THE EFFECTS OF CONSTANT AND VARYING ENVIRONMENTS ON LITTER SIZE IN CONTROL POPULATIONS OF MICE OF DIFFERENT ORIGINS

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SUMMARY

The mean and variance of first parity litters of 8 control populations of mice of different origins, each maintained in two environments were examined (N=22422). The main populations were maintained with 25 single pair matings for 70 generations in a controlled environment. A replicate was sampled from each population around generation 18 and maintained with 15 single pair matings in an uncontrolled environment. The populations were crosses between two and four inbred lines, non-inbred strains and their crosses. The mean and variance of litter size in the replicates were significantly larger in almost half of the cases than those in the main populations. Despite significant differences in litter size between generations in almost all the populations, the between generations component of variance was much smaller than the within generations component of variance in every case. A fairly good agreement existed between the expected genetic heterogeneity of the populations and their within generation mean-squares.

INTRODUCTION

The effect of varying environment on genetic structure of populations has been an appealing subject to researchers both from theoretical and applied points of view. Positive association between environmental heterogeneity and genetic heterozygosity have been reported by Beardmore and Levine (1963), Gillespie and Langley (1974), Gillespie (1976) and Mackay (1981). It has been suggested (Felsenstein, 1976) that environmental heterogeneity is sufficient to maintain genetic variability. There are evidences which indicate that the positive association between genetic heterogeneity and environmental variation is likely due to the higher fitness of the heterozygote individuals by virtue of their superior biochemical flexibility, which makes them developmentally more stable (Lewontin, 1958; Mackay, 1980). The objective of this study was to assess the long-term performance of control populations of mice with different genetic heterogeneity each maintained in two environments.

MATERIALS AND METHODS

Four inbred lines of mice; A/J, RFM, DBA/1 and C57-BR/cd, which will be referred to as A, R, D, and C respectively, were mated reciprocally and six crossbred groups; RC, RA, DA, DR, AC, and CD were generated, but only AC and CD survived. The progeny of the 2-way crosses were reciprocally crossed to form generation zero of the population IC. Four non-inbred strains of mice; Q, JH, NB and XL were obtained from the Institute of Animal Genetics, Edinburgh, Scotland, and were maintained as

straightbreds. The JH showed some infertility and young mortality, and could not be maintained for more than 3 generations. The XL and Q were called LX and QL respectively. The 4-way crossbred progeny of the non-inbred strains were designated as generation zero of the population OC. Population GL was formed by reciprocal crossing of the OC and IC. The populations were maintained from 1961 to 1979 (67 to 73 generations). The OC and GL were genetically the most heterogeneous of all the populations, and AC and CD had the narrowest genetic background. One replication from each of the 8 main populations was sampled between 1964 and 1966 by taking 15 pairs of mice from each population. The replicate of the NB population originated from a full-sib family, because other families in the sample did not produce any live progeny. The replicates will be designated by adding the letter "R" to the name of the main populations.

The main populations were kept in an environmentally controlled laboratory with 22±1° C temperature and 45±5 % relative humidity. The replicates were maintained in a poorly heated, poorly air conditioned building. Maximum temperature in this building, which fluctuated with outside temperature, was around 30° C, and minimum occasionally reached the freezing point. The mice were fed a pelleted mouse breeder ration *ad libitum* throughout the experiment. Matings were made every 91 days, resulting in four generations per year. The mice were between 8 and 9 weeks of age when bred for the first time. Only the first parity litters were used for breeding in so far as possible. Males and females were together for 17 days after pairing. All the main populations, except the GL, were maintained with 25 single pair mating per generation. The population GL was maintained with a breeding sample of 50 males each mated to 2 females. The replicates were raised with 15 single pair matings per generation. One male and one female were selected from each litter as the parents for the next generation and were used in a cyclical mating system.

Data on 22422 first parity litters were used in this study. Infertile matings were not considered, and litter size was defined as the total number of young born dead and alive in the first litter. Means of litter size of the main populations and their replicates were compared by the two-tailed T-test for samples with unequal numbers and variances. Differences between mean litter size over generations within each population were tested by the one-way analysis of variance, and the between generations component of variance ($\sigma^2 b$) was estimated.

RESULTS AND DISCUSSION

The means of litter size were significantly ($P<.01$) greater in the replicates compared with those in the corresponding main populations in the GL, OC, IC and CD, and were similar in all the other populations except QL which had larger average litter size than in the QL-R ($P<.01$, Table 1). The replicates were maintained under a rather harsh environment with smaller population size

which resulted in faster rate of inbreeding compared with the main populations. Yet these populations somehow managed to keep their average litter size larger or equal to that of the main populations.

