses and therefore a more powerful test of heterosis.

Heterosis

The crosses showed heterosis for 6-week weight, the age at which the lines had been selected, but not for 3-week weight. This lack of difference at three weeks may have partly been accounted for by maternal limitations for there was a slightly greater litter size among crossbred litters, 4% for numbers born and 8% for numbers weaned (see Bhuvanakumar et al. 1985). The more rapid subsequent growth may then have reflected compensatory growth, and it is notable that there was more heterosis in males than females at 6-weeks.

For 6-week weight the crosses among large and control lines showed more heterosis, on average, than did crosses of small lines (Table 2). On a logarithmic scale there was no difference in the amount of heterosis between crosses of similar sized lines or dissimilar sized lines, and no evidence of other interaction between specific crosses. On an arithmetic scale large × small crosses showed negative heterosis, but that can be explained by assuming multiplicative action of the genes for size.

How can the differential heterosis according to size of line be explained? A completely plausible explanation is hard to find, but presumably the low lines were fixed for the same recessive or partially recessive allele at each locus showing dominance for growth, so there was little or no heterosis among the small lines. At generation 23, when selection ceased, there was considerable variation among the small lines in performance (e.g. Falconer 1973) and this variability must have been due to differences in frequency or fixation of additive genes. Among the high and control lines the frequencies of dominant or partially dominant genes must have differed. At the time selection ceased at generation 23 there was less between-line variability among the large lines than the others, suggesting a limit with fixation of the same genes

(Falconer 1973). The lines did vary subsequently, however, (RL Baker, unpublished; Bhuvanakumar 1980), indicating that, in conjunction with the present results on heterosis, the large lines were not fixed for the same genes. The difficulty with this model of identical fixation among the small but not the large lines is to explain why there is no more heterosis between control × control than between large × large crosses, and no more between large × small than control × control.

The lack of interaction (after the logarithmic scale transformation) among crosses of different size (Table 3) is in itself of some interest. In this experiment, approximately the same level of inbreeding was approached in all lines, both selected and unselected. The results suggest that genetic distance (unrelatedness) is a better indicator of how much heterosis a cross will show than either the selection history or mean performance of the lines. Of course, we cannot say how the crosses would have performed at the time selection ceased. About one-third of the differences in 6-week weight between large and control lines had been lost between generations 23 and 60 and, as will be reported subsequently, some of the poor reproductive performance of the selected lines, particularly the lows, had been recovered (Bhuvanakumar et al. 1985).

The extent of heterosis for all the growth and composition traits examined was rather small, in line with previous experience. Thus for six-week weight, the average heterosis was 0.51 g whereas the large-small purebred difference was 13.3 g. The only indications of larger heterosis were in post-weaning rates of gain, suggesting some earlier development of crosses. In common with some previous studies (e.g. Jamison et al. 1975) more heterosis was observed at intermediate ages (e.g. 6 weeks) than at later ages. These observations on gain could be explained as compensatory growth occurring post-weaning: for example L × S crosses were 1.5 g smaller than S × L crosses at 3 weeks and only 0.1 g smaller at 6 weeks (Table 1).

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