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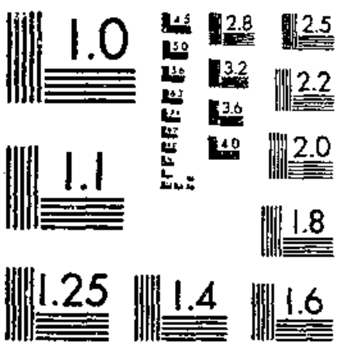

MICROCOPY RESOLUTION TEST CHART
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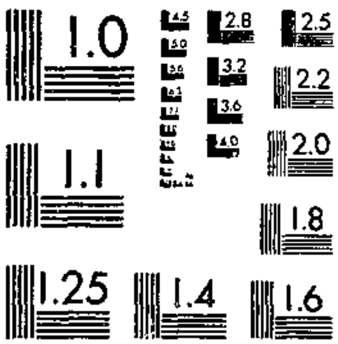

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Technical Bulletin No. 765 • *March 1941*

UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

Effect of Crossing Inbred Lines of Guinea Pigs [1]

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CONTENTS

INTRODUCTION

Much has been written concerning cross-breeding in plants and animals. Some cases have been reported in which the gene combinations of the strains crossed are apparently unfavorable, and poor results follow. This finding is most marked in crosses of different species, in which sterility frequently results in the F_1 offspring. In most instances, however, cross-breeding increases the fertility, growth rates, and resistance to disease and to adverse environmental conditions.

Little work has been done in crossing inbred strains of livestock or of laboratory animals, mainly for the reason that few such strains exist. With plants, however, outstanding work has been done with corn and wheat. According to Wallace (7),[2] private breeders and workers at the various State experiment stations and at the United States Department of Agriculture have developed thousands of inbred strains of corn and have made hundreds of thousands of crosses. Of the thousands of inbred strains produced, only 40 to 50 are outstanding. Jenkins (5) summarizes corn-improvement work by hy-

[1] Received for publication August 10, 1940.
[2] Numbers in parentheses refer to Literature Cited, p. 18.

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bridizing as follows: Crosses between promising inbred strains have given marked increases in yield varying from 10 to 30 percent above the parent varieties. Inbred strains have been developed which differ in resistance to disease, insect injury, cold, drought, composition of the plant and grain, and productivity, but practically nothing has been accomplished in transferring these desirable qualities from one line to another. The high increase in yield holds only for the first hybrid generation. The best results have been obtained through two-way crosses, i. e., four inbred strains have been combined by crossing F_1 hybrids, each resulting from the crosses of two distinct inbred lines. At present (1936) 44 different hybrids have been released for commercial production.

In experiments carried on with guinea pigs, the United States Department of Agriculture has shown that inbred strains vary considerably in such characters as fertility, growth rate, and mortality percentages, as reported by Wright (*8, 9*), McPhee and Eaton (*6*), and Eaton (*3*). The strain that ranks highest in one of these respects does not necessarily rank high in others. Comparisons of the inbred strains with a noninbred control stock have shown the inbreds to be inferior to the control stock in most of the factors considered. As measured by these factors, there has been a gradual decline in the inbred stocks over a period of years, but this fact cannot be attributed solely to inbreeding since the control stock has shown a similar decline, although it has consistently maintained a higher level than have the inbreds.

Crosses between the various inbred strains have shown that much of the vigor lost by inbreeding can be recovered in the hybrids, according to Wright (*9*). Since his paper was published additional data have been obtained. The present bulletin gives a more complete analysis of the crossbreeding experiment, particularly with respect to the hybrids.

MATERIAL AND METHODS

The guinea pigs used in this study consisted of five inbred strains—families 2, 13, 32, 35, and 39—and a noninbred, control-strain B. Families 2 and 13 and control-strain B were derived from guinea pigs that had been bred within the Bureau of Animal Industry for a long period of time previous to the beginning of the inbreeding experiment. Families 32, 35, and 39 were descended from crosses of the original Bureau stock and animals purchased from a dealer. The inbred strains had been maintained wholly by brother-sister matings from the beginning of the experiment in 1906. The control stock was begun in 1911 and contained no matings more closely related than third cousins. Crosses between the different families were not made until 1916. The data presented in this bulletin cover the period from January 1, 1916, through December 31, 1937. Crosses between all the lines were not made throughout this entire period but were scattered over various years, with the result that the various crosses overlap in period of time. This fact tends to eliminate somewhat influences that good or poor seasons may have had on the growth and mortality of the animals. Otherwise, the crossbred animals were subjected to the same environment as the inbred and control strains. Data were obtained on F_1 and F_2 hybrids from various 2-way crosses as well as on hybrids of three 3-way crosses.

The criteria used for evaluating heterosis include various measures of fertility, growth, and mortality. Under fertility are included number of young per litter, age of dam at birth of first litter, and intervals between litters. Growth data include birth weight of young raised to weaning, weaning weight at 33 days, and weight every 30 days (beginning with the 53-day weight) of those animals that were mated and raised to maturity. The criteria of mortality were the percentages of young born alive and the percentages raised to weaning of those born alive. These two factors therefore measure prenatal mortality and mortality between birth and weaning. Data are also presented which show the longevity of the hybrid adult animals in comparison with that of their parent strains.

Sufficient numbers of young for satisfactory analysis of data were not obtained from all the crosses. Only those crosses producing 100 or more young were included in the results reported in this bulletin. In order to obtain numbers large enough for an analysis of the 3-way crosses, the data presented include litters from inbred and crossbred dams. This procedure undoubtedly affects the results somewhat, since Wright (*9*) has shown that hybrid dams produced more young per litter, the weights of their young at birth and at weaning were greater, and the percentage of their young born alive was greater than in litters from inbred dams. In the crosses of families 2×13×35, 8 of the 14 dams were crossbred, and in the crosses of families 2×13×39 and families 2×32×35, 8 of 22 dams were crossbred. However, in view of the similarity of the results, as reported later, it was considered valid to present the results of the 3-way crosses in comparison with the other data. Weights at birth and at weaning were corrected to a standard litter size of 2.5, thus eliminating differences due to number of young per litter.

RESULTS

Litter Size, and Growth and Viability to Weaning Age

Table 1 shows litter size and growth and viability to weaning age of the various crosses indicated, together with comparisons with the inbred parent strains and with the noninbred control stock in the various characters studied. Table 2 shows the ratings, for the various characters, of the inbred families and their hybrids, on the basis of 100 for the control-stock B.

