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THE EFFECTS OF INBREEDING AND CROSSBREEDING ON GUINEA PIGS.

I. DECLINE IN VIGOR.
II. DIFFERENTIATION AMONG INBRED FAMILIES.

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CONTENTS.

I. DECLINE IN VIGOR.

EARLIER VIEWS ON INBREEDING.

Inbreeding and crossbreeding are subjects on which there has been much discussion for centuries. The marriage customs of primitive peoples indicate that definite views on them were entertained long before the beginning of history. These views, however, were apparently different among different peoples, as the customs of some seem designed to prevent inbreeding, while the reverse seems true in other cases. A diversity of views continues to exist.

Livestock breeders have generally endeavored to prevent close inbreeding, holding that such breeding is likely to produce a progressive degeneration, exhibited by reduction in size, constitutional

vigor and fertility, and leading ultimately to the appearance of monstrosities. On the other side, however, we find that most of the modern improved breeds of livestock originated in rather close inbreeding of selected stock. Systematic livestock breeding began in England about the middle of the eighteenth century with the attempt of Robert Bakewell to improve the native Leicester sheep and Longhorn cattle. Bakewell had definite views on the characteristics which he wished to combine in his animals, but he departed most from the prevailing customs of his time in his use of close inbreeding for the purpose of fixing these desired characteristics. His methods were followed in the foundation period of most of the other British breeds. In the course of time, however, certain unfortunate characteristics, such as low fertility in the Duchess family of Shorthorns, came to be attributed to the inbreeding. At the present time there is much difference of opinion among practical breeders about the effects of inbreeding.

The remarkable increase in size and vigor which often follows the crossing of different varieties was noted by the early plant breeders. Darwin made carefully controlled experiments on the effects of self-fertilization and crossing of various plants. In general, those species with mechanisms facilitating cross-fertilization suffered an obvious decline in vigor when self-fertilized, while those without such a mechanism suffered no ill effects. He found that little or no improvement followed crossing within a self-fertilized strain, while marked improvement was the rule in crosses between such strains. In applying his results to livestock breeding Darwin pointed out that the advantage of close inbreeding in retaining characteristics might outweigh some loss in constitutional vigor.

Darwin's work on plants was followed by the experiments of Crampe and Ritzema-Bos with rats and of Weismann and Von Guaita with mice. The decrease in fertility and increase in sterility noted by all of these writers and the increased susceptibility to disease and the appearance of abnormalities noted by Crampe have long done duty as the stock examples of degeneration through inbreeding.

The problem has been attacked from a new viewpoint since the rediscovery of Mendel's law. The experiments of Castle, Moenkhaus, Hyde, Wentworth, and others with the fruit fly, *Drosophila melanogaster*, those of G. H. Shull, East, Hayes, Jones, Collins, and others with maize, and those of Miss King with rats have been rapidly bringing this subject into line with the current theory of heredity.

The experiments with guinea pigs described in this bulletin have given results which agree in the main with those of the authors mentioned above, although appearing at first sight somewhat difficult

to reconcile with the results in the only other recent extensive experiment on inbreeding of mammals, namely, those which Miss King obtained with rats. It will be shown, however, that the two experiments are complementary rather than contradictory. It may be well to call attention to the excellent summaries of the present state of knowledge on the subject to be found in Miss King's series of papers and in "Inbreeding and Outbreeding" by East and Jones.

PLAN OF THE EXPERIMENTS.

An extensive investigation of the effects of inbreeding was planned in 1906 by George M. Rommel, Chief of the Animal Husbandry Division of the Bureau of Animal Industry. The work was commenced in that year at the Experiment Station of the bureau at Bethesda, Md., with guinea pigs as material. Since 1911 the experiments have been carried on at the Experiment Farm of the Bureau of Animal Industry at Beltsville, Md. Over 30,000 guinea pigs have been recorded. The work has been conducted successively by Ralph J. Carr, Dr. E. H. Riley, F. R. Marshall, and the writer. Essentially the same system of records has been kept throughout. On taking charge in September, 1915, the writer found the previous records in excellent condition. In analyzing these and later data a great amount of tabulation and calculation has been necessary. The writer has been assisted successively by Walter J. Hall and Orson N. Eaton, to whose painstaking care in this laborious work the carrying through of the project is in a large measure due. All tabulations and calculations have been carefully checked.

HISTORY OF THE GUINEA-PIG STOCK.

Dr. E. C. Schroeder, superintendent of the experiment station at Bethesda, Md., has kindly furnished the following account of the early history of the stock:

The history of the station's stock of guinea pigs is as follows: When I took charge of the experiment station of the bureau (at that time located at Benning Road and Eighteenth Street NE., Washington, D. C.), during the summer of 1894, I found on hand about 250 to 300 guinea pigs, of all sizes and ages, about the history of which no records were available. The general character of the animals indicated that some attempts had been made to breed special varieties, such as curly haired guinea pigs, white guinea pigs with black-smudged muzzles, long-haired guinea pigs, etc.

As there was a superabundance of other work which urgently required attention at the station, I at once abandoned all attempts to breed guinea pigs of special types and kinds, and made of the breeding pens a strict business project, with no other purpose in mind than the production of a sufficient number of satisfactory animals for the technical work of the bureau. I used the stock on hand, eliminating the fancy types as much as possible, because they are less satisfactory than the plain, varicolored, smooth-haired type for laboratory use.

In the year 1895, as nearly as I can remember, I purchased a number of plain, ordinary male guinea pigs, which, after a lengthy period of quarantine, were introduced into the breeding pens.

Toward the latter part of the year 1896 it became evident that I would be able to move the experiment station from Benning Road and Eighteenth Street to some larger and more desirable place; hence I concluded that it would be wise to save as many young and vigorous pigs for breeding purposes as possible, and to start the guinea-pig pens at the prospective new station with this young stock.

A new place for the station was found at Bethesda, Md., its present site, in May, 1897, but it was not ready to be occupied until the following November, during which month the whole stock of guinea pigs was moved from Benning Road to Bethesda. The stock at that time consisted of about 300 old breeders and about 400 young animals, unbred but specially selected for breeding purposes, also 100 to 150 young pigs.

During the journey from Benning Road to Bethesda, Md., a distance slightly more than 11 miles, a sudden, unexpected, heavy, cold shower of rain occurred, and many of the guinea pigs, though they were in cages and in a covered wagon, got thoroughly wet.

From 10 days to 2 weeks later the guinea pigs began to die at the rate of from 30 to 50 a day. The disease which caused the deaths was a combination of inflammation of the bowels and lungs. When the outbreak finally terminated just 63 guinea pigs were left alive, and of them 9 were in such hopeless condition that they were killed. This left 54 guinea pigs, varying in age from a few weeks to about 2 years.

The 54 guinea pigs are the stock to which all the guinea pigs that are now in the breeding pens at the experiment station, or that ever have been in the guinea-pig breeding pens at the Bethesda station, trace their origin.

The method of raising guinea pigs at the station has been always to select the best animals for breeding purposes, not only with reference to size and weight, but also with reference to smoothness of hair and productivity.

Unprolific breeders have always been eliminated from the pens as quickly as possible, and the progeny of such breeders have always been carefully avoided in selecting fresh breeders.

The total number of guinea pigs produced since the latter end of 1897 and the present time I can not give without spending several weeks searching our records. At present, however, the station is producing about 12,000 guinea pigs per annum, all of which trace their ancestry back to the 54 which were left after the disastrous outbreak of disease in the year 1897.

To judge from the information I have been able to obtain from various persons who are informed about guinea pigs, the stock we have at the station, so far as health, vigor, and productivity are concerned, in spite of the inbreeding to which they have been subjected, is, strictly speaking, very superior.

The beginning of the inbreeding experiment is described as follows in a report by Dr. E. H. Riley:

Investigations were begun in July, 1906, to study the effects of inbreeding when continued for successive generations. Guinea pigs were selected for this work because larger numbers could be housed and cared for with greater convenience than any other animal at our disposal, and, being prolific breeders, the data from succeeding inbred generations accumulated rapidly, thus enabling one to draw conclusions in a comparatively short time. Since large numbers of guinea pigs are used annually in the bureau laboratories, all stock which has served its purpose in the breeding experiment is readily made use of.

Two inbreeding tests were planned in this experiment. In Test No. 1 the foundation stock was line-bred for 12 years at the Bureau of Animal Industry Experiment Station. This foundation stock was selected from a group of 150 guinea pigs. The largest and most vigorous individuals of both sexes were selected for breeders. No attention was paid to color or color markings, except that no albinos were selected.

