OPEN-FIELD BEHAVIOR IN MICE: SELECTION RESPONSE AND SITUATIONAL GENERALITY[1]

J. C. DeFries, J. R. Wilson & G. E. McClearn

Institute for Behavioral Genetics
University of Colorado, Boulder, Colorado

ABSTRACT—The response to selection for open-field activity in each of six lines of mice (two selected for high activity, two selected for low activity and two controls) is presented. Change in activity as a function of selection during the last five generations was found to be somewhat less than that during the first five generations, although the correlated response in open-field defecation has continued. The realized heritability of open-field activity was estimated to be 0.13 ± .02 and the realized genetic correlation between open-field activity and defecation was — 0.80 ± .13.

During the tenth generation of selection, second litters were obtained so that full-sibs of S_{10} subjects could be tested in an extensive activity battery and thus assessed for the situational generality of the response to selection. In general, selection for open-field activity has produced lines which differ markedly in both activity and defecation in apparatus which have some elements in common with the open field. Apparatus which result in significant differences between the high- and low-active lines are boxlike and illuminated, but do not necessarily possess the "openness' of the open field. However, significant differences were not observed in more confining apparatus nor in exercise wheels.

THE open-field test was devised by Hall (1934) to provide an objective index of emotionality in rodents. The test consists of placing a subject in an enclosure (usually brightly lit) and observing its behavior for several minutes. When confronted with this novel situation, the subject may tend to "freeze," defecate and urinate, or it may explore its environment. Conventionally, animals with relatively low activity and high defecation scores are referred to as "emotional" or "reactive," whereas those with relatively high ambulation and low elimination scores are "non-emotional" or "non-reactive." The evidence for the validity of this measure has been discussed in some detail (Broadhurst 1960, 1969; Eysenck and Broadhurst 1964; Whitney 1970).

Because of the paucity of information concerning the inheritance of behavioral characters and because of the importance of

---

[1]This research was supported in part by Research Grant GM-14547 from the National Institute of General Medical Sciences. We thank E. A. Thomas, T. W. Klein, J. Howard, and Misses Barbara Johnson and Dianne Ross for their assistance.

a character which may be related to emotionality or fearfulness, DeFries initiated an extensive genetic analysis of open-field behavior in mice in 1964 at the University of Illinois. Open-field behavioral data were obtained on individuals from two inbred strains which were known to differ widely in open-field behavior, and from their derived F_1, backcross, F_2 and F_3 generations. In addition, replicated, bi-directional selection for open-field activity was initiated, using members of the F_3 generation as the foundation population for selection. Six closed lines were formed: two were selected for high open-field activity (H_1 and H_2); two were selected for low activity (L_1 and L_2); and two were randomly mated without selection to serve as controls (C_1 and C_2). With replicated selection lines and controls, spurious correlated responses to selection are unlikely. After five generations of selection, the experiment was transferred to the University of Colorado. The results of this genetic analysis, through generation five of selection (S_5), have been presented elsewhere (DeFries and Hegmann 1970). The purpose of the present communication is twofold: (1) to present the direct and correlated response to selection in this experiment through S_{10}, and (2) to assess the situational generality of this response by testing full-sibs of S_{10} subjects in an extensive activity battery (McClearn, *et al.*, 1970).

SELECTION RESPONSE

Method

Subjects. The foundation population for the selection experiment consisted of 40 F_3 litters which were descendants from an original cross of two inbred strains of mice (*BALB/cJ* and *C57BL/6J.)* The most active male and female from each of ten randomly chosen litters were selected and then mated at random at about sixty days of age; their offspring constituted the first selected generation (S_1) of one high-active line (H_1). From these same ten litters, the least active male and female were also selected and mated to produce the first selected generation of one low-active line (L_1). In a similar manner, high-active and low-active males and females from ten other randomly chosen litters were selected and mated to produce offspring constituting generation S_1 of lines H_2 and L_2. From each of ten other litters, one male and one female were chosen at random and then mated at random, resulting in generation one of control line C_1. Control line C_2 was constituted similarly from the remaining ten litters.

In each generation, selection for open-field activity was done on a comparative, within-litter basis. The most active male and female from each litter in lines H_1 and H_2 and the least active male and female from each litter in lines L_1 and L_2 were selected and then mated at random within line; within lines C_1 and C_2, one male and one female were chosen at random from each litter. In order to maintain an effective mating population of ten pairs of parents per line, it was occasionally necessary to select more than one male and one female from each litter. With an effective mating population of ten pairs of parents per line and within-litter selection, the increase in the coefficient of inbreeding should be less than 1.5 percent per generation.