Litter size (table 1) differed significantly in the inbred strains except between families 2 and 35 and between families 35 and 39, and all differed significantly from strain B. Since the dams of the F_1 animals were inbred, such a character as litter size, which is largely dependent on the dam, would not be expected to show the effect of crossing until the F_2 litters. However, about half of the

F_1 and F_2 hybrids differed significantly in litter size from one or the other of the parent strains. The size of the F_2 litters was about 6 percent greater than that of the F_1 litters and in two cases, family 35 × family 13 and family 39 × family 2, the F_2 litters were larger than those of either inbred parent family. The greatest increase in fertility (32×13) resulted from crossing two strains, one high, the other low, for this character. In all three of the three-way crosses, litter size exceeded that of the parent strains and also that of the F_1 hybrids from any two of these strains. Differences were not significant in all cases, however. The control-stock B exceeded most of the F_1 and F_2 hybrids in litter size. Litter sizes in F_1 of family 32 × family 13 and in the three-way cross of families 2×13×35 exceeded that of control-stock B by 11.5 percent, and litter sizes in F_2 of families 35×13 and in the three-way cross of families 2×32×35 excelled that of control-stock B by about 9 percent (table 2).

TABLE 1.—*Comparison of inbred and hybrid strains of guinea pigs in various measures of vigor* [1]

Strain or cross	Litters	Animals	Average litter size	Average birth weight	Average weaning weight	Young born alive	Young raised to weaning of those born alive
	Number	*Number*	*Number*	*Grams*	*Grams*	*Percent*	*Percent*
B stock (control)	2,241	6,023	2.69±1.16	93.4±21.4	260.1±68.9	83.0± .48	81.2±0.55
Inbred family:							
2	2,340	5,683	2.43± .93	72.0±13.9	175.4±43.0	77.7± .55	70.2± .61
13	2,293	5,979	2.61±1.11	87.3±18.2	243.8±61.7	74.8± .56	72.0± .67
32	1,091	2,288	2.10± .89	70.6±12.8	150.7±37.8	82.1± .80	71.0±1.05
35	1,657	4,115	2.48±1.04	83.4±16.7	230.6±50.8	73.0± .69	76.3± .78
39	462	1,177	2.54±1.05	75.6±13.2	198.3±47.8	74.2±1.27	63.5±1.63
F_1 hybrids from families: [2]							
2×13	186	451	[3] 2.44±1.07	[3,5] 79.6±17.0	[3,4,5] 215.5±50.0	[3,4] 85.7±1.64	[3] 81.8±1.06
13×2	236	549	[4] 2.33± .85	[4,5] 70.9±15.1	[3,4,5] 181.8±48.1	79.6±1.72	[5] 80.3±1.90
2×32	69	168	[3] 2.43± .97	[3,4] 83.7±16.2	[3,4] 216.8±49.7	[4] 96.3±2.65	[5] 75.2±3.59
32×2	76	201	[4] 2.64± .99	[3,4] 80.6±15.6	[3,4] 226.0±48.2	[3] 88.6±2.24	[3,4,5] 92.1±2.02
2×35	86	233	[4,5] 2.71±1.16	[3,4,5] 89.0±19.1	[3,4,5] 250.5±61.1	[3] 84.1±2.39	[3,4,5] 93.4±1.77
35×2	83	197	[5] 2.37± .87	[3,4,5] 74.9±13.5	[3,4,5] 203.7±44.7	78.7±2.92	[5] 81.3±3.13
13×35	123	310	2.52± .96	[3] 87.6±21.1	[3,4] 255.1±58.7	[5] 72.6±2.53	[3,4] 90.2±1.98
35×13	201	505	2.51±1.15	[4] 87.6±21.5	[3,4] 252.1±59.8	[3,4,5] 83.6±1.65	[3,4] 87.0±1.64
32×13	37	111	[3,4] 3.00±1.04	[3,4] 98.0±19.7	[3,4] 287.2±59.5	[3] 89.2±2.95	[3,4] 95.0±2.19
39×2	75	195	2.60± .98	[3] 76.0±13.1	[3,4] 215.1±54.3	[4] 84.6±2.58	[4] 86.1±2.69
39×13	84	216	2.57±1.01	[3,4] 83.2±16.1	[4] 245.7±58.6	74.1±2.98	[3,4] 85.6±2.77
39×32	56	137	[3] 2.45±1.07	[3,4] 79.3±15.8	[3,4] 216.6±56.6	[4] 85.4±3.02	[4] 82.0±3.55
F_2 hybrids from families: [2]							
2×13	214	550	[4] 2.57± .95	[3,4] 79.8±15.5	[3,4,6] 194.6±49.5	[3,4] 84.0±1.56	76.6±1.97
13×2	220	559	[6] 2.54±1.05	[3,4,6] 78.8±16.0	[3,4,6] 192.3±50.6	[3,4,6] 89.3±1.31	77.0±1.58
13×35	47	118	2.51± .92	[4,6] 79.8±15.6	[3,4,6] 211.6±60.2	78.8±3.76	[6] 66.7±4.89
35×13	44	129	[4,6] 2.93±1.22	[3,4,6] 93.8±21.6	[4] 253.5±75.9	[4] 83.7±3.25	[6] 73.2±4.26
39×2	39	101	2.67±1.05	[3,4,6] 81.1±17.2	[3] 210.6±61.1	84.6±3.54	[4] 83.0±4.00
3-way crosses of families:							
2×13×35	45	135	[7,8] 3.00± .97	[7] 91.9±18.7	247.9±60.5	[7,8] 87.4±2.85	[7,8] 91.0±2.02
2×13×39	51	135	2.65±1.23	81.4±18.2	223.3±57.0	[7,8] 91.8±2.36	[7,8] 91.9±2.45
2×32×35	34	100	[7,8] 2.94±1.00	[7] 90.3±18.6	240.8±52.5	[8] 88.0±3.24	[7,8] 92.0±2.89

[1] Standard errors, and not probable errors, are shown after the ± sign.
[2] Throughout the text and tables, the family first named is the male.
[3] Differs significantly from female-parent line.
[4] Differs significantly from male-parent line.
[5] Differs significantly from its reciprocal cross.
[6] Differs significantly from hybrids from same parent strains.
[7] Significantly higher than best parent strain in a 3-way cross.
[8] Significantly higher than control-stock B.