Record was made of the coat color patterns as a means of identification. This record has later served as a means of noting certain family characteristics, which, in many cases, were transmitted to succeeding generations of inbred stock with quite uniform regularity. All animals of the foundation stock were between 5 and 6 months old when mated.

Twenty-four females of uniform size and conformation were selected and numbered consecutively from 1 to 24. The males were selected in a like manner and numbered in another series beginning with 1. The number of each of these females of the foundation stock was given to the family of guinea pigs which descended from her. Generation 1 is the progeny of the foundation stock, and is, therefore, not inbred. In order to follow the closest line of inbreeding, brother and sister of the same litter were mated. In all cases the best individuals in the litter were selected for breeders. Their progeny were selected and mated in a like manner. This method is being continued, and at present (1913) individuals in a few of the families have been inbred for 13 generations. All breeders in each of the families have been inbred through 4 generations.

In Family 4, parents were bred to their progeny: that is, sires were mated with their daughters, granddaughters, etc., of each succeeding generation during the breeding period of their lives. In a similar manner dams were mated with their sons, grandsons, etc., of succeeding generations.

In Test 2 of this experiment the animals of the foundation stock were unrelated to each other. Some of the breeders were selected from the same general stock at the Bureau of Animal Industry Experiment Station as were those in Test 1, but in all cases they were mated with stock which was obtained from a different source. The alien stock was apparently as healthy and vigorous as the other. The foundation females used in this test were numbered consecutively from 31 to 42, inclusive. The families were numbered in the same manner as those in Test 1. All animals were housed, fed, and cared for in the same manner. Practically no change has been made in the method of rearing our breeding stock since the experiment was started. The methods which we use are those which have been followed successfully for the past 14 years by the Bureau of Animal Industry Experiment Station, where thousands of guinea pigs are raised annually for laboratory purposes.

It was found that more satisfactory results could be obtained by having one male and only one female occupy each breeding cage, because frequently two females gave birth to young at about the same time, making it impossible to tell to which female the young belonged. In all such cases these mixed litters were eliminated from the experiment. In a few instances young females became pregnant by their sires before they were weaned, which was at the age of 33 days. Young from these matings were also eliminated from the experiment.

According to this report, 35 families were started, 24 wholly from the line-bred stock of the Bureau of Animal Industry and 11 from a cross between this stock and guinea pigs obtained from a local dealer. All were carefully selected, for vigor, from large stocks. In all but one family, matings were made exclusively between full brothers and sisters. The data from Family 4, in which matings were made between parent and offspring, have not yet been analyzed. Seven of the remaining 23 families in Test 1 (from the line-bred stock) went out of existence before the second generation was produced, for various reasons, such as the early death of the female or the failure to produce living young of both sexes. Four of the 12 families in Test 2 failed for similar reasons, and another was disposed

of in the third generation because a skin disease had become established in it. These failures can not be ascribed to inbreeding.

There were thus 23 families with which the inbreeding experiment really started. One of these (Family 15) became extinct in 1911. Family 1 followed in 1914 and Families 3, 11, and 21 in 1915, leaving 18 families in existence at the end of 1915. Families 14, 19, and 34 became extinct before the middle of 1917. In the summer of 1917 several other experiments had become so extensive that it seemed best not to attempt to maintain all of the inbred families. Five families—2, 13, 32, 35, and 39, were selected for perpetuation, while the others were gradually eliminated. (Pls. I to VI.) The condition of the families in November, 1915, is shown in Table 1.

TABLE 1.—*Number of matings in each generation of inbreeding in each family on November 15, 1915.*

[The original matings are called the zero generation.]

Family.	Generation—										Number of matings.
	6	7	8	9	10	11	12	13	14	15	
2			4	10	11	6					31
7					4	3	1	3	1		12
9				1	1	4	4	1			17
13					6	13	15	5			39
14	1	1									2
17				1	1	3	6	6	3	1	21
18				1	3	3	4	4			15
19					3	4	1				8
20				5	7	5	1				18
23			1	4	2	2	1				12
24				2	2	2	1				7
31					1	4	6	4			15
32						3	4	12	7	1	27
34					2	1					3
35				1	2	5	10	11	8	1	38
36				1	5	11	6	2			25
38				1	0	6	7	3	1	1	19
39				1	7	18	14	2			42
Total	1	1	5	28	59	93	83	56	21	4	351

The 23 families which have been made the basis of analysis were descended from 23 different females, but are not so distinct from one another on the male side. Only nine males were in fact used in the foundation stock. Male 1 was used with Females 1, 2, 3, and 7 to found the families named from these females. Male 13 was the male ancestor of Families 9 and 11 and parts of Families 13 and 14. Male 2 was the male ancestor of the remaining lines in Families 13 and 14 and all of Family 15. Families 17 to 24 are all descended from Male 3; Families 31 and 32 from Male 9; Families 35 and 36 from Male 11, while Families 34, 38, and 39 had separate male ancestors. It may be seen that Families 13 and 14 are really composite and each might well have been treated as two families. In Family 13 the line descended from Male 2, began to decline after three genera-

tions, and produced its last litter in January, 1913, having reached the ninth generation. The family characters may in the main be considered to represent the large stock descended from Male 13. In Family 14 the two lines kept about the same ratio to each other in strength. The line from Male 2 was the strongest in numbers. It ran out in the tenth generation, while the line descended from Male 13 lasted only to the ninth generation.

The families other than 13 and 14 all descend from a single original pair but yet are of varying degrees of homogeneity. Some idea of the degree of homogeneity of the various families can be obtained from Table 2. This table shows the number of matings made in each family in two periods, 1906 to 1909, inclusive, and 1910 to 1914, inclusive, and the maximum percentage of these matings which can be traced back to a single mating in each generation of inbreeding. The original mating is called the zero generation.

The table reveals that certain families, such as 18 and 39, became dominated by a particular subfamily in their early history and remained so later. At the other extreme are families, such as 11, 14, 17, and 32, which remained split up into many subfamilies even through 1914. Most of the families became more homogeneous as time went on. Families 2 and 38 are extreme examples of the emergence of one subfamily into predominance. In a few cases (19, 24, 31, and 35) the most important subfamily in the first period became supplanted by another in the second. The most remarkable case of this sort, that of Family 35, is not fully brought out by the table. One of the four matings made in the second generation produced only 10 out of 59 matings of the third to seventh generations. Its only pair of descendants in the seventh generation produced 49 out of the 75 matings of Family 35 of the eighth to twelfth generations and produced all matings following the twelfth. This family has reached the twenty-third generation (1921) and now traces entirely to a single mating of the twelfth generation. There seems to have been no conscious effort to bring about the predominance of the descendants of the single mating of the seventh generation.

In interpreting the results in the various inbred families, it will be important to bear in mind that those in which one subfamily was predominant from the first or in which several subfamilies remained about equally important should maintain about the same average of hereditary characteristics throughout their history, while a marked change in the hereditary characteristics of the family as a whole need not be surprising in cases in which a subfamily, which is unimportant at first, later emerges into predominance.

TABLE 2.—*The relative homogeneity of the inbred families.*

[The number of matings made in each family from 1906 to 1909 (first line of each family) and from 1910 to 1915 (second line of each family) is given in the second column. The maximum percentage of these matings descended from a single mating in each generation is shown in the following columns. Change in the dominant subfamily is indicated by an asterisk.*]

Family.	No.	Generation.						
		0	1	2	3	4	5	6
1	11	100	91	27	....	....	....	....
	13	100	100	92	92	85	62	31
2	36	100	44	31	....	....	....	....
	65	100	89	89	86	74	57	34
3	41	100	63	44	....	....	....	....
	40	100	98	55	33	....	....	....
7	43	100	51	40	23	....	....	....
	77	100	69	65	47	....	....	....
9	26	100	96	46	19	....	....	....
	59	100	100	88	76	46	....	....
11	73	100	75	25	....	....	....	....
	71	100	72	45	....	....	....	....
13	67	55	54	28*	....	....	....	....
	94	100*	100*	80*	46*	....	....	....
14	42	50	48	....	....	....	....	....
	41	71	68	41*	....	....	....	....
15	23	100	44	....	....	....	....	....
	8	100	75*	....	....	....	....	....
17	38	100	63	42	....	....	....	....
	88	100	66	41	....	....	....	....
18	25	100	96	56	52	20	....	....
	62	100	100	76	76	37	....	....
19	19	100	95	88	32	....	....	....
	43	100	100	84*	84*	49*	....	....