Apparatus. The open field (91.44 x 91.44 x 20.32 cm high) used throughout this experiment is constructed of clear Plexiglas painted white. In order to automate the recording of activity scores, holes (5 mm diameter) were drilled at intervals of 15.24 cm in the walls at a height of 15 mm; two sets of five light sources each were then attached to adjacent sides of the field and beamed through infrared filters and the holes to photo-conductive cells on the opposite side. This grid of light beams effectively divides the floor of the field into 36 15.24 cm squares. Interruption of these beams activates counters which thus record activity scores. Illumination during testing is provided by two 20-watt fluorescent tubes mounted 94 cm above the floor of the field; these yield incident light levels of approximately 48 ftc. in both the center and corners of the field.

Procedure. Beginning at 40 $\pm$ 5 days of age, each mouse is tested for three minutes on each of two successive days. The subject is placed in a clear Plexiglas cylinder in one corner of the field and then released to start the test period. The total number of beams interrupted during the two three-minute tests is each subject's activity score. The total number of fecal boli dropped is the defecation score. Between tests, the floor of the field is rinsed with tap water and dried with a paper towel. In previous reports (see DeFries and Hegmann), activity and defecation scores were routinely subjected to transformations prior to statistical analysis. However, since the untransformed data are more readily interpreted and since the raw and transformed data yield similar results when subjected to various statistical analyses, only untransformed data are presented in this communication.

Results and Discussion

The mean open-field activity scores of the six lines are plotted as a function of generation of selection in Figure 1. The means of the foundation litters (S_0) from which the lines were derived are also presented. Females have somewhat higher activity and lower defecation scores than males (DeFries and Hegmann); thus, mean values were calculated separately for each sex and an unweighted average obtained. The number of mice tested in each line each generation is presented in Table 1. During generations S_0-S_{10}, 4,642 mice have been tested.

Each generation the mean of the mice selected to be parents is compared to the mean of the litters from which they were chosen. The difference between these means is the selection differential and indicates the amount of selection which has been applied. To correct for variable litter size, these selection differentials were weighted according to the number of offspring produced by each mating pair. These weighted selection differentials, summed across generations, resulted in the cumulative selection differential.

As indicated in Figure 1, a response to selection has clearly

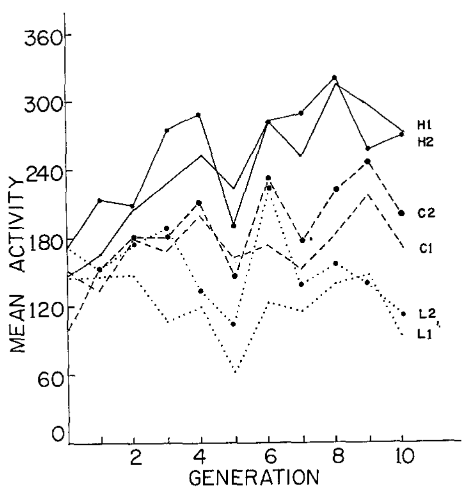

FIGURE 1. Mean open-field activity scores of two lines of mice selected for high open-field activity (H_1 & H_2), two selected for low activity (L_1 & L_2) and two controls (C_1 & C_2).

TABLE I

Number of Mice Tested Each Generation during Selection for Open-Field Activity

Generation	H_1	H_2	C_1	C_2	L_1	L_2
S_0	75	90	93	74	75	90
S_1	74	76	83	62	74	59
S_2	72	69	52	54	63	70
S_3	88	82	88	71	79	82
S_4	71	79	76	72	73	85
S_5	70	74	67	77	66	71
S_6	81	75	71	74	69	73
S_7	73	52	66	69	81	64
S_8	89	79	81	79	64	66
S_9	82	74	66	73	74	62
S_{10}	85	48	61	80	44	76

been realized. After ten generations of selection, subjects in the high-active lines are well over twice as active as those in the low-active lines. The similarity of the replicate means (H_1 vs. H_2; C_1 vs. C_2; and L_1 vs. L_2) after ten generations of selection is particularly striking. In addition, the means of the high-active and low-active lines in S_{10} are still about equally distant from controls, indicating a relatively symmetrical response to selection. However, considerable intergeneration variability in the line means is evident.