TABLE 2.—*Rating of the inbred and hybrid strains of guinea pigs, on the basis of 100 for the control-stock B, for the various measures of vigor*

Strain or cross	Litter size	Birth weight of young raised to weaning	Weaning weight	Percentage of young born alive	Percentage of young raised to weaning of those born alive	Average for all characters measured
Inbred family:						
2	90.3	77.1	67.4	93.6	97.5	85.2
13	97.0	93.5	93.7	90.1	88.7	92.6
32	78.1	75.0	69.5	98.9	87.4	81.9
35	92.2	89.3	88.6	87.9	94.0	90.4
39	94.4	80.0	76.2	89.4	78.2	83.8
F_1 hybrids from families:						
2×13	90.7	[1] 85.2	[1] 82.8	[1,2] 103.2	[1,2] 100.7	92.5
13×2	86.6	75.9	[2] 71.0	95.9	[1] 98.9	85.7
2×32	[2] 90.3	[1,2] 89.6	[1,2] 83.4	[1] 104.0	92.6	92.0
32×2	[1] 98.1	[1,2] 86.3	[1,2] 86.9	[2] 106.7	[1,2,3] 113.4	98.3
2×35	[1] 100.7	[1,2] 95.3	[1,2] 96.3	[2] 101.3	[1,2,3] 115.0	101.7
35×2	88.1	[2] 80.2	[2] 78.3	94.6	100.1	88.3
13×35	93.7	[2] 93.8	[1,2] 98.1	87.5	[1,2,3] 111.1	96.8
35×13	93.3	[1] 93.8	[1,2] 96.9	[1,2] 100.7	[1,2,3] 107.1	98.4
32×13	[1,2] 111.5	[1,2,3] 104.9	[1,2,3] 110.4	[2] 107.5	[1,2,3] 117.0	110.3
39×2	90.6	[2] 81.4	[1,2] 82.7	[1] 101.9	[1] 106.0	93.7
39×13	95.5	[1] 89.1	[1] 94.5	89.3	[1,2] 105.4	94.8
39×32	[2] 91.1	[1,2] 84.9	[1,2] 83.3	[1] 102.9	[1] 101.0	92.6
F_2 hybrids from families:						
2×13	96.5	85.4	74.8	101.2	94.3	90.2
13×2	94.4	84.4	73.9	[3] 107.6	94.8	91.0
13×35	93.3	85.4	81.4	94.9	82.1	87.4
35×13	108.9	100.4	97.4	100.8	99.1	99.5
39×2	99.2	86.8	81.0	101.9	102.2	94.2
3-way crosses of families:						
2×13×35	[3,4] 111.5	[4] 98.4	95.3	[3,4] 105.3	[3,4] 116.9	105.5
2×13×39	98.5	87.2	85.8	[3,4] 110.6	[3,4] 113.2	99.1
2×32×35	[3,4] 100.3	[4] 96.7	92.6	[3] 106.0	[3,4] 113.3	103.6

[1] Significantly higher than male-parent strain.
[2] Significantly higher than female-parent strain.
[3] Significantly higher than control-strain B.
[4] Significantly higher than best parent strain in a 3-way cross.

Weights at birth and at weaning (table 1) differed significantly in the inbred strains and between each of these and control-strain B. Characters such as growth and mortality, which are less dependent on the dam than fertility, should show heterosis in the F_1 animals. This result was manifested in the present crosses, especially when two families low in weight, such as families 2, 32, and 39, were crossed. Under such conditions, average gains of 8 percent in birth weight and of 13 percent in weaning weight resulted (table 2). When heavy families, such as 13 and 35, were crossed with the lightweight families, the weights of the hybrids were in general greater than those of the lighter parents, the average gains being 11 percent for birth weight and 20 percent for weight at weaning. Except for two F_1 crosses (32×13 and 2×35) such hybrids weighed less at birth than the heavier parents, the average difference being about 10 percent for birth weight and 14 percent for weaning weight. A third exception (39×13) exists for weaning weight. In the hybrids from family 32 × family 13 and family 2 × family 35, weights of young at birth and at weaning averaged greater than those of either parent family. A consistent difference in growth was observed in the F_1 reciprocal crosses. The weights of the young at birth and at weaning tended to follow the average of the dam's family for these characters. Average birth and weaning weights of F_1 young from family 32 × family 13 were significantly greater than those of the B stock. The three-way crosses of families 2×13×35 and families 2×32×35 exceeded their parent families in weights at birth and at weaning, and practically equaled or were slightly better than the F_1 hybrids of the parent families for these characters. Families 13 and 35 ranked highest among the inbreds in growth characteristics, and hybrids of these two families also maintained a high rank for this character.

Differences in the inbred strains and between each of these and strain B were significant for percentage of young born alive, except between families 13 and 39 and between family 32 and strain B. For percentage raised to weaning of young born alive, differences were significant except between families 13 and 32 and between family 2 and strain B. In nearly all crosses the viability of the F_1 hybrids increased approximately 8 percent for young born alive and 17 percent for young raised to weaning of those born alive. The percentage born alive was about the same in F_1 and F_2 litters except for 13×2 cross, but percentage raised to weaning was greater in the F_1 litters. The greater number of the hybrids exceeded the B stock in percentage of young born alive, the average gain being about 3.5 percent. Nearly all the F_1 hybrids excelled the B stock in percentage of young that were raised to weaning, the exceptions being hybrids of families 13×2 and families 2×32. The average increase of the F_1 hybrids over the B stock in percentage raised to weaning was about 6 percent. Percentages of young born alive and raised to weaning were higher in the 3-way crosses than in the parent strains and in most cases than in the hybrids from 2-way crosses. The percentage of young born alive averaged about 7 percent higher in the three-way crosses than in control-stock B, and the percentage of young raised averaged about 14 percent higher. In the hybrids the only factors which consistently showed improvement over the parent lines were percentages born alive and raised to weaning.

In table 2, the average rank of the five characters considered as a whole, in which each character was given equal weight, shows that the F_1 hybrids from families 32×13 ranked highest, two three-way hybrids second and third, and the F_1 hybrids from families 2×35 fourth. These excelled strain B from 1 to 10 percent in the characters measured. The remaining crosses were approximately 1 to 14 percent lower than the control strain.

Growth After Weaning

Weights of the animals that were saved for mating were taken at 53 days of age and every 30 days thereafter. Males only were used in this study, since weights of females are highly variable on account of recurring pregnancies. Comparison was made with the growth curves for males of the parent families as given by McPhee and Eaton (*6*). Growth of the hybrids and their parent families is shown in figures 1 to 5, inclusive.