Family.	No.	Generation.							
		0	1	2	3	4	5	7	8
20	23	100	61	52	13	....	....	....	....
	48	100	98	98	83	52	42	....	....
21	20	100	95	50	35	....	....	....	....
	96	100	100	89	48	....	....	....	....
23	12	100	83	50	25	....	....	....	....
	45	100	100	96	49	....	....	....	....
24	66	100	55	29	....	....	....	....	....
	63	100	59*	59*	29*	....	....	....	....
31	32	100	53	28	....	....	....	....	....
	64	100	53*	53*	45*	....	....	....	....
32	103	100	62	23	....	....	....	....	....
	107	100	40	....	....	....	....	....	....
34	11	100	91	64	19	....	....	....	....
	34	100	100	44	....	....	....	....	....
35	45	100	98	29	....	....	....	....	....
	95	100	100	59*	59*	59*	59*	58	33
36	47	100	96	47	....	....	....	....	....
	94	100	100	60	41	....	....	....	....
38	40	100	43	....	....	....	....	....	....
	61	100	92	92	49	....	....	....	....
39	14	100	93	86	71	64	29	....	....
	77	100	100	100	100	100	56	56	31

From 1906 to 1911 the inbred stock, as already stated, was kept at the bureau Experiment Station at Bethesda, Md., with many other guinea pigs raised for pathological experiments. In 1911 the inbred stock was taken to the experiment farm at Beltsville, Md. Shortly before moving, 40 pairs of normally bred guinea pigs were selected on the basis of vigor and set aside as a control stock to be maintained without inbreeding. They were from the same stock from which Families 1 to 24 and the original females of Families 31 to 39 were derived. They had, however, been maintained up to 1911 without records. This control stock was called Experiment B. It has been kept at Beltsville since 1911 under the same conditions as the inbred families except that matings as close as those between second cousins have been avoided.

SYSTEM OF MATING, CARE, AND FEED.

With rare exceptions, the matings in the inbred families have been made between litter mates at the time of weaning at 33 days. This was to avoid mistakes in identity which would make the strictness of the inbreeding doubtful. Females occasionally are sufficiently mature at 33 days to bear litters sired by their own sire at about 100 days of age. They do not appear to suffer ill effects, and as the males do not become mature until over 2 months of age, the system of breeding followed is not believed to be injurious to the animals to an appre-

ciable extent. Most but not all of the matings in the control stock were made between immature guinea pigs. A single pair has been kept in each pen as already stated, except for cases in the early generations.

Large wooden pens, 23 by 16 by 29 inches on the inside, were used until 1916. They had got into rather bad condition by this time and had become infested with bedbugs. They were replaced in December, 1916, by metal pens, 16 by 14 by 24 inches, with removable trays for ease in cleaning. Whether the improvement in cleanliness and freedom from bedbugs compensates for the smaller amount of room for exercise and the greater difficulty in maintaining an even temperature in winter is not certain. In any event, experiments conducted in different years must be compared with due caution.

The guinea pigs have been given oats and fresh water every day. Green feed is supplied three times a week and hay once a week when the pens are cleaned. Green oats and fresh grass in spring and summer, and cabbage and kale in fall and winter have been used most successfully as green feed. The greatest difficulty in procuring good green feed comes in late winter and early spring, after other winter conditions have depressed the stock. All records indicate that the stock is in the poorest state at this time. Conditions are also better as a rule in the early part of summer and in fall than during the hot weather in July and August.

THE DATA RECORDED.

All litters are recorded on the day on which they are born, except that litters born on Sunday or a holiday are recorded on the next day. At birth the date, pen, number, sex, color, and weight are recorded for each young one. Drawings are made of the coat pattern of each guinea pig in a rubber-stamp outline. The variety of the colors, including intense and dilute agouti, black with red, yellow, or cream spotting, and albinism, together with the almost endless variety in the tricolor pattern, make color and pattern an almost certain means for the identification of individuals. Ear punches are also used as a help to identification. All mated animals are identified at death to insure that no confusion has occurred in the matings. Each of the young is weighed at the ages of 3, 13, 23, and 33 days as well as at birth. Up to 1916 the mated animals were weighed when 1 year old. Since 1917 more frequent weighings have been made.

THE CHARACTERS STUDIED.

Possible effects of inbreeding have been looked for in age of maturity, fertility, rate of growth, mortality among the young, resistance to tuberculosis, sex ratio, the production of monstrosities, and coat color.

Under the head of fertility, both the size and frequency of litters have been considered. Little attempt has been made to distinguish complete and partial sterility, as cases of complete sterility have been rare and uncertain in all stocks. The failure of a mating to produce litters has usually been due to the early death of one member of the pair.

The data on the rate of growth up to the age of weaning (33 days) are naturally much more extensive than those on later growth, and have been studied in more detail. The principal characters which are used in this connection are the weight at birth of all of the young born, the birth weight of those which survive to 33 days, and the gain between birth and 33 days.

The losses among the young are considered under two heads, death at or before birth and death between birth and weaning. The characters used are the percentage born and found alive and the percentage raised to 33 days of those born alive. The product of these two, namely, the total percentage raised, is also used.

LIFE HISTORY.

Guinea pigs are born in litters of 1 to 9. Litters of from 2 to 4 are most common, and litters of more than 6 have been decidedly rare in the present work. The young are born in a very advanced state of development, with thick fur, open eyes, and the ability to run about at once. They soon begin nibbling at the leaves of cabbage or other green food in the pen. They are, in short, rather better able to take care of themselves from the time of birth than the young of any other familiar domesticated mammal. They grow rapidly and reach about half the adult weight when between 2 and 3 months of age. The final weight is nearly reached at a year, but there is slow growth for a longer time. Guinea pigs are in their prime between 1 and 3 years. After reaching 3 years there seems to be a distinct decline. The present experiments, however, have not been designed to study longevity, as matings have often been disposed of to make room for those of a later generation. The oldest dam recorded had reached 47 months. The average age of dams has been between 14 and 16 months. One female is reported to have died at an age of 59 months. Her last litter was born at 38 months.

Sexual maturity is reached early. In nearly every family and experiment there have been a few cases in which females have had young when about 100 days old. As the gestation period is about 68 days, this means that these litters were sired by the dam's sire before she was weaned at 33 days. The minimum age at which a male may sire a litter seems to be about 60 days, although we have one apparently reliable record at about 48 days (litter born at 117 days).

The average age under ordinary conditions seems to be about 3 months, bringing the first litter between 5 and 6 months.

The birth of a litter is followed at once by an œstrus period. In 50 to 60 per cent of the matings in a vigorous stock, fertilization takes place at this time, and one litter follows another after an interval of 65 to 74 days. If fertilization does not take place, there is a period of about 17 days before the next œstrus, and recurrence thereafter at about this period. The average interval from one litter to another, if there is no delay, is about 69 days (68. 93 $\pm$ 0.04 in 1,332 cases among inbreds and controls in which the interval was between 65 and 74 days). The true gestation period would of course be slightly shorter. The gestation period is subject to much variation, its standard deviation, judging by that of the intervals between litters, being almost two days (1.91 $\pm$ 0.03 in the above data). The most important cause of variation is the size of litter. Large litters are born earlier than small ones. The correlation between size of litter and interval in the data mentioned above was -0.457 ± 0.015. Under unfavorable conditions the average gestation period is slightly shorter than under favorable conditions. Young born before 65 days are seldom raised, or even born alive.

FERTILITY.

The number of litters produced per year depends in the main on whether many of the litters succeed one another without delay, which doubtless depends in part on whether or not ovulation takes place immediately after the birth of the preceding litter. Evidence which will be presented later, however, shows that the sire is more apt to be responsible than the dam for irregularity in this respect. The most important factors are associated with the conditions at this time. If the preceding litter is small, if environmental conditions are improving (as in April and May as a rule), or if the female is above the average weight for her age, there is considerably more likelihood that a second litter will start on its career at once than if, for example, a large litter is born in December leaving the dam much under weight. The age of the dam, at least up to 3 years, does not seem to be an important factor. There is, however, a trifle more regularity between 1 and 2 years of age than before or after. Regularity or irregularity is not characteristic of particular matings to any marked extent. The correlation between successive intervals, classified as more or less than 77 days, came out virtually zero in the control stock (-0.01 ± 0.03). This excludes both heredity and condition of health over long periods of time as important factors. Other results show the small importance of heredity in particular cases, the correlations between parent and offspring matings, in litters per year, being insignificant in both controls and inbreds. On the other hand, as we

shall see later, by comparing the averages of whole families significant differences can be found which must be attributed to heredity.