In order to express the response to selection independently of intergeneration variability which affects all lines in the same direction, the divergence between the means of the corresponding high and low lines is presented in Figure 2. Differences in diverg-

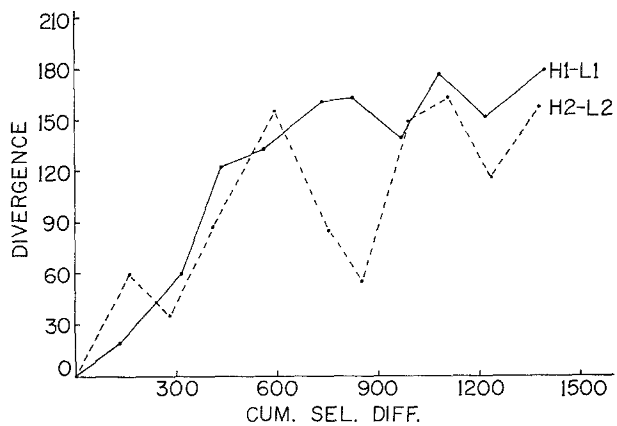

FIGURE 2. Divergence of response to selection for open-field activity between lines H_1 and L_1 and between lines H_2 and L_2, plotted as a function of the cumulative selection differential.

ence between replicates (H_1 - L_1 vs H_2 - L_2) could be due to sampling error or to different selection pressures. To examine the latter possibility, divergence is plotted in Figure 2 as a function of the cumulative selection differential. From the position of the points on the abscissa, however, it may be seen that the amount of selection applied in the two replicates is almost identical. Although the trend in Figure 2 is more systematic than that in Figure 1, some fluctuations are still apparent. However, except for generations S_5 and S_6, the divergence of response in the two replicates is in good agreement. The values plotted in Figure 2 indicate that the rate of response to selection has been somewhat less during generations S_6 through S_{10} than during S_1 through S_5. Although this reduced response in the later generations may be indicative of an approach to a selection plateau, recent data from S_{11} subjects (unpublished) indicate that the response is continuing.

The mean defecation score for each of the six lines in each generation is presented in Figure 3 and a striking correlated response to selection is evident. It is interesting to note that the difference in defecation scores between the high- and low-active lines has continued to increase in S_6 through S_{10}, in spite of the lower rate of response in open-field activity. The agreement between replicates within the high- and low-active groups is again impressive. In contrast, the control lines have fluctuated rather widely. Nevertheless, these results are clearly indicative of a sub-

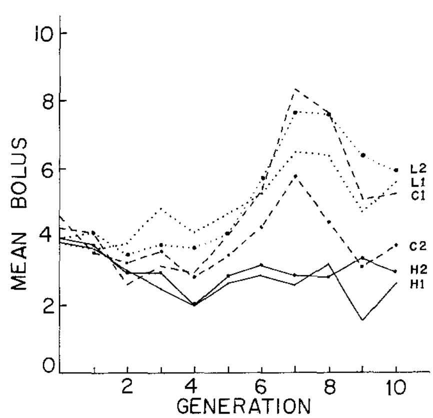

FIGURE 3. Mean open-field defecation scores of two lines of mice selected for high open-field activity (H_1 & H_2), two selected for low activity (L_1 & L_2) and two controls (C_1 & C_2).

stantial negative genetic correlation between open-field activity and defecation.

The realized heritability of open-field activity may be estimated from the regression of the response on the cumulative selection differential, adjusted for within litter selection (see DeFries and Hegmann). Since the response to selection was relatively symmetrical, the divergences of response for H_1—L_1 and H_2—L_2 were each regressed on their cumulative selection differentials and a pooled (from corrected sums of squares and crossproducts) estimate was obtained. Realized heritability estimated in this way is 0.13 ± 0.02. From a comparison of scores of F_3 subjects and their F_2 mid-patental values, DeFries and Hegmann previously obtained an estimate of 0.22 ± 0.09. In addition, from the response to selection through S_5, the realized heritability was found to be 0.26 ± 0.03. Since selection results in changes in gene frequency and thus in changes in genetic variance, one might expect that the realized heritability should be lower than that estimated from the foundation population. However, it has often been observed that estimates of heritability from foundation populations are reasonably robust, at least through several generations of selection. In the present experiment, the realized heritability estimated from the response through S_5 was in excellent agreement with that from the foundation population, both of which were somewhat larger than that estimated from the response through S_{10}. This apparent decline in heritability could be due to an actual decrease in genetic variance as a function of continued selection or it may be transient. In long term selection experiments, temporary selection plateaus followed by bursts of response have frequently been observed (see Mather and Harrison, 1949). Such periodic bursts of renewed response are likely due to the action of selection on genetic variation released through crossing over.