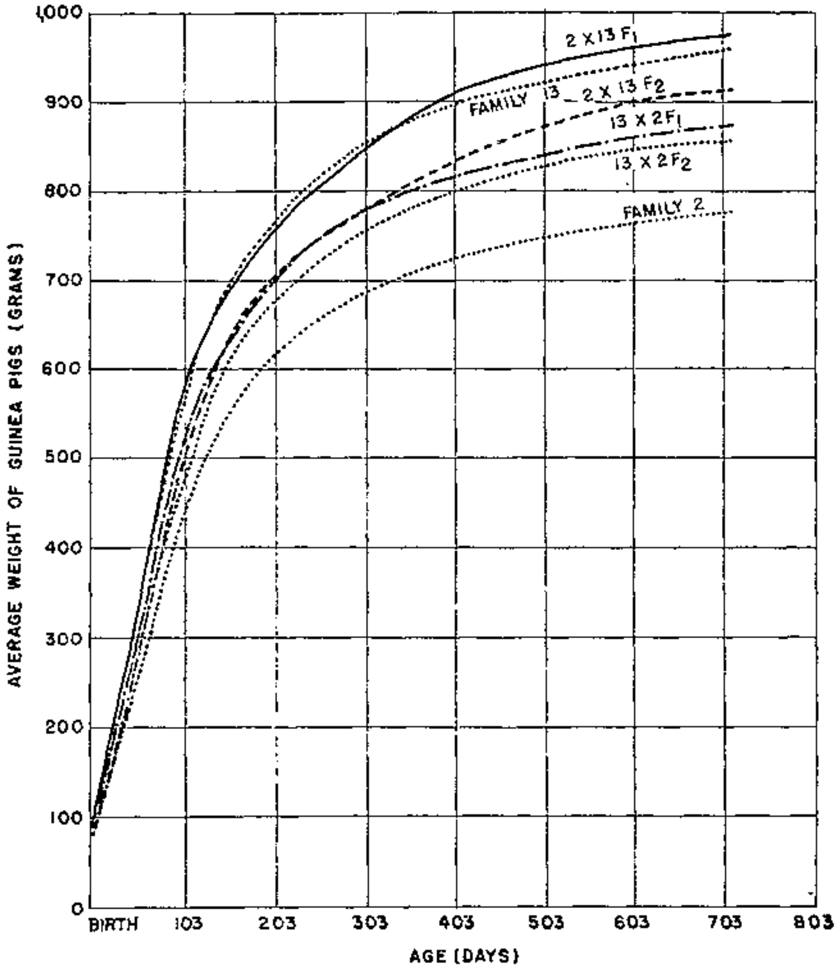

FIGURE 1.—Growth of inbred families 2 and 13 and their F_1 and F_2 reciprocal hybrids.

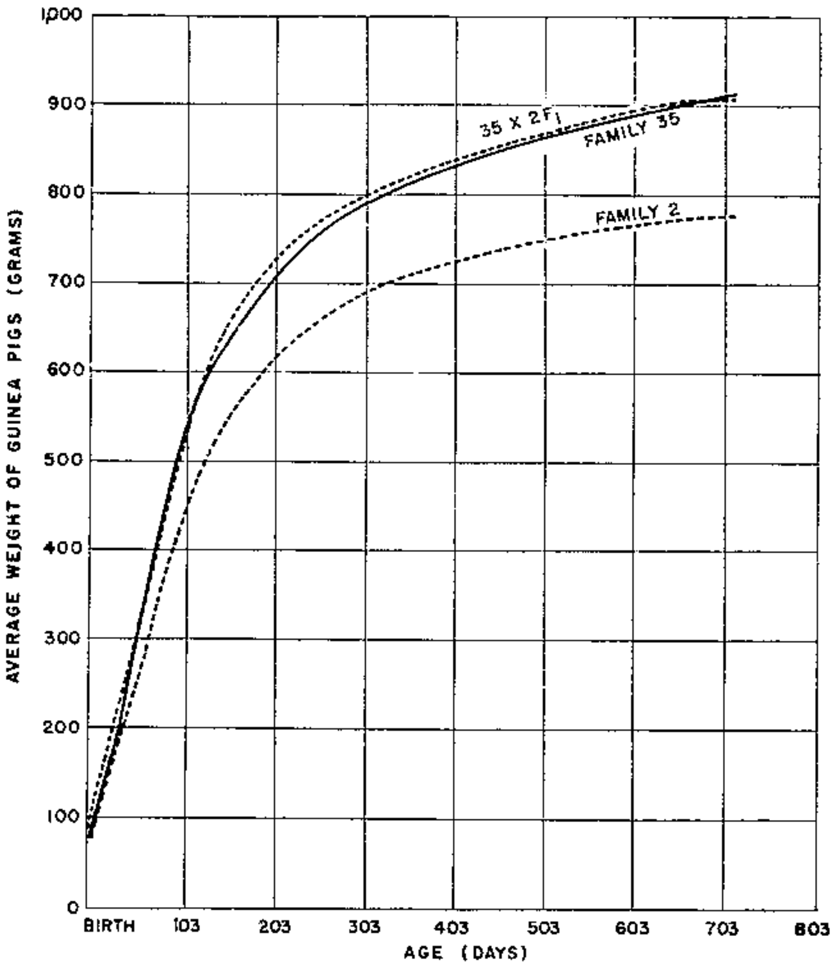

FIGURE 2.—Growth of inbred families 2 and 35 and the F_1 hybrids of family 35 × family 2.

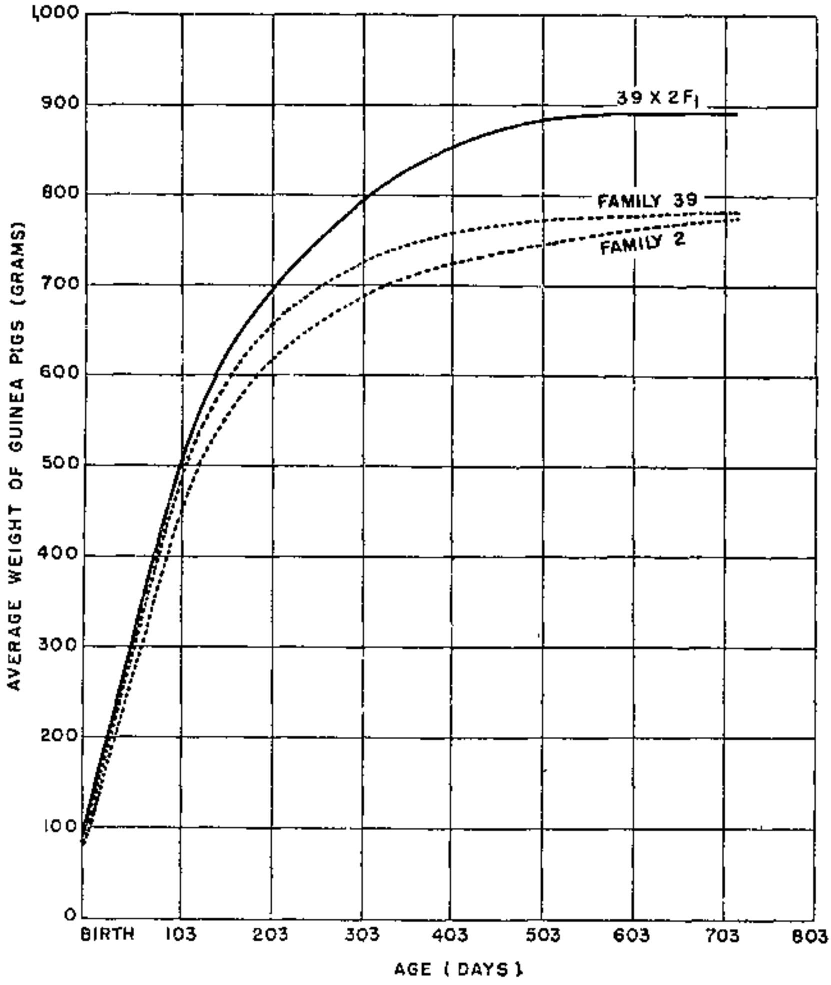

FIGURE 3.—Growth of inbred families 2 and 39 and the F_1 hybrids of family 39 × family 2.