The phenotypic variances of litter size were larger in the replicates than those in the corresponding main populations, and the differences were significant in the LX, CD, IC and GL. The only exception was the NB in which the variance of litter size was significantly ($P<.01$) larger than that in the NB-R (Table 1). The ranking order of the main populations with respect to their phenotypic variance were QL> OC=GL=LX=NB> IC=AC=CD, showing a fairly good agreement between the expected genetic heterogeneity and total phenotypic variance in the controlled environment. Except for the NB-R, which had the smallest variance amongst all the populations, the ranking order of the replicates for their expected genetic heterogeneity and variance were the same. The significantly smaller variance of the NB-R than the NB was most likely due to its genetically narrow base, as this population originated from a family of full-sibs.

The between and within generation components of variance (σ^2b and σ^2w respectively) and $100(\sigma^2b/\sigma^2w)$ are presented in Table 2. Significant differences between generations were observed for litter size in all the populations, except for the QL-R. There was no easy to explain relationship between the expected genetic heterogeneity of the populations and their σ^2b, while the main and replicate populations originated from crosses between inbred lines had generally a smaller σ^2w compared with the other populations. Amongst the main populations, σ^2w was minimum in the crosses between inbred lines, intermediate in the LX and NB and maximum in the GL, OC and QL, indicating a fairly good agreement between the genetic heterogeneity and σ^2w of each population. The ranking order for the genetic heterogeneity and σ^2w in the replicates was almost similar to that of the main populations, except for the NB-R which had the smallest σ^2w of all the populations and the IC-R which had larger σ^2w than the LX-R and NB-R. The QL-R was the only population whose within generation mean-squares was larger than its between generation mean-squares, resulting in a negative σ^2b which was considered to be an estimate of zero.

The difference in the environmental conditions under which the main populations and their replicates were raised and the differences in population size did not have a consistent effect on the magnitude of σ^2w. The σ^2b's in the replicates were larger than those in the main populations, except for the QL and CD. Considering that the total phenotypic variance (Table 1) is equal to $\sigma^2b+\sigma^2w$, the results indicated that the larger phenotypic variances of litter size in the replicates compared with that in the main populations was partly due to their larger σ^2b's, and the smaller total phenotypic variances of the crosses between inbred lines compared with those in the non-inbred populations in

Table 1. Number of generations (G), number of litters (L), mean and phenotypic variance (V) of litter size estimated from pooled data in different populations†

Pop.	G	L	Mean	V	Pop.	G	L	Mean	V
QL	72	1649	9.81**	9.46	QL-R	59	809	8.98	10.60
LX	73	1608	9.37	6.68	LX-R	50	580	9.15	7.13
NB	73	1421	8.92	6.35**	NB-R	54	699	8.94	5.02
OC	69	1531	9.60**	7.25	OC-R	59	806	10.28	7.43
AC	69	1471	8.56	5.63	AC-R	51	612	8.63	6.01
CD	69	1477	7.66**	5.12**	CD-R	53	708	8.31	6.22
IC	69	1628	8.30**	5.55**	IC-R	42	539	8.71	7.13
GL	67	6196	10.30**	7.21**	GL-R	50	688	10.69	10.04

†Significant difference between the main populations and their replicates are shown by ** (P<.01) and * (P<.05)

the controlled environment was largely due to their smaller σ^2w's. The estimates of σ^2b, although significant, were a small fraction of σ^2w, ranging from 1.6% in the GL to 8.7% in the CD amongst the main populations, and from zero in the QL-R to 21.2% in the LX-R in the replicates.

The σ^2b was much smaller than the variance of the observed generation means (σ^2m) in all the populations (Table 2). Difference between these two parameters is attributable to the sampling variance (σ^2s), which is expected to be $1/k\sigma^2$w, where k is the harmonic mean of the number of litters per generation (Table 2). The variances of observed generation means were very close to the σ^2b+σ^2s in all the populations, indicating that the variance of observed generation means was fully accounted for by the true between generation variance (σ^2b) and the sampling variance (σ^2s). The σ^2b's were generally smaller than the σ^2s's in the main populations, but the reverse was true in the replicates. These results show that the larger variances of observed generation means in the replicates compared with those in the main populations were not entirely due to their smaller sample sizes.