The realized genetic correlation between open-field activity and defecation was estimated from the regression of the correlated response on the direct response, adjusted for differences in heritabilities and standard deviations of the two characters. The pooled estimate of the realized genetic correlation was -0.80 ± 0.13, in close agreement to that of -0.86 ± 0.14 previously reported by DeFries and Hegmann. The agreement between the two estimates again indicates the sustained response in the correlated character throughout the ten generations of selection.

Another response which has continued throughout the ten generations of selection is the change in the frequency of albinism. One of the inbred strains from which the foundation population was derived was albino *(BALB/cJ)*, whereas the other *(C57BL/6J)* was pigmented. Thus, the frequency of this recessive character in the foundation population was approximately 25 percent. As reported previously (DeFries, 1969), the frequency of albinism has increased markedly in the low-active lines and decreased in the high-active lines, supporting the hypothesis of a major gene effect at the *c*-locus on open-field behavior. These observed genotypic frequencies are presented for the first time through S_{10} in Figure 4. As indicated in Figure 4, one low-active line (L_2) reached fixation for albinism in S_8. The frequency of albinism in the other low-active line (L_1) increased sharply during S_9 and S_{10} and thus may also be nearing fixation. The frequency of albinism in the high-active lines decreased steadily until they are now fluctuating near zero. However, neither line has yet reached fixation for the dominant allele since both were segregating for albinism in S_{10}. Since selection is obviously being directed against albinism in the high-active lines (indirectly through the major gene effect on open-field activity) and since the response to selection against rare recessives is notoriously slow, these lines may be expected to continue segregating for albinism for a number of generations. In the control lines, the frequency of albinism has

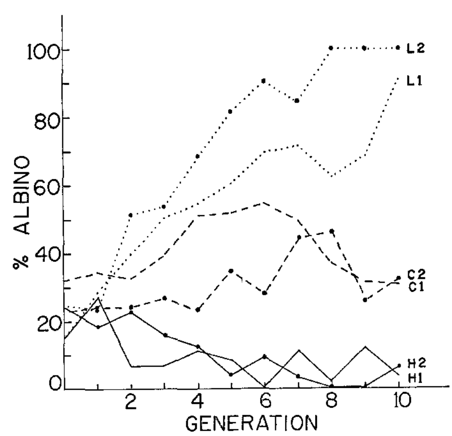

FIGURE 4. Percent albino subjects in two lines of mice selected for high open-field activity (H_1 & H_2), two selected for low activity (L_1 & L_2) and two controls (C_1 & C_2).

fluctuated about somewhat; however, about 30 percent of these animals were albino in S_{10}, indicating relatively little departure from the expected frequency of 25 percent in the absence of selection.

SITUATIONAL GENERALITY

Method

Subjects. After the subjects from the S_{10} generation had been tested, their parents were remated to produce second litters. From each second litter which was produced, one male and one female were chosen at random. These representatives from each of the six lines served as subjects. The numbers tested are shown in Table II.

Apparatus. The test battery consisted of a number of devices for measuring ambulatory activity under different conditions. Unless noted otherwise, apparatus was constructed of red or green opaque Plexiglas, with the matte-finished side next to the subject to eliminate reflections. Responses were observed via an overhead mirror angled toward an observer seated in a chair fitted with clocks, counters, and timers electrically integrated with the test apparatus. The DeFries *open-field* apparatus described above was used as one of the activity testing devices for this experiment. The *arena* apparatus employed is similar to a smaller open-field (50.8 x 50.8 x 14.0 cm high), but the "openness" has been eliminated by affixing six vertical barriers to the floor which is marked off into 16 12.7 cm squares. Two 15-watt fluorescent lamps light the apparatus; one is mounted on each side, and both illuminate the interior through white translucent Plexiglas panels which form the side walls of the apparatus. The top is transparent and hinged at the back for access. A circular opening in a corner of the top permits introduction of a transparent cylinder which serves to restrain the subject until the start of the test period when the cylinder is removed and the opening in the top is capped with a transparent plate. During the three-minute test period, a crossing was scored any time the subject placed any two feet into a different square. Presence or absence of urine, and number of fecal boli dropped were scored in this and the other apparatus described below.

The *Y-maze* consists of three dead-end alleys (5.08 cm wide x 25.40 cm long) interconnected and symetrically arranged in the

TABLE II.

Means and Standard Deviations of Activity Battery Scores Obtained by Subjects from the Tenth Generation of Selection for Open-field Activity.