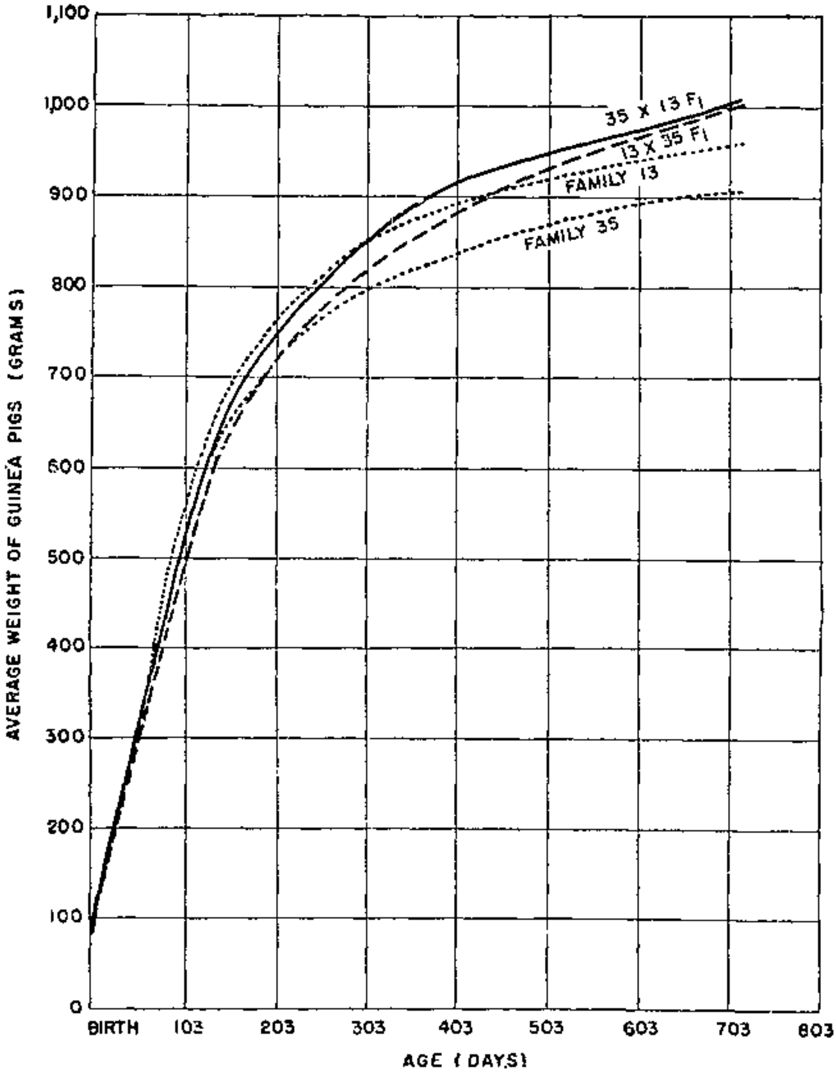

FIGURE 4.—Growth of inbred families 13 and 35 and their reciprocal F_1 hybrids.

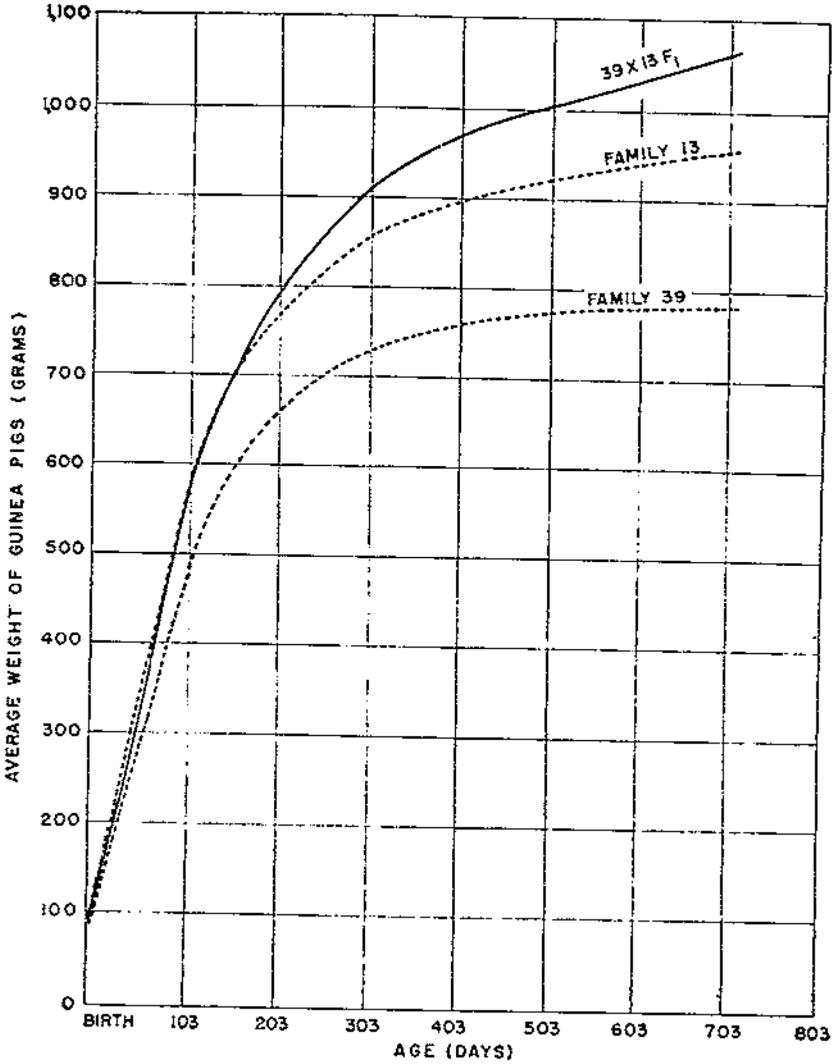

FIGURE 5.—Growth of inbred families 13 and 39 and the F_1 hybrids of family 39 × family 13.

The growth of the hybrids from weaning (33 days of age) to about 2 years of age illustrates strikingly the phenomenon of heterosis as exhibited by growth. In all the crosses studied, the growth of the hybrid was significantly higher than that of the smaller parent and in two crosses exceeded significantly that of the heavier parent. In most cases the weight of the hybrid followed closely that of the heavier parent strain. Although small numbers of animals were used in deriving the upper ends of the curves, only a small amount of smoothing out was required for the last 200-day period, indicating that the growth curves as presented represent those of the entire group of animals studied. Growth of the animals after weaning is not necessarily determined by growth prior to weaning, since some of the hybrid young were lower in weight previous to weaning than either parent family, but equaled or exceeded their parents in final weight. In the case of a cross between two families low in weight at all ages—for instance, families 2 and 39—there must have been a combination of growth genes which gave practically the same result as that obtained by combining a family low in body weight with one already possessing genes for heavy body weight. The progeny resulting from family 39 × family 13 were the only ones that reached the weight of the control-stock B at about 2 years of age.