For the purposes of the present work, frequency of litter has been measured in a somewhat rough way. Matings are entered in a table under the month in which the male reaches 4 months of age (an average of 3.5 months) or under the month following that in which the mating was made if the male was already more than 3 months old. The mating is dropped from the table the month after the death or disposal of the female. The number of litters produced by a given group of matings, divided by their effective duration in years, as calculated by the above method, gives the average number of litters produced by a mating in a year. In comparing experiments it must be borne in mind that difference in the age of maturity as well as in the regularity in producing litters may be responsible for observed differences in frequency of litter as calculated by this method.

The production of a given size of litter, as in the case of frequency, is only to a slight extent characteristic of matings. The correlation between successive litters produced by the same mating among the controls was -0.011 ± 0.023 and that between litters which were not successive was $+0.064 \pm 0.014$. Similarly insignificant correlations were obtained from extensive tabulations among the inbred families. The correlation between parent and offspring in the average size of the litters produced is in all cases so small as to be of doubtful significance. Here, again, the only satisfactory evidence of heredity is found on comparing different inbred families raised under identical conditions.

Variations in environmental conditions have a marked influence on size of litters. The average is usually higher in summer and fall than in winter and spring. In the controls (first 112 matings, 588 litters) averages of 2.75, 2.84, 3.26, and 3.16 were found for successive periods of three months beginning with January to March. This decrease in the average size of litter under unfavorable conditions seems to be due to a reduction of large litters to medium-sized ones (perhaps by death and absorption of some of the embryos), rather than to increase in the percentage of small litters. The percentage of litters of 1 and 2 in these data was found to be nearly constant at all seasons of the year, but the percentage of litters of three increased greatly in winter and spring at the expense of litters of 4 or more, litters of 3 rising from 25.5 per cent in summer to 45.9 per cent in spring. In such of the inbred families as were characterized by a markedly smaller average size of litter the percentage of small litters was much greater than in the controls. Such inbred families under good conditions might produce litters of the same average size as the controls under poor conditions, but the distribution of litter

sizes has been strikingly different in these cases. The average size of litter among the controls born in the years 1911 to 1916 under the unfavorable conditions from January to June was 2.77. The average for the eight poorest inbred families during the months July to December in 1906 to 1910 was nearly the same, 2.74. The difference in distribution may be seen in Table 3. It appears that inferior heredity reduces the size of litter in a different way from inferior environmental conditions.

TABLE 3.—*Percentage of litters of each size in two stocks of guinea pigs—a vigorous stock under poor conditions and a weak stock under good conditions.*

Kind of stock.	Number of litters.	Average size of litters.	Percentage in litters of 1 to 6.					
			1	2	3	4	5	6
Controls (conditions unfavorable).............	386	2.77	11.4	27.5	40.7	15.0	4.4	1.0
8 inbred families (conditions favorable)........	372	2.74	16.9	31.7	24.5	16.4	8.6	1.9

The age of the dam has an influence on the size of the litter, but not an important one. First litters are smaller than later ones on the average (2.77 compared with 3.05 in the first 112 matings of the controls). This difference, however, exists mainly because first litters are especially apt to be born in winter and spring. Most matings have been made in summer and fall, when conditions are favorable, and the first litter, born when the dam is about 6 months old, has thus been smaller on the average than litters born at 12 months or 24 months, but not much smaller than litters born in the neighborhood of 18 months. Females from 1 to 2½ years old, however, produce slightly larger litters than younger or older females, apart from the seasonal complication.

Among the controls, litters which follow others without delay are slightly larger than those born after a long interval (3.16 compared with 2.91 in the tabulation referred to above). Presumably the same causes which were favorable to immediate fertilization were favorable also to a large size of litter. Curiously enough, a tabulation among the inbreds born in 1916 gave a contrary result. The average was 2.22 after a short interval and 2.46 after a long one. In this case only 36 per cent of the litters were born after an interval of less than 75 days as compared with 56 per cent in the controls in the former tabulation. Apparently in this case the advantage of the recuperation furnished by the delay outweighed the unfavorableness of the conditions which was indicated by the mere fact of a delay.

Taking the record of each mating as a whole, there is no significant correlation between the size and frequency of litters.

All the factors which have been considered—constitutional vigor, heredity, season, age of dam, and interval since preceding litter—if combined, determine the size of litter only to a small extent, probably less than one-tenth. The determination of the size of any particular litter must be due largely to rather temporary conditions. The immediate direction of change in the condition of the dam at a critical period, for example, may be the important factor. From the standpoint of the condition of the female, during an appreciable period of time, it appears that variations in size of litter are largely a matter of chance. The most vigorous female may have a litter of 1 under what seems the best of conditions, and a litter of 4 may be born when everything seems opposed.

MORTALITY AMONG THE YOUNG.

Guinea pigs may be born dead for a variety of reasons. A large percentage of those classified as born dead are born prematurely, and the average weight is much less than that of those born alive. There are, however, not infrequent cases of animals which are unusually large at birth, but are found dead apparently because of difficulties in parturition. Many of those classified as born dead undoubtedly were born alive but died before being recorded. In general the percentage born alive obviously depends largely on the health of the dam. Unfavorable environmental conditions act in the main indirectly on the young. The inherent vigor of the young, however, plays some part, as is shown by the improvement in the percentage born alive when inbred females are mated with unrelated males, instead of with their brothers, a point which will be discussed in a bulletin to follow.

The percentage of the young which is raised among those born alive also depends much on the health of the dam, but to a less extent than the percentage born alive. There have been cases in which the young reached 33 days largely through their own efforts, the mother having died a few days after their birth. Environmental influences act on the young directly as well as indirectly in this case. The inherent vigor of the young counts for much. Thus we find that the percentage raised of those born alive shows a more marked improvement when inbred females are crossed with unrelated males instead of with brothers than is the case with the percentage born alive.

Both of these percentages reflect closely the changes in environmental conditions. Inadequate or inferior green feed causes a large number of stillbirths and an increased mortality among the living young. A change from alfalfa to timothy hay has been observed to have the same effects. The records are usually much better in both respects in summer than in winter. In years in which one of

these percentages was high, as 1910 and 1914, the other was also high, the same years showing, moreover, high records in size and frequency of litter and rate of growth.

It will be shown later that there are significant differences among the inbred families, differences which must be hereditary. It will be shown also that success in bearing living young is not correlated with success in rearing them. Genetically the constitutional vigor of the young themselves and the qualities of the dam which favor their successful rearing seem to be largely independent of the qualities which insure against stillbirth.

The size of litter naturally makes a difference in the percentages born alive and reared. The effect, however, is different in different stocks. In the vigorous control stock there was not much difference even up to litters of 6. Litters of 3, however, were most successful in both respects, with litters of 2, 4, and 5 following closely. In the inbred families the most favorable size of litter has shifted to 2 or even 1, and litters of 3 or more are at a disadvantage. Apparently in a vigorous stock a litter of 1 is itself so much of an indication of lack of vigor that smaller percentages are born alive and reared. This effect is not a seasonal one, since litters of 1 and 2 were hardly more numerous in winter than in summer among the controls, while litters of 3 were much more numerous in winter.

There is no appreciable difference between males and females in the percentages born alive and reared. Among the controls (112 matings) 87.1 per cent of the males and 87.5 per cent of the females were born alive. Among those born alive, 84.9 per cent of the males and 85.4 per cent of the females were reared. Equally insignificant differences, reversing, however, the slight advantage of the females, were found among the inbred families.

The age of the dam has little bearing on the percentage born alive or reared, except as it is correlated with seasonal changes. The cyclical tendency toward maxima at 12 and 24 months and minima at 6 and 18 months, noted in the case of size of litter, is also pronounced in the mortality percentages.

There is naturally a strong tendency for the young in the same litter to share the same fate.

RATE OF GROWTH.

The birth weight of guinea pigs varies greatly. Animals which ultimately reach maturity may have weighed anywhere from 40 to 150 grams at birth. The average is about 80 grams. About half fall between 64 and 91 grams. There is little difference between the sexes. An extensive tabulation among the controls gave a difference of only 2.7 ± 0.8 grams in favor of the males. There was a difference of 11.1 ± 2.6 grams in favor of the males at 33 days. The males con-

tinue rapid growth longer and are much heavier at 1 year. A tabulation among the inbred families (1910 to 1914) gave averages of 888 grams and 763 grams, respectively, for the weight at a year in males and females.