	H_1		H_2		C_1		C_2		L_1		L_2	
Variable	*Mean*	σ	*Mean*	σ	*Mean*	σ	*Mean*	σ	*Mean*	σ	*Mean*	σ
Open-field:												
Activity	188.9	63.6	162.9	47.8	183.7	37.0	200.1	66.6	99.1	50.0	85.6	55.9
Defecation	.77	1.74	1.73	1.94	2.82	2.11	1.44	1.67	2.56	2.37	2.75	1.51
Arena:												
Activity	106.7	67.4	110.5	34.7	105.6	34.5	105.2	57.0	81.8	45.1	69.8	37.2
Defecation	1.08	1.42	.73	1.14	1.92	1.55	.38	.91	2.25	2.34	1.50	1.78
Urination	.23	.44	.20	.43	.20	.41	.06	.25	.19	.41	.20	.37
Barrier:												
Crossings	8.24	9.28	13.19	9.89	9.71	10.51	11.88	10.05	8.19	12.16	1.35	2.53
Defecation	1.19	1.45	1.34	1.50	2.52	2.59	.69	1.53	1.31	1.36	2.15	1.73
Hole-in-wall	22.77	16.84	28.39	17.12	32.12	15.10	31.38	19.14	15.00	14.54	12.00	14.73
Y-maze:												
Activity	49.24	28.10	59.49	14.52	61.44	20.87	65.75	21.57	43.94	29.16	55.40	24.52
Defecation	2.01	1.67	2.03	1.95	2.78	2.14	1.26	1.62	2.06	2.70	2.20	2.25
Urination	.21	.43	.13	.34	.20	.41	.06	.25	.19	.37	.10	.32
Staircase	39.95	25.36	38.49	23.61	49.89	19.80	67.81	20.13	45.62	25.71	50.45	26.79
Emergence	.056	.228	.206	.421	.056	.252	.125	.354	.062	.250	.100	.298
Reaction-to-												
Handling	9.27	3.95	9.46	3.66	9.29	3.35	8.69	2.64	11.19	3.38	10.65	4.00
Wheel 1	1,896	2,611	4,680	5,470	262	719	4,497	5,686	1,459	2,294	2,468	3,868
Wheel 2	5,809	2,499	10,513	10,864	1,351	3,092	7,377	9,299	3,549	4,004	9,000	9,936
N	19[a]		15		16		16		16		20	

a One Subject not Tested in arena.

form of a *Y* whose arms join at 120° angles. The walls of the alleys are constructed of translucent white Plexiglas; the floor is green opaque and the top is transparent. Lighting is provided through the translucent sides by a 15-watt fluorescent lamp on each side. The subject is introduced at the junction of the Y-maze which is then capped. During each of three subsequent minutes, crossings are scored whenever the mouse crosses a line which is painted on the floor at either end of the alley.

The *barrier* apparatus consists of a box (30.5 x 30.5 x 14.0 cm high) with a barrier inserted in the form of an *X*. The sides and barrier are green opaque Plexiglas and the top is transparent. Illumination is provided through a white translucent floor by a 22-watt Circline fluorescent lamp. The barrier insert reaches to the top of the apparatus in the central position, but is cut down to form a 3.18 cm vertical barrier in the outer portion. The mouse is placed in one compartment and the number of crossings from compartment to compartment during the three-minute test is recorded.

The *hole-in-wall* apparatus has the same overall dimensions as the barrier and is generally similar. However, the *x*-shaped insert reaches from bottom to top and divides the box into four wedge-shaped compartments. Communication among compartments is via holes (3.5 cm) placed 0.6 cm from the floor in the center of each barrier wall. Two opposing compartments are lighted from below through their translucent white floors; the other two compartments are essentially dark. The subject is placed into a lighted compartment and the number of entries into different compartments during the three-minute test is recorded.

The *staircase* apparatus consists of eight wooden stairs (3.8 x 7.6 cm, each) mounted in a wooden frame between a back of painted plywood and a removable transparent front. The subject is placed on the bottom step through a small door on the side of the apparatus and the total number of steps traversed up and down the stairway during the three-minute test is recorded.

For the *emergence* test, the cage of each mouse is placed into a rectangular hole cut into a red opaque platform so that the top edge of the cage is even with the platform surface. The wire mesh top of the cage is removed and the animal is permitted a maximum of five minutes to emerge. A subject is assigned a score of zero or one, depending upon whether it stayed in its cage or climbed onto the platform.

In the *reaction to handling test,* each mouse is subjectively rated on a five-point scale for each of the following: ease of catching, resistance to handling, muscular tension, and response to prodding. In addition, presence or absence of vocalization, defecation and urination are each scored by zero or one. These scores are then summed to give the total rating.