The fact that the full effect of heterosis was not manifested at the younger age would tend to decrease the benefit from cross-breeding of inbred strains in livestock production if the same relations were to hold for the larger animals. Most cattle are marketed at about 60 percent of their mature weight and most hogs at about 40 percent. In guinea pigs these percentages correspond to weights at about 120 and 60 days, respectively, before the effect of heterosis as regards growth has become manifested significantly.

Age of Dam at Birth of First Litter, Length of Gestation, and Regularity of Breeding

The female guinea pig is considered to be sexually mature at about 30 days of age, the male about 1 month later. The normal gestation period averages 69 days. Therefore, the dam should be approximately 130 days of age at the birth of her first litter if the male and female are placed in the breeding cage at weaning time. As a matter of fact, Wright (*8*) has shown that the dam is actually about 1½ months older than this at the birth of her first litter.

Comparison of the hybrids as to age of dam when first litters are born was made with Wright's (*9*) data for the inbred strains. He used age of males at birth of first litter, but since males and females are usually placed in the breeding cage when they are weaned at 33 days of age, the age of dam at birth of first litter would be equal to that of the male in most cases. The greatest departure from this would be in control-stock B, in which there may be a few days of variation between age of males and females at time of placing the young animals in the breeding cages.

In the present comparison only hybrid matings in which the animals were 45 days of age or less when put in the breeding cages were considered. The data are given in table 3. Among the inbreds, families 35 and 39 probably differ significantly from the others in age at which first litters were produced, and all probably differ significantly from the B stock. Significance of differences between the inbreds and their hybrids cannot be determined definitely since only means were given for Wright's data. Reciprocal crosses between families 2 and 13 differ significantly in age of dam at birth of first litter, and the cross of family 2×family 13 probably differs significantly from both parent strains in this respect. Reciprocal crosses of families 2 and 35 and of 13 and 35 show similar differences in age of dam at first litter. In these three cases the younger age at which the first litters were produced occurred when the dams were from one of the heavy strains (13 and 35). This fact seems to indicate that sexual maturity of the female is related to general body size. The great variability in age at which first litters were born among the hybrids and the small numbers of first litters in many instances make the results of little significance.

Table 3.—*Comparison of inbred and hybrid strains of guinea pigs in age of dam at birth of first litter, length of gestation, and measures of regularity of breeding following first litters*[1]

Strain or cross	First litters	Average age of dam at birth of first litter[2]	Average length of gestation[2]	Total litters	Premature litters	Conceptions first estrus after parturition	Conceptions after skipping 1 or more estrous periods
	Number	*Days*	*Days*	*Number*	*Percent*	*Percent*	*Percent*
Control B stock	20	151	69.6	1,025	1.1	47.9	51.0
Inbred family:							
2	62	175	68.7	1,106	1.5	60.6	37.9
13	55	174	69.0	996	2.5	46.2	51.3
32	40	173	70.9	510	.6	43.9	55.5
35	76	162	70.3	743	.8	33.8	65.4
39	25	188	68.7	316	1.6	38.6	59.8
F_1 hybrids from families:							
2×13	34	[3] 157±24	69.4±2.5	151	[3,4] .7	[3,4] 55.6	[3,4] 43.7
13×2	30	[3] 179±51	68.6±3.0	186	[3,4] 3.7	[3,4] 45.2	[3,4] 51.1
2×32	8	149±33	70.0±2.3	60	1.7	58.3	40.0
32×2	10	210±94	69.0±1.8	64	.0	[5] 65.6	[5] 34.4
2×35	19	[3] 149±21	69.9±1.6	62	[4,5] 4.8	[4,5] 46.8	[4,5] 48.4
35×2	19	[3] 211±68	69.2±2.0	60	[5] 3.3	[5] 61.7	[5] 35.0
13×35	21	[3] 192±60	70.0±3.4	89	[5] 2.3	[3,5] 24.7	[3,5] 73.0
35×13	34	[3] 150±41	70.0±2.6	152	[3,5] 3.3	[3,5] 46.0	[3,5] 50.7
32×13	5	152±18	69.7±2.1	30	.0	43.3	56.7
39×2	10	192±59	68.1±2.0	65	[4,5] .0	[4,5] 55.4	[4,5] 44.6
39×13	11	194±68	69.0±2.3	69	2.9	34.8	62.3
39×32	8	161±36	69.4±1.8	45	2.2	48.9	48.9
F_2 hybrids from families:							
2×13	29	166±55	68.9±2.3	191	1.6	56.0	42.4
13×2	33	172±35	69.8±2.6	181	1.1	54.7	44.2
13×35	8	172±33	70.2±2.3	39	[6] 5.1	[6] 46.2	[6] 48.7
35×13	20	163±57	69.6±2.7	30	.0	60.0	40.0
39×2	18	186±50	69.2±2.2	31	.0	58.1	41.9

[1] In the data included for the inbred families and the control stock, ages of dam at birth of first litter are those reported by Wright (*9*); lengths of gestation period, by Eaton (*2*); and total number of litters and percentages born prematurely or conceived after one or more estrus periods, by Eaton (*3*).
[2] Standard errors, and not probable errors, are shown after the ± sign.
[3] Differs significantly from its reciprocal cross.
[4] Differs significantly from female-parent line.
[5] Differs significantly from male-parent line.
[6] Differs significantly from hybrids from same parent strains.

Length of gestation period (table 3) is apparently a rather constant character, varying but little between the families. Families 32 and 35 carry their litters 1 to 2 days longer than the other inbred strains. Among the F_1 hybrids, length of gestation appeared to average practically the same as for the inbred family to which the dam belonged. Length of gestation for the F_2 hybrids did not vary appreciably from that of F_1.

Normally the guinea pig breeds immediately following the birth of a littler. If mating does not take place at this time a period of 15 to 17 days elapses before estrus occurs again. The percentage of litters conceived immediately following the birth of a litter should give a partial measure, at least, of the regularity of breeding in the different strains. Comparison of the hybrids was made with Eaton's (*3*) data for the inbred strains and control-stock B, using as criteria the percentage of premature births, percentage of conceptions immediately following a normal gestation, and percentage of conceptions after skipping one or more estrus periods, and then determining the significance of the differences by means of the χ^2 test (chi square) as given by Fisher (*4*) for a $2 \times n$ table.

Most of the inbred families and control-stock B differed significantly from one another in the percentage of conceptions occurring in the first estrus after parturition. In family 2 more than 60 percent of the litters were conceived at this time, whereas in family 35 only about one-third of the litters were conceived as regularly (table 3). F_2 litters were conceived somewhat more regularly than the F_1 litters.