A little experience is enough to demonstrate that the size of litter is a very important factor in determining the variations in birth weight. Single guinea pigs are not only conspicuously larger as a rule but also have longer hair and are more active than those in large litters. The correlation between the size of litter and mean weight of litter mates came out -0.658 ± 0.007 as the average of determinations in 11 inbred families and in the controls. The correlation between size of litter and individual birth weights is, of course, somewhat less (about -0.57). The correlation between mean birth weight of litters and interval since last litter was $+0.533 \pm 0.013$ in the cases in which this interval was less than 75 days. The correlation between interval and litter size was -0.457 ± 0.015, as previously stated. Analysis of these and other data shows that size of litter has considerably more effect on birth weight through its effect on rate of growth than by merely determining a longer or shorter period of growth, a conclusion contrary to that reached by Minot.[1] The analysis further indicates that the rate of growth is affected by the general condition of the dam even more than by the size of the litter. The hereditary potentialities of the fetus itself are in addition important factors in a crossbred stock.

Hereditary differences are, however, relatively unimportant in a random-bred stock. The correlation between the mean birth weights in successive litters was found to be -0.051 ± 0.023 in the control stock and that between litters which were not successive was $+0.058 \pm 0.014$. Nevertheless, it will be shown later that hereditary variation was sufficiently great in this stock to permit the isolation of marked differences among the inbred families derived from it.

Even when all of the above factors are constant, as within a litter produced by an inbred stock, there may be considerable variation. There was an average standard deviation of about 10 grams within litters of any given size from 2 to 7 in the control stock, after making due corrections for the small numbers. The standard deviation of the mean birth weights of litters, again making the necessary corrections, was of about the same size, declining from 13.7 in litters of 2 to 7.4 in litters of 7. Thus in this case variations within litters and among litters means are about equally important. Only an insignificant part of the variation within litters is genetic in the controls as

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[1] Minot, C. S., 1891. Senescence and rejuvenation. Jour. Physiol. v. **2** p. 97–153.
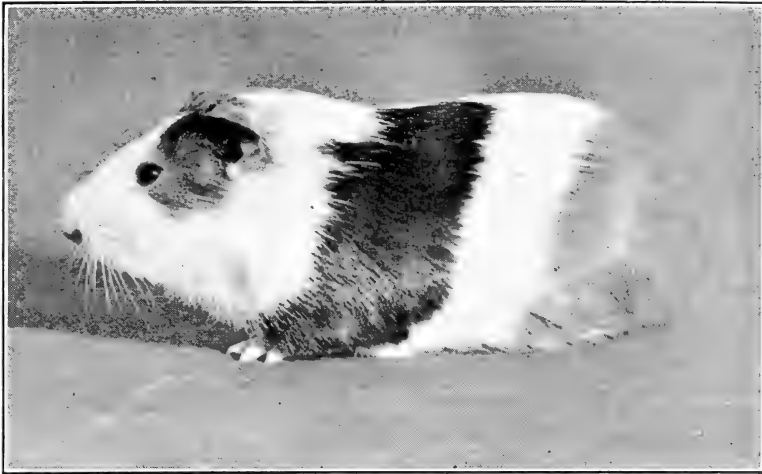
FIG. 1.—MALE OF FAMILY 2, BELONGING TO THE TWELFTH GENERATION
OF INBREEDING.

FIG. 2.—FEMALE OF FAMILY 2, FULL SISTER OF THE MALE SHOWN ABOVE.

This family is characterized by frequent but rather small litters, heavy mortality at birth but
great vitality and longevity thereafter. It is second in resistance to tuberculosis.

FIG. 1.—MALE OF FAMILY 13, BELONGING TO THE EIGHTEENTH GENERATION OF INBREEDING.
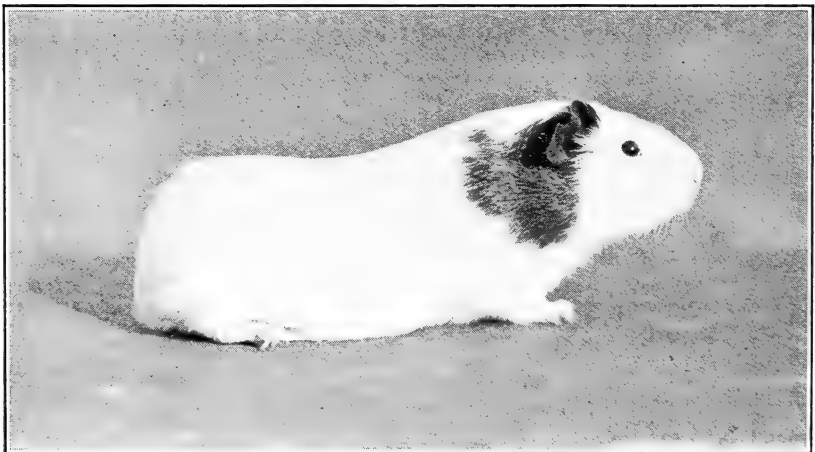
FIG. 2.—FEMALE OF FAMILY 13, FULL SISTER OF THE MALE SHOWN ABOVE.

The heaviest animals and the largest litters come in this family. It is above the average in most other respects but is next to the poorest in resistance to tuberculosis. The large amount of white is characteristic.

FIG. I.—MALE OF FAMILY 32, BELONGING TO THE SEVENTEENTH GENERATION
OF INBREEDING.
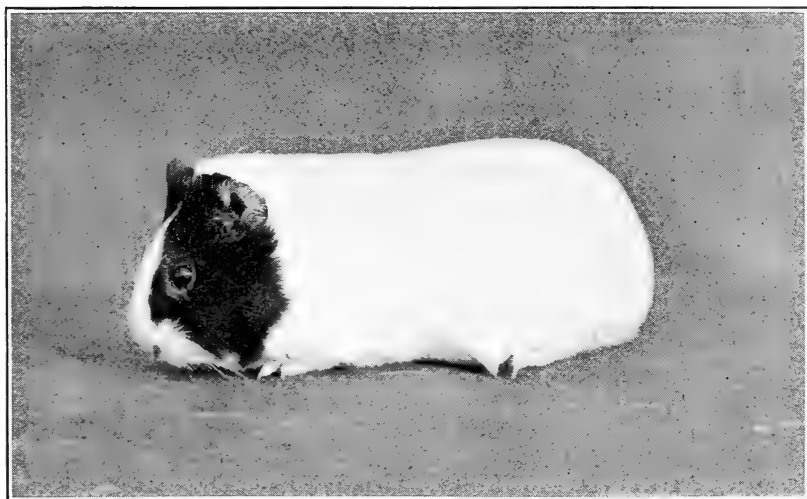
FIG. 2.—FEMALE OF FAMILY 32, FULL SISTER OF THE MALE SHOWN ABOVE.

This family is below the average in most respects. It contrasts with Family 13 in its light
average weight and small litters, but resembles that family in the large amount of white in
the coat and in its only very slightly greater resistance to tuberculosis.
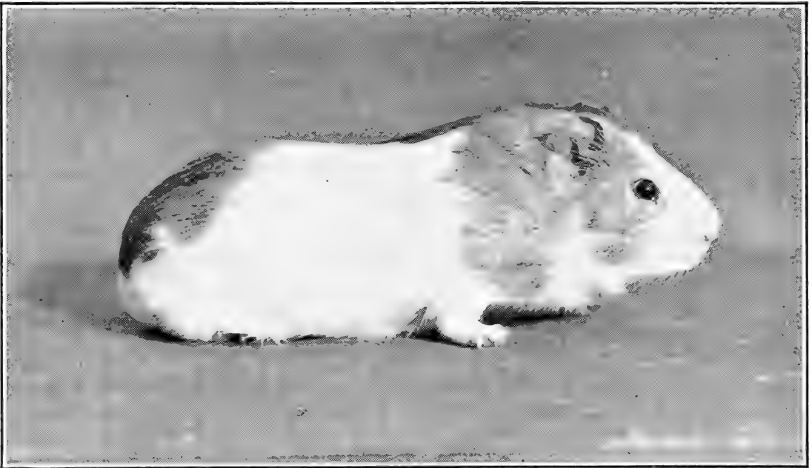
FIG. 1.—MALE OF FAMILY 35, BELONGING TO THE NINETEENTH GENERATION OF INBREEDING.
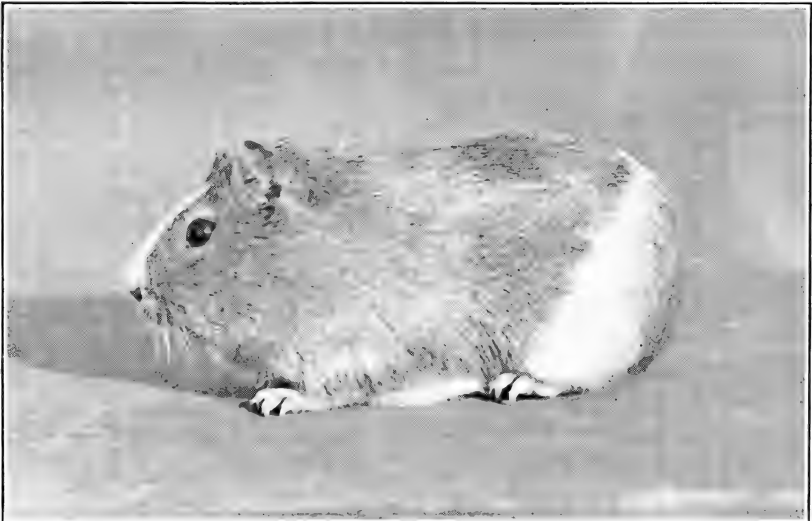
FIG. 2.—FEMALE OF FAMILY 35, FULL SISTER OF MALE SHOWN ABOVE. NOTE THE LARGE AMOUNT OF NONGENETIC VARIATION IN AMOUNT OF WHITE.