The *activity wheels* consist of a set of fifteen exercise wheels made from 15.24 cm diameter plastic pans. Each pan is connected via a short transparent tube to a regular living cage which has been cut out to accommodate the connecting tube. The subject thus has free access between its home cage and the activity wheel. An eccentric on the shaft of each wheel trips a microswitch on each revolution and a count of wheel revolutions is thus recorded automatically. Mice are assigned randomly to a wheel and left in the apparatus for twenty-two hours on each of two days, resulting in Wheel 1 and Wheel 2 scores.

Procedure. The entire testing procedure for each subject in this activity battery required two weeks plus one day. Since it was not possible to begin more than fifteen subjects on the activity battery during a given week, the 102 subjects included in this study were assigned to groups of twelve or less each. When possible, one male and one female from each of the six lines were included in a group. On Monday of Week 1, each subject in one group (ranging in age from 85 to 95 days) was administered the *reaction to handling* test. Then, between 4:00 and 5:00 PM, subjects were placed in the *activity wheels.* On Tuesday, between 1:00 and 2:00 PM, mice were removed from the wheels, held in the experimenter's hand for thirty seconds, and then placed for familiarization on a floor constructed from plastic for sixty seconds. On Wednesday, between 1:00 and 3:00 PM, the mice were administered the *emergence test.* On Thursday, between 4:00 and 5:00 PM, the mice were again placed randomly into the activity wheels. On Friday, between 1:00 and 2:00 PM, the animals were removed from the wheels and handled for thirty seconds.

During each weekday of Week 2 and Monday of the following week, the subjects were tested on one of the following six apparatus: *open-field, arena, barrier, hole-in-wall, Y-maze* and *staircase*. For the initial group, apparatus were assigned in random order; for subsequent groups, permutations of this order were followed to counterbalance possible order effects.

RESULTS AND DISCUSSION

The mean and standard deviation corresponding to each of sixteen variables measured in the activity battery are presented for each line in Table II. Prior to pooling the data across sex, each variable was subjected to a 6 x 2 (6 strains, 2 sexes) analysis of variance for unequal subclass numbers (Winer, 1962). The main effect due to sex was significant for only one variable (arena urination, $F = 4.42$, $p < .05$, $df = 1/89$) and in no case was there a significant interaction between line and sex. The significance of the main effect due to line differences will be discussed separately for each variable.

The main effect due to differences between lines was significant for both open-field activity and defecation ($F = 13.35$, $p < .005$; $F = 3.24$, $p < .025$, respectively, both with $df = 5/90$). From Table II it may be seen that the mean open-field activity of H_1 and H_2 is about twice that of L_1 and L_2. This relative proportion is in good agreement with that found for S_{10} subjects, although the data are not directly comparable since the scores of subjects in the selection experiment were based upon two-day totals. However, the open-field activity scores of control subjects tested in the battery do not fit the expected pattern. In fact, the mean for C_2 is higher than that of either H_1 or H_2 and the mean for C_1 is higher than that for H_2. This unexpected result could be due to sampling errors since relatively small numbers of subjects were tested in the battery or it could be due to procedural differences. Subjects in the selection experiment are about forty days of age when tested in the open field and are experimentally naive. In contrast, full-sibs of S_{10} subjects were about ninety days of age and, perhaps more importantly, were exposed to at least one week of testing prior to being placed in the open field. Open-field defecation scores, on the other hand, tend to follow the expected pattern, although the C_1 mean does slightly exceed those of L_1 and L_2.

With regard to the variables measured in the arena, only arena defecation was significant ($F = 3.31$, $p < .01$, $df = 5/89$). In general, arena defecation followed the same pattern as open-field defecation. Although non-significant, arena activity also tended to follow the same pattern as open-field activity, that is, means of high and control lines were similar and greater than those of the low lines. Both variables measured in the barrier apparatus were significant (crossings, $F = 3.28$, $p < .01$; defecation, $F = 2.51$, $p < .05$). Again, these variables tended to follow the same pattern across lines as those measured in the open field. This is also true for activity (entries) measured in the hole-in-wall apparatus ($F = 4.37$, $p < .005$, $df = 5/90$).

None of the variables measured in the *Y*-maze yielded a significant line difference. This lack of any consistent pattern is also evident from the means presented in Table II. It is interesting to note that the shape of this apparatus is quite different from the other apparatus considered above, all of which have some common elements. No significant line difference was found for emergence from home cage or for the reaction-to-handling test. However, significant line differences were found for staircase activity and activity in both wheel 1 and 2 ($F = 3.27$, $p < .01$; $F = 3.50$, $p < .01$; $F = 3.05$, $p < .025$, respectively, all with $df = 5/90$). With regard to staircase activity, the two lines with the highest means are C_2 and L_2, whereas those with lowest means are H_1 and H_2. With regard to wheel activity, the high lines are more active on the average than the low lines, although the control lines are least active on the average in Wheel 2. In addition, considerable differences between replicates are evident in wheel activity. In fact, the difference between H_1 and H_2 exceeds the difference between H_1 and L_1 and that between H_2 and L_2 for both Wheels 1 and 2.

Although the analysis of variance described above provides a valid test of line differences, it does not provide a direct test for the presence of genetic correlations between these variables and open-field behavior. For example, random fixation of alleles could give rise to real differences between replicates for characters which are uncorrelated with open-field activity. On the other hand, for characters closely related to open-field activity, the difference between replicates would be expected to be small. This could reduce the power of the test to the extent that real differences between the high and low lines might not be recognized. Thus a more direct test of a correlated response was attempted. Because of the considerable effort required to test each subject in the complete battery, only a relatively small number of subjects was tested in each line. This small sample size undoubtedly accounts for much of the variability between replicates seen in Table II. In order to remove this sampling error to some extent and utilize only one test of significance for each variable (thereby minimizing Type I error), a t-test of the difference between the unweighted mean of H_1 and H_2 and that of L_1 and L_2 was utilized. These means of the high- and low-active lines and the corresponding t-tests are presented for each variable in Table III. It is interesting to compare these results with those of the analysis of variance for line differences discussed above. Of the nine cases in which there were significant line differences, five are also significant when the mean of the high group is compared to that of the low group (open-field activity and defecation, arena defecation, barrier crossings, and a hole-in-wall entries). In the case of arena

TABLE III.

Mean of the High and Low Lines, Pooled Across Replicates.

Variable	High	Low	$t(62)$	$p\leqslant$
Open-field:				
Activity	175.9	92.3	5.95	.001
Defecation	1.25	2.66	2.95	.005
Arena*				
Activity	108.6	75.8	2.62	.02
Defecation	.90	1.88	2.18	.05
Urination	.21	.19	.16	—
Barrier:				
Crossings	10.72	4.77	2.63	.02
Defecation	1.27	1.73	1.19	—
Hole-in-wall	25.58	13.95	2.90	.01
Y-maze:				
Activity	54.37	49.67	.74	—
Defecation	2.02	2.13	.20	—
Urination	.17	.14	.26	—
Staircase	39.22	48.04	1.36	—
Emergence	.131	.081	.65	—
Reaction-to-Handling	9.37	10.92	1.61	—
Wheel 1	3,288	1,963	1.41	—
Wheel 2	8,161	6,274	.97	—

*For arena scores, $df=61$.

activity there was a significant difference between the means of the high and low lines, but no significant line difference in the previous analysis of variance. With regard to barrier defecation, staircase activity and activity in Wheels 1 and 2, the significant differences observed between the line means were apparently not due to a difference between the means of the high and low groups.

In general, the results of this study indicate that differences between lines produced by selective breeding for open-field activity are also present when the lines are tested in other apparatus. Lines selected for high open-field activity have relatively low defecation scores, whereas those selected for low activity have relatively high open-field defecation scores. Differences in these behaviors were also observed when the lines were tested in the arena, barrier and hole-in-wall apparatus, all of which are boxlike, illuminated and thus somewhat resemble the larger open field. However, unlike the open field, these apparatus all have some obstacles inside the enclosure. Thus, it is apparent that the "openness" of the open field is not an essential feature of the apparatus in which the animals were selected. These differences, however, do not generalize to more confining situations like the *Y*-maze or staircase. In addition, no evidence for a difference in "general activity" as traditionally measured by performance in an exercise wheel was found between the high- and low-active lines.

REFERENCES

Broadhurst, P. L. 1960. Experiments in psychogenetics. Applications of biometrical genetics to the inheritance of behaviour. In *Experiments in personality,* Vol. 1, *Psychogenetics and psychopharmacology,* ed. H. J. Eysenck. London: Routledge & Kegan Paul, pp. 1–102.

Broadhurst, P. L. 1969. Psychogenetics of emotionality in the rat. In *Experimental approaches to the study of emotional behavior.* Annals N. Y. Acad. Sci. 159: 806–824.