The dam apparently accounts largely for the regularity with which litters are produced. Females from family 2, except when mated with males of families 13 and 39, produced litters in succession much more regularly than females of other families. Females of family 35 were the most irregular in producing. There may be a preference of certain males or females for one another, since females of family 13 bred much less regularly with family 39 males than with males from the other inbred families. This statement also applies to females of families 2 and 35 when mated with family 13 males.

There was also a considerable difference in the percentage of litters born prematurely in the different families. Furthermore, the percentage of premature litters from females mated to males not of their own family was much higher than from females mated in the family to which they belong. This fact may be due to several causes, such as increased size of the young in certain crosses, more young per litter, or some physiological reaction due to differences of the parent strains that might be manifested in the developing fetuses.

Longevity of the Hybrids

Enough hybrids from which data could be obtained for the construction of reliable longevity curves were available only from crosses between families 2 and 13 and 13 and 35. A comparison of these curves with those for the parent families, as given by Eaton (*3*), are shown in figures 6 to 9, inclusive. From the graphs presented it appears that longevity of the sire's or dam's family had little influence on the longevity of the hybrid.

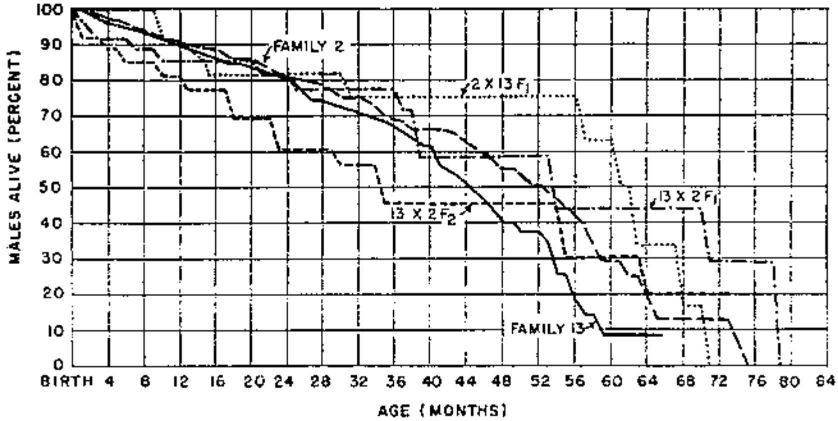

FIGURE 6.—Longevity, at various ages, of males of inbred families 2 and 13 and their reciprocal hybrids.

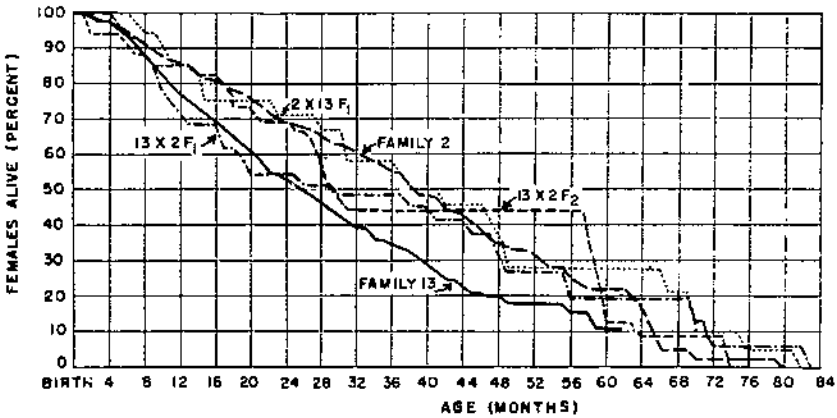

FIGURE 7.—Longevity, at various ages, of females of the same inbred families and hybrids as in figure 6.

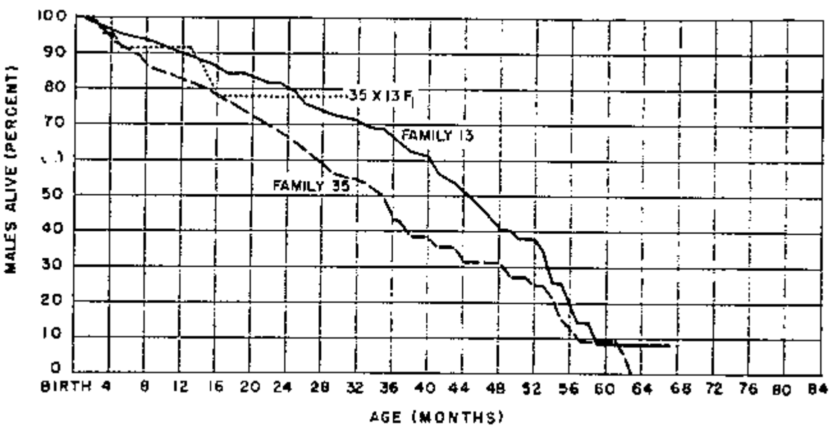

FIGURE 8.—Longevity, at various ages, of males of inbred families 13 and 35 and the F_1 hybrids of family 35 × family 13.

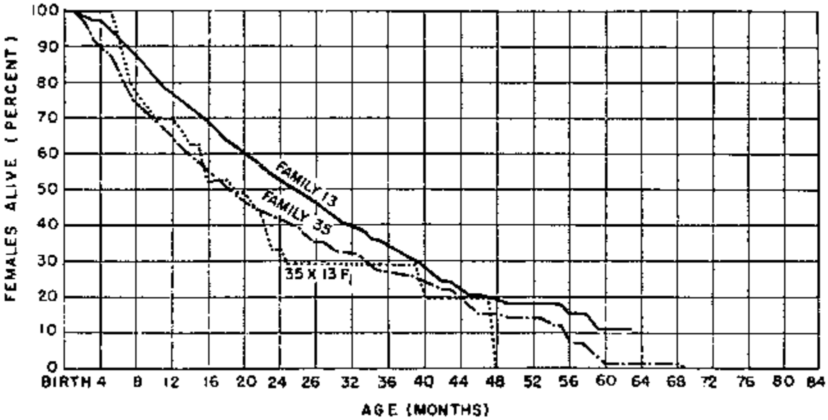

FIGURE 9.—Longevity, at various ages, of females of the same inbred families and hybrids as in figure 8.

To get a better idea of the influence of family on longevity, all hybrids that were descended from the same inbred family—either sire or dam—were combined into one group to give greater numbers, and percentages alive at 6-month intervals were determined. The results are presented in table 4.