Inbreeding has gone further in this family than in any other, possibly because it is above the average in nearly all elements of vigor. It is much the most resistant to tuberculosis.
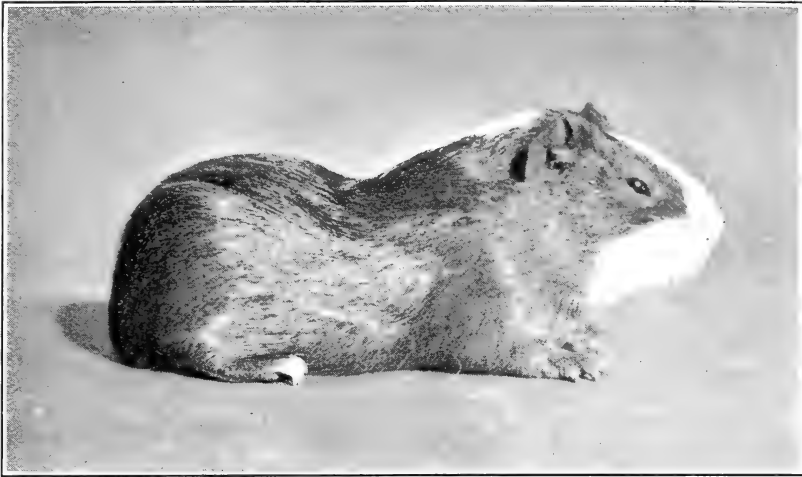
FIG. 1.—MALE OF FAMILY 39, BELONGING TO THE THIRTEENTH GENERATION OF INBREEDING.

FIG. 2.—FEMALE OF FAMILY 39, FULL SISTER OF THE MALE SHOWN ABOVE. THE SMALL AMOUNT OF WHITE AND THE SWAY BACK ARE CHARACTER-ISTICS FIXED IN THIS FAMILY.

Other characteristics are the greatest success in bearing young alive, but lack of success in rearing them, irregularity in producing litters, and the greatest susceptibility to tuberculosis.

PLATE VI.
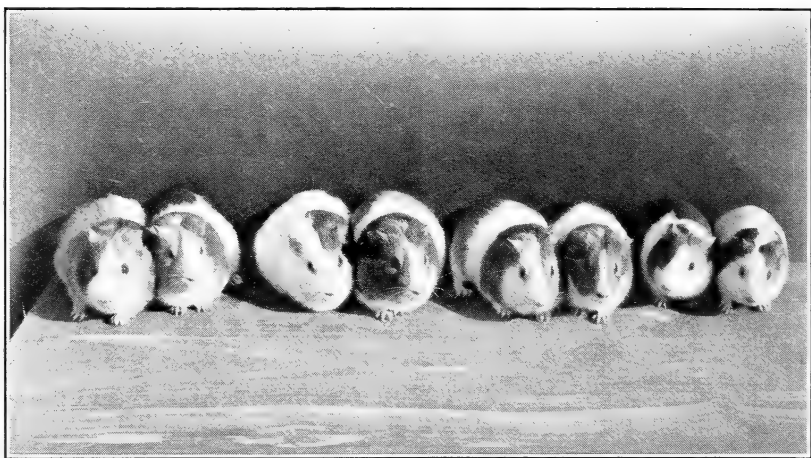
FOUR GENERATIONS OF FAMILY 35.

The young pair at the right is descended from 19 generations of matings of brother with sister. Their parents, grandparents, and great-grandparents were all found to be alive and are shown in the picture. There is little if any genetic variation left in this stock. The variation in pattern, which persists, seems to be due to nontransmissible irregularities in development.

shown above. Most of the variation within litters thus must be due to such a cause as position in the uterus.

Seasonal conditions have a marked effect on birth weight through their influence on the condition of the dam. The age of the dam is not an important factor.

The gain in weight between birth and 33 days is affected by the same factors which affect the prenatal rate of growth, namely, size of litter, condition of dam, and heredity.

The correlation between gain and size of litter in the same data as those used above was -0.381 ± 0.011. That between gain and interval was $+0.283 \pm 0.018$. There is naturally considerable correlation between birth weight and gain, the figure being $+0.533 \pm 0.009$. Heredity plays a larger part than in the case of birth weight, and the condition of the dam a smaller one. This was shown, as in the case of the percentages born dead and reared, by the relatively greater improvement in gain than in birth weight among the offspring of inbred dams when mated with unrelated males instead of with brothers.

Hereditary variation, however, is not of much importance within the control stock. The correlation between the mean gain of successive litters was $+0.221 \pm 0.026$, and that of litters which were not successive was $+0.062 \pm 0.016$. Common environmental factors may play a part in the former case as well as heredity.

Comparison of the gains made in different seasons and years demonstrate the importance of differences in environmental conditions in the present experiments.

The effect of size of litter on the early growth is soon lost. There is no correlation between size of litter and weight at a year among the inbreds ($r= +0.010 \pm 0.018$, in males; $r= -0.029 \pm 0.019$ in females). The common influence of heredity, however, is seen in the correlations of $+0.395 \pm 0.031$, $+0.375 \pm 0.024$, $+0.374 \pm 0.035$, and $+0.494 \pm 0.051$, between weight at birth and weight at a year in litters of 2 to 5 respectively among males. The correlations were smaller among females ($+0.339 \pm 0.032$, $+0.160 \pm 0.029$, $+0.187 \pm 0.041$, $+0.134 \pm 0.070$), owing, doubtless, to the greater unreliability of their weights at a year. It was shown in an earlier paper [2] that the correlation of $+0.375 \pm 0.024$ for males in litters of 3 was in part due to a correlation of $+0.630 \pm 0.083$ between average birth weight and average year weight among 24 inbred families (including Family 4) and in part to an average correlation of $+0.308 \pm 0.026$ between birth weight and year weight within a family. The value

[2] Wright, S. 1917. The average correlation within subgroups of a population. Proc. Wash. Acad. Sci. v. 7, p. 532–535.

for the correlation of family means is doubtless wholly due to the common factor, heredity of size. The correlation within families is probably due in part to genetic differentiation within the families and in part to environmental causes.

SEX RATIO.

Sex follows closely the laws of random sampling in guinea pigs. The sexes have been produced in nearly equal numbers in all experiments. Thus, in the tabulation of the controls born in 1906 to 1920 there were 2,051 males and 2,007 females. Among the inbreds born in the same years were 12,831 males and 12,529 females. Extensive tabulations have given no indications of any connection between sex ratio and size of litter or season or year of birth. In every other character considered, by far the highest records were obtained in the year 1910. The percentage of males in this year was 50. Again, if there were any important extraneous causes determining sex, litters exclusively of males and exclusively of females should be more numerous than expected by the laws of random sampling. The actual numbers, however, have been very close to those expected; (580 males and females were born in litters of 2 to 5 containing only one sex, during 1916 and 1917, where 590 was the expected number.) The only contrary indication was in an apparent differentiation of the inbred families with respect to sex ratio, which was somewhat greater than would be expected by random sampling.