DeFries, J. C. 1969. Pleiotropic effects of albinism on open-field behaviour in mice. *Nature* 221: 65–6.

DeFries, J. C., & Hegmann, J. P. 1970. Genetic analysis of open-field behavior. In *Contributions to behavior-genetic analysis: The mouse as a prototype,* ed. G. Lindzey, & D . D. Thiessen. New York: Appleton-Century-Crofts, pp. 23–56.

Eysenck, H. J., & Broadhurst, P. L. 1964. Experiments with animals: Introduction. In *Experiments in motivation,* ed. by H. J. Eysenck. New York: The Macmillan Co., pp. 285–91.

Hall, C. S. 1934. Emotional behavior in the rat. I. Defecation and urination as measures of individual differences in emotionality *J. comp. Psychol.* 18: 385–403.

Mather, K., & Harrison, B. J. 1949. The manifold effect of selection. *Heredity* 3:1–52; 131–62.

McClearn, G. E., Wilson, J. R., & Meredith, W. 1970. The use of isogenic and heterogenic mouse stocks in behavioral research. In *Contributions to behavior-genetic analysis: The mouse as a prototype,* ed. G. Lindzey, & D. D. Thiessen. New York: Appleton-Century-Crofts, pp. 3–22.

Whitney, G. D. 1970. Timidity and fearfulness of laboratory mice: An illustration of problems in animal temperament. *Behav. Genet.* 1:77–85.

Winer, B. J. 1962. *Statistical principles in experimental design.* New York: McGraw-Hill.

Manuscript received May 4, 1970

RÉSUMÉ—On présente les résultats d'une sélection pour activité dans un espace ouvert pour chacune des six races de souris (deux races sélectionnées pour leur niveau élevé d'activité, deux pour leur niveau bas d'activité et deux races "controles.")

Pendant les cinq premières générations l'activité changait en fonction de la sélection plus que dans les dernières cinq générations, quoique la défécation en espace ouverte, qui est liée a l'activités continuât d'augmenter.

L' "héritabilité réaliseé" de l'activité en espace ouvert fut estimeé à $0.13 \pm .02$ et la corrélation génétique réaliseé entre l'activité en espace ouvert et la défécation était—$0.80 \pm .13$.

A la dixième génération de séléction on a obténu des littlères secondes de sorte que des "full sibs" des souris S_{10} peuvaient être examinés avec une batterie extensive de mesures d'activité pour voir la généralité de sélection dans toutes les situations.

Généralement la sélection pour activité en espace ouvert a produit des races qui différent beaucoup quant à leur activité et leur défécation quand ils sont dans des appareils qui ont des éléments semblables à l'appareil "espace ouvert".

Des appareils qui mènent à certaines différences significatives entre les races d'activité élevée et basse sont semblables à une boite et sont illuminés mais ne possèdent pas la qualité d' "ouverture" de l'appareil "espace ouvert". Cependant aucune différence significative ne fut observée dans des appareils plus confinants ou dans des roues d'exercise.

ZUSAMMENFASSUNG—Resultate der Selektion für Aktivität im offenen Raumet werden dargestellt von Maüsen in jedem von sechs Stämmen (zwei selektiert für hohe und zwei für niedrige Aktivitätsniveauen, und zwei Kontrollinien) Die Änderung der Aktivität als Funktion der Selektion in den letzten fünf Generationen war kleiner als die der ersten fünf Generationen, obgleich die korrelierte Response der Defekation im offenen Raum anhielt. Die realisierte Heritabilität von Aktivität im offenem Raum wurde auf $0.13 \pm .02$ geschätzt und die realisierte genetische Korrelation zwischen Aktivität im offenen Raum und Defekation war $-0.80 \pm .13$.

Während der zehnten Generation der Selektion wurden zweite Würfe gewonnen damit Vollgeschwister der S_{10} Mäusen mit einer grossen Batterie von Aktivitätmäszen undersucht und so die Allgemeinheit des Selektion responses in verschiedene Situationen geschätzt werden konnte.

Im Allgemeinen hat die Selektion für Aktivität im offenen Raume Linien produziert die für Aktivität sowie für Defekation in Apparaten die einige Elemente mit dem offenen Raum Apparat gemeinsam haben, ziemlich verschieden waren. Aparate die signifikante Unterschiede zwischen den Mäusen mit viel und wenig Aktivität produzierten waren schachtelartig und beleuchtet, aber hatten nicht den "offenen" Charakter des offenen Raum Apparates.

Signifikante Unterschiede wurden weder in Apparaten die mehr begrenzt waren weder im Übungsrad beobachtet.