The components of the total phenotypic variance provided at least a partial explanation for the cause of variation in litter size. The small but significant between generations component of variance in almost all the populations is in agreement with the finding of Falconer (1960) for a control population of mice over 28 generations. The result of the present study showed that the effects of factors which influence litter size in different generations of a population maintained in a constant environment might in fact be relatively small, as σ^2b's of the replicates were larger than those of their corresponding main populations. Furthermore, the contemporaneous individuals within each generation were possibly subjected to much larger environmental

Table 2. Between (σ^2b) and within (σ^2w) generations components of variance, harmonic mean of the number of litters per generation (k), $100\sigma^2b/\sigma^2w$, variance of observed generation means (σ^2m), sampling variance (σ^2s), $\sigma^2b+\sigma^2s$, and $100\sigma^2b/\sigma^2s$

Pop.	σ^2w	k	σ^2b†	$100\sigma^2b/\sigma^2w$	σ^2m	σ^2s	$\sigma^2b+\sigma^2s$	$100\sigma^2b/\sigma^2s$
QL	9.15	22.9	0.323**	3.5	0.724	0.400	0.723	81.0
QL-R	10.70	13.7	-.099	0.0	0.669	0.780	0.780	0.0
LX	6.56	22.0	0.122**	1.8	0.450	0.298	0.420	40.9
LX-R	5.91	11.6	1.250**	21.2	1.740	0.510	1.760	245.1
NB	6.11	19.4	0.246**	4.0	0.607	0.314	0.560	78.3
NB-R	4.32	12.9	0.687**	15.9	1.044	0.334	1.021	205.7
OC	6.99	22.2	0.268**	3.8	0.579	0.315	0.583	85.1
OC-R	6.83	13.7	0.610**	8.9	1.105	0.500	1.110	122.0
AC	5.53	21.3	0.107**	1.9	0.410	0.259	0.366	41.3
AC-R	5.42	12.0	0.610**	11.2	1.057	0.452	1.062	134.9
CD	4.72	21.4	0.409**	8.7	0.684	0.221	0.630	185.1
CD-R	5.84	13.4	0.387**	6.6	0.837	0.437	0.824	88.6
IC	5.43	23.6	0.120**	2.2	0.366	0.230	0.350	52.2
IC-R	6.49	12.8	0.658**	10.1	1.462	0.506	1.164	130.0
GL	7.10	93.9	0.117**	1.6	0.207	0.076	0.193	154.8
GL-R	9.78	13.8	0.272**	2.8	0.966	0.710	0.982	36.3

† ** Differences between generations were significant at $P<0.01$.

variations than expected. The ranges in litter size variability in population- generation subclasses rarely were below 10. This large within generation variability, which seems to be a characteristics of litter size, could have been due to the complex genetic and environmental factors controlling litter size. Death losses at various stages of embryonic development due to many genetic and environmental factors would increase the variance of litter size in each generation. Falconer (1960) reported that approximately 50% of the variability of mean litter size between generations was attributable to sampling and 50% to real difference between generations. These estimates are in the lower boundary of the corresponding estimates for the main populations in the present study.

Inspection of the frequency distributions of litter size pooled over generations reveal that the mode class in the GL-R, OC-R, AC-R and CD-R, and the maximum litter size in the GL-R, OC-R, AC-R and IC-R were larger than those in their corresponding main populations. The limits of fluctuation of mean litter size per generation in the replicates were larger than those in the main populations, and wider ranges of the fluctuations in the former were not only due to the smaller minimum values but also to the larger maximum values of the mean litter size. There was

no general correspondence between the expected genetic heterogeneity of the populations and the differences between the two limits within which the generation means fluctuated.

The higher levels of heterozygosity of the replicates compared with those in the main populations is probably a reasonable explanation for this phenomenon. Based on the evidence provided in the introduction, it may be hypothesized that the amount of heterozygosity in the replicates was higher than that in the main populations. If this hypothesis is true, the larger means of some of the replicates could be attributed to their higher degree of heterozygosity. Automatic selection was avoided insofar as possible by selecting two individuals from each litter. However, since some small size litters contributed only one sex, and occasionally only one individual was born, some selection for large litter size had inevitably taken place. Automatic selection could have been more effective in increasing the litter size in the replicates than in the main populations on the account of their larger variance. It is not, however, clear why the means of litter size in some of the replicates were the same or below that of the main populations, as there was not any association between the differences in the performance of the main and replicate populations in the two environments and their expected genetic heterogeneity.

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