INDEXES FOR GROWTH AND MORTALITY.

The purpose in going into the causes which affect the various characteristics of guinea pigs has been to bring out the precautions necessary in studying the effects of inbreeding and crossbreeding upon them.

Size of litter, for example, has such important effects on the rate of growth and the mortality among the young that it would be unfair to compare such characters as the average weight at 33 days and the percentage raised, in stocks with different average sizes of litter. It is, however, desirable to obtain a single figure to express the record of each experiment with respect to each character. Accordingly, indexes have been calculated for the weights and mortality percentages for each stock, based on a fixed number of litters of each size. The averages of litters of 1, 2, 3 and 4 have been assigned weights of 1, 3, 4, and 2, respectively, the resulting sum being divided by 10. An index in a given stock is thus the average which would be obtained if 100 guinea pigs were picked at random from litters of 1, 300 from litters of 2, 400 from litters of 3, and 200 from litters of 4. The different weights assigned to the different sizes of litter measure

roughly the relative reliability of the averages. The number of litters of each size produced by the inbred families between 1906 and 1915 was as follows:

Size of litter.	Number.	Size of litter.	Number.
1	1,187	5	387
2	2,230	6	100
3	2,253	7	19
4	1,111	8	2

Data for later years are discussed in more detail in Bulletin 1121. There was a considerable smaller average size of litter than in the preceding years, which made a different index desirable. In this bulletin the same index is used for 1916 to 1920 as in the earlier years.

In the above data we see that litters of 1, 2, 3, and 4 occurred approximately in the ratio of 1 : 2 : 2 : 1, while large litters were much less numerous. The young in these litters were in the ratio 1 : 4 : 6 : 4. Use of the latter ratio would give too much importance to the larger litters, because of the obvious tendency for litter mates to resemble each other in birth weight, rate of gain, and fate. On the other hand, averages based on a given number of litters of 4 are more reliable than ones based on the same number of litters of 1. In the case of birth weight it has been noted that variations within litters and variations among the means of litters of a given size are about equally important. It has accordingly seemed best to adopt a compromise between the ratio based on litters and the ratio based on individuals. The ratio 1 : 3 : 4 : 2 has thus been arrived at. Where two stocks differ consistently in all sizes of litters it makes little difference what ratio is used in calculating indexes. Where they do not differ consistently, no index is of much value.

ENVIRONMENTAL CONDITIONS.

Tabulations of the various characters among the inbred families were originally made according to generation. The results, however, were irregular. Family 2, for example, reached its highest point in size of litter in the fifth generation of inbreeding. The high point in Family 23 was a generation earlier. The variations in other characters tended to agree with those for size of litter in a given family. A study of the curves suggested that much of the variation was probably due to variations in conditions from year to year. In order to interpret the results with safety it is necessary to bring out as fully as possible all causes of change other than inbreeding. Thus tabulations were made with the year instead of the generation as a unit. As all inbreeding began in 1906 and the original matings produced no young after the spring of 1907, each year can safely be assumed to represent a higher average degree of inbreeding than the preceding year.

Table 2 gives the number of matings in each generation of each family near the end of 1915. The average number of brother-sister matings in the ancestry of the young from these matings was 11.4.

Sex has a slight influence on birth weight and slightly more influence on gain to weaning. These effects, however, are so small in comparison with those of other causes of variation, and the ratio of the sexes is so close to equality in all experiments, that it has not seemed necessary to make tabulations of these characteristics with the sexes separate. On the other hand, in studying the growth after weaning, separate averages must be made for the males and females. Similarly the influence of sex on the juvenile mortality can be neglected, although very important in dealing with the death rate of adults.

The age and previous record of the dam have been found to have slight effects on some of the characteristics studied, but so slight that they can safely be neglected in comparing different experiments with each other.

Summing up, size of litter and environmental conditions, together with sex, in the case of adult characteristics, are the only factors for which constant allowance must be made. Tabulations have thus been made separately for each size of litter and for each year. A method by which the averages for different sizes of litters are combined in a single index has been described.

CHANGES IN THE INBRED AND CONTROL STOCKS.

The averages for each character in each size of litter in the inbred and control experiments are given by years in Tables 6 to 22. The indexes for each year, calculated as described above, are also given. The results are presented graphically for the indexes in Figures 1 to 11.

Turning first to the indexes, we see that there are considerable fluctuations from year to year. These fluctuations are evidently significant, being based on quite large numbers. There is, moreover, not only a remarkable degree of parallelism between the fluctuations among the inbreds (A) and the controls (B) in most respects, but also a high degree of parallelism between the fluctuations of different characters. In the year 1910 all characters were at a maximum. There was a sharp drop in 1911, improvement in 1912, decline in 1913, and a marked improvement in 1914. There was a pronounced decline in 1915, continued to 1918, and followed by a rise in 1919. The only departure from parallelism that requires comment is the much greater decline in the mortality curves in 1916 and 1917 among the inbreds than in the control stock. The marked decline in 1916 was undoubtedly due to the severity of the winter of 1915–16 and a shortage of green feed in winter and early spring. The decline in the inbreds, however, is probably somewhat exaggerated, since the pens which they occupied were decreasing in number during 1916 and 1917
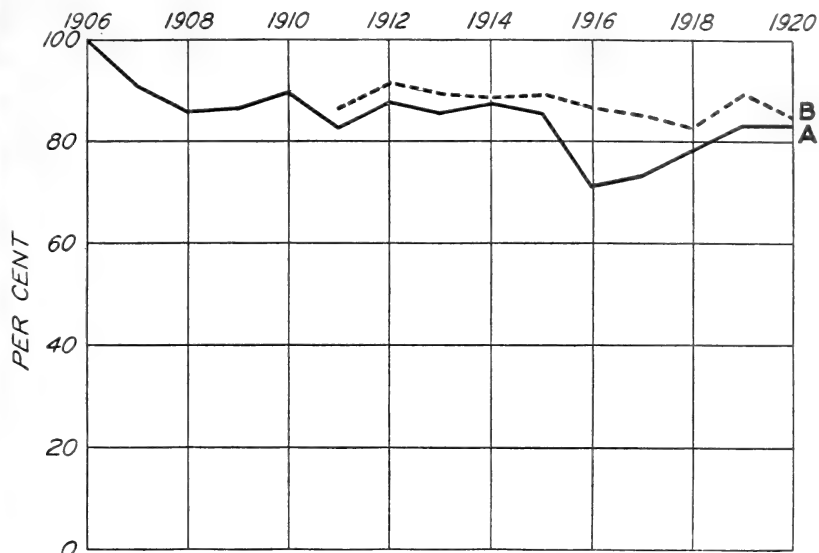
Fig. 1.—The percentage born alive among the inbreds (A) and controls (B) in successive years 1906 to 1920. Correction made for effect of size of litter by assigning weights of 1, 3, 4, and 2 to the averages for litters of 1, 2, 3, and 4, respectively.
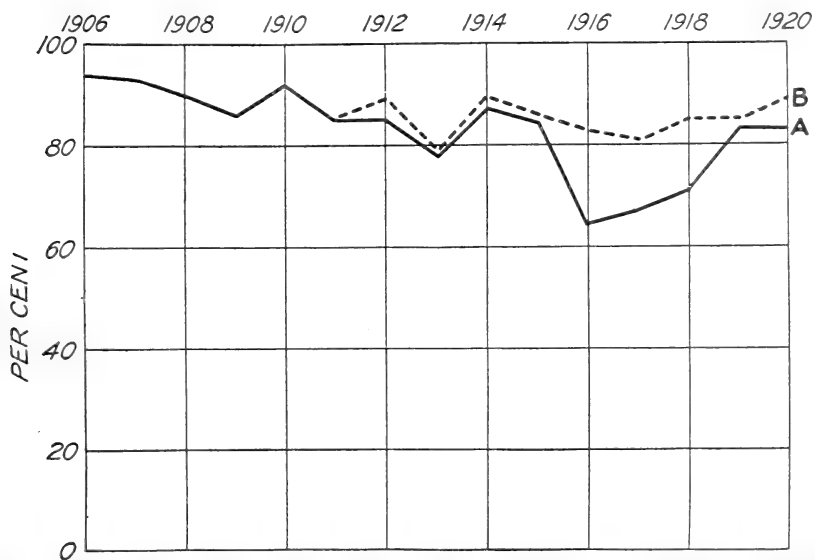
Fig. 2.—The percentage raised of those born alive. Inbreds (A) and controls (B), 1906 to 1920. Corrected for effect of size of litter as in Figure 1.