TABLE 4.—*Percentages of males and females of the inbred families of guinea pigs and their hybrids alive at various ages*

Genetic group	Sex of animals	Guinea pigs alive at age of—						
		6 months	12 months	18 months	24 months	30 months	36 months	42 months
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Family 2 (inbred)	Males	95.8	91.0	86.9	81.0	75.4	68.6	65.7
	Females	94.1	86.1	78.6	69.7	63.0	55.4	44.8
F_1 hybrids of family 2	Males	96.0	89.5	85.4	81.5	79.4	75.0	66.3
	Females	92.0	75.8	65.4	57.3	51.9	47.3	39.9
F_2 hybrids of family 2	Males	92.9	85.4	76.9	69.3	61.1	50.9	46.7
	Females	87.1	81.1	69.3	57.2	41.1	33.3	30.9
Family 13 (inbred)	Males	94.9	89.3	84.8	80.3	71.9	66.9	54.8
	Females	93.2	77.2	63.9	52.7	42.9	34.2	21.6
F_1 hybrids of family 13	Males	95.2	91.9	86.1	84.7	83.1	80.9	68.9
	Females	96.4	75.6	62.3	53.1	47.4	43.4	36.3
F_2 hybrids of family 13	Males	92.6	56.5	79.1	72.0	66.6	55.5	50.8
	Females	90.8	65.4	52.8	43.5	31.9	27.2	25.3
Family 32 (inbred)	Males	94.8	91.0	83.5	79.4	72.0	58.1	40.8
	Females	92.9	78.3	61.6	48.5	35.4	28.5	20.2
F_1 hybrids of family 32	Males	96.3	92.3	81.8	81.8	81.8	81.8	81.8
	Females	89.6	73.1	65.4	54.5	41.5	35.5	30.4
Family 35 (inbred)	Males	90.5	82.6	75.9	66.7	55.2	43.5	35.4
	Females	82.7	63.7	50.7	42.1	33.2	27.0	22.3
F_1 hybrids of family 35	Males	94.0	91.6	85.0	80.7	80.7	80.7	64.6
	Females	90.9	69.8	54.6	37.6	33.9	31.1	24.2
F_2 hybrids of family 35	Males	95.4	85.9	78.6	78.6	78.6	-------	-------
	Females	88.0	66.7	36.7	15.3	15.3	-------	-------
Family 39 (inbred)	Males	88.1	83.7	75.6	71.1	65.7	62.5	47.1
	Females	87.2	64.3	46.3	37.2	30.8	20.6	17.2
F_1 hybrids of family 39	Males	96.1	96.1	91.8	91.8	91.8	-------	-------
	Females	91.0	73.3	59.5	55.5	37.8	28.4	28.4

F_1 hybrid males of families 13, 32, 35, and 39 were longer lived than males of the parent inbred families. The F_2 male hybrids were generally shorter lived than the F_1 hybrids and males of the inbred parent strains. F_1 females from families 13, 32, and 39 had greater longevity than inbred females from the same families. Most F_2 females were shorter lived than the F_1 and inbred females from the corresponding inbred strains. Inbred family 2 had a tendency to live longer than its F_1 or F_2 male or female hybrids.

DISCUSSION

It appears from the results presented that different sets of genes govern the physiological processes which make up fertility, growth, and viability. None of the inbred families apparently contain gene combinations favorable to superiority in all the three factors mentioned. The sets of genes governing a single character may even be different in the several strains. By crossing the various strains new gene combinations are thus formed, in some cases favorable to increased vigor in one of the several characteristics measured, in other cases perhaps unfavorable to one another, resulting in the production of individuals inferior to the parent races.

The history and results of the guinea-pig families concerned in this study lend themselves well to the foregoing postulations. As already stated, families 2 and 13 were derived from guinea pigs that had been bred within the Bureau of Animal Industry for a long period previous to the beginning of the inbreeding experiment, whereas families 32, 35, and 39 were descended from crosses of the original Bureau stock and animals purchased from a dealer. The results obtained from these two groups of families have been different through the period of the inbreeding experiments.

It is possible that the purchased stock introduced gene combinations not present in the original Bureau stock. When the stocks from the two different sources of origin were crossed, new gene combinations that could well account for the different results obtained may have resulted. In the case of differences in reciprocal crosses, it is possible that some of the growth and fertility characteristics may be due to sex-linked genes. However, the correlation of weight of dam at the birth of a litter to the growth characteristics of the young, even to a year of age, as shown by Eaton (*2*), indicates a strong maternal inheritance relationship, probably physiological in nature. Greater improvement over the parent strains resulted when three families entered into the hybrid than when only two were used. This is probably due to a larger number of favorable genes being brought together. These assumptions are in harmony with the theory of heterosis as explained by East (*1*) and other students of this subject.

Heterosis in livestock breeding has not been manifested to the same extent as in the breeding of corn and other plants. Greater difficulties doubtless will be encountered in establishing inbred strains of animals from which to make the crosses. Most experiments with livestock have shown that they will not stand so intensive inbreeding as plants and laboratory animals. The length of time between generations makes it impossible for the individual breeder to accomplish much. The expense of maintaining a large number of individuals from which to choose and build up lines is prohibitive except for cooperative efforts on the part of individual breeders and institutions. Unfortunately, the outcome of a cross cannot be predicted from the performance of the strains composing it. Until there is more knowledge concerning the genetic factors that control the various life functions, it appears that the improvement of livestock by hybridizing will necessarily continue to depend on the method of trial and error. Once inbreds that produce favorable hybrids are located, the practice from that point on should not be so difficult.

SUMMARY AND CONCLUSIONS

Comparisons involving five inbred strains of guinea pigs, a noninbred control stock, and reciprocal crosses between the inbred strains were made on the basis of various measures of fertility, growth, and mortality. The data presented cover the period from January 1, 1916, through December 31, 1937.

The inbred families and the control stock differed in the measures of comparison. No one strain was superior in all characteristics. Crosses between the strains also differed in the characters compared.

In crosses between strains of high and low fertility, the hybrid was usually higher in fertility than the poorer parent but lower than the better parent. The greatest improvement in fertility was obtained when two strains medium in this respect were crossed. The same relationship held for growth as for fertility. It was shown that mature-growth characteristics cannot be determined from weights at birth and weaning. In most cases crossing the strains increased the viability.

Reciprocal crosses varied in their performance. The dam appeared to affect the fertility and growth of the young more than did the sire.

Mating took place somewhat more regularly when the sires and dams were unrelated, but there was little difference in the age at which first litters were born.

Greater fertility and viability resulted from combining three inbred families in a cross than from combining two.

The performance of the hybrids cannot be predicted from the performance of their inbred parents.

The results in general seem consistent with the manifestations of heterosis as found in hybrid corn and in other plants and animals.

The fact that the full effect of heterosis, especially as regards growth, was not manifested at an early age tends to offset the benefits of crossing in livestock raised for market. The crossbred animals would still be in a period of rapid growth, and therefore less likely to attain a good finish, at the age when more rapidly maturing stock would ordinarily be finished for market. The feeder, therefore, would have to keep his stock for a longer period to attain the proper finish, or he would have to market at the usual age and weight at a sacrifice of price per pound for the animals.

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