as room was made for other experiments. This meant that an unusually large percentage of the inbred young were born in both years in the winter and spring months, when conditions were unfavorable. Unfavorable conditions have a more immediate effect on the mortality among the young than on other characters. This explanation, however, is not wholly adequate to account for the disproportionate decline in the inbreds as compared with the controls in one set of characters only. It therefore seems probable that the inbreds had reached a critical stage, in which a given change for the worse in environmental conditions actually produced a disproportionately great effect on the mortality.
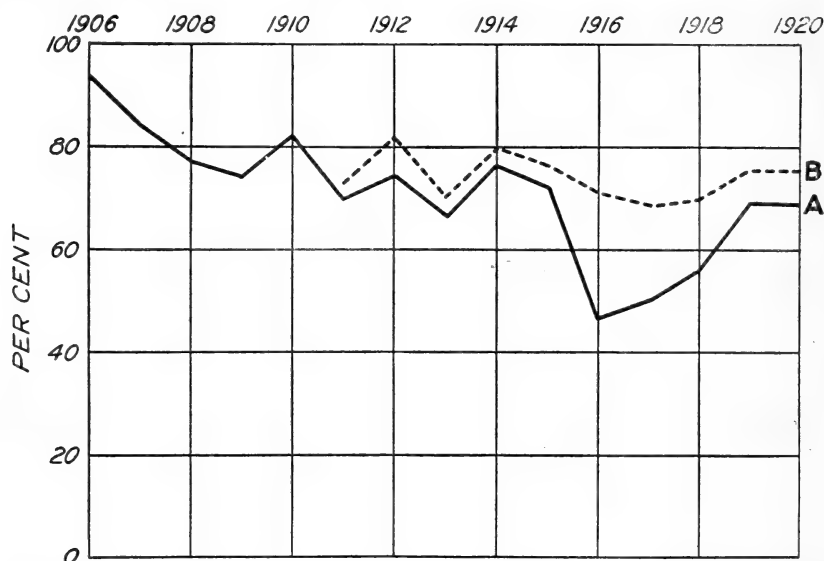
FIG. 3.—The percentage raised of all young born. Inbreds (*A*) and controls (*B*), 1906 to 1920. Corrected for effect of size of litter as in Figure 1.

Disregarding the fluctuations from year to year, a downward trend is apparent in all characters. The trend can be measured by fitting the best straight line to the graphs. This has been done by Pearson's method of moments for the characters given below, for the years from 1907 to 1915. It is, of course, recognized that a straight line would not be appropriate for changes in percentages over a very wide range. A uniform decrease in the ability to rear young would be represented by a curve starting from 100 per cent as an asymptote and falling away ever more rapidly for some distance. Fitting with a straight line, however, brings out the fact of a decline.

TABLE 4.—*Linear equations representing the trend in the inbred stock relative to each characteristic.*

(In these equations y is the measure of the character in question and x is the number of years from 1906.)

Size of litter	$y=\ \ \ 2.885-0.043x$
Litters per year	$y=\ \ \ 4.210-\ .110x$
Young per year	$y=\ 12.092-\ .450x$
Percentage born alive	$y=\ 88.27\ -\ .29x$
Percentage raised of those born alive	$y=\ 92.10\ -1.04x$
Percentage raised of all born	$y=\ 81.30\ -1.16x$
Birth weight of young raised (grams)	$y=\ 86.17\ -\ .19x$
Gain, 0 to 33 days (grams)	$y=163.70\ -1.96x$
Weight at 33 days (grams)	$y=249.87\ -2.15x$

Both elements in fertility, gain, and percentage raised of those born alive have shown considerable decline, while the birth weight and percentage born alive have shown very little decline, according to these figures.

A downward trend can of course be interpreted in two ways. It may be due in some way to the inbreeding, or it may be due in some way to progressively deteriorating environmental conditions. In regard to the latter hypothesis, arguments could be advanced on both sides. There are, however, certain considerations which show that some at least of the decline was genetic in character.

Consider first the inequalities in the decline in different characters. The record for 1914, after eight years of inbreeding, surpassed any preceding year except 1910 in gain, weight at 33 days, and birth weight. The records surpassed five earlier years in percentage born alive, and four earlier years in percentage of the latter which were raised and in total percentage raised. These points indicate that in 1914 environmental conditions were at least as good as in any earlier year, with the probable exception of 1910. Nevertheless the average size and frequency of litters in 1914 is markedly inferior to all years before 1911. Two inbred families had become extinct by 1914, but these two families (1 and 15) were the two lowest in fertility and their elimination should have resulted in genetic improvement of the average. Thus, whatever may have been the case with other characters, the conclusion seems unavoidable that fertility had suffered a real genetic decline after eight years of inbreeding.

A comparison between the inbreds and controls shows that in every respect the controls, born in a given year under identical conditions, were more vigorous than the inbreds. The difference is most marked in the case of size of litter, a result which agrees with the greater decline in size of litter than in other characters. It will be noted that the controls were taken from the same line-bred stock from which the inbred families were mainly derived. The most vigorous guinea pigs were selected in both cases. The inbred families (31 to 39)
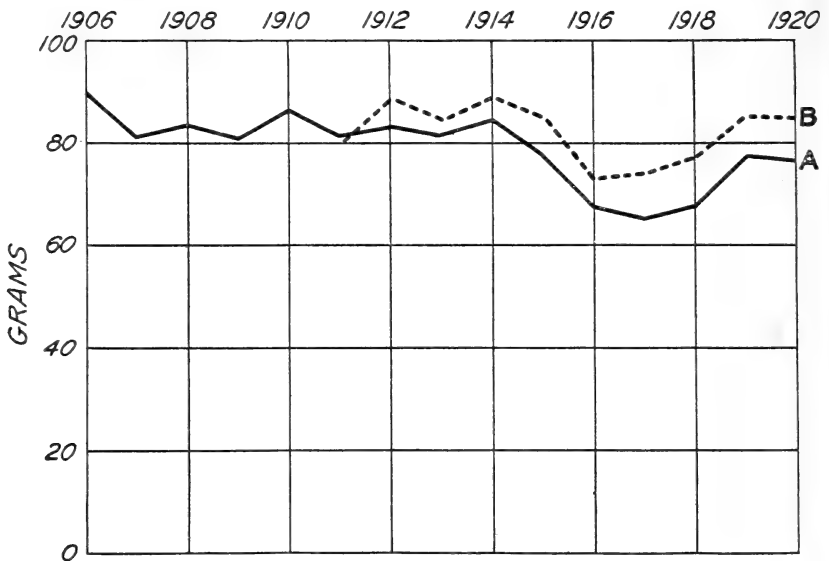
FIG. 4.—The average birth weight.   Inbreds (A) and controls (B), 1906 to 1920.   Corrected for effect of size of litter as in Figure 1.
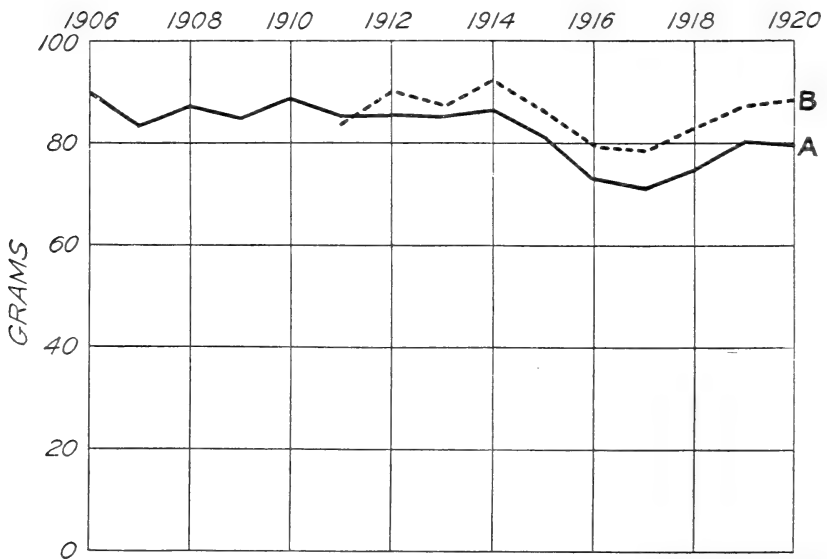
FIG. 5.—The average birth weight of young raised to 33 days.   Inbreds (A) and controls (B), 1906 to 1920. Corrected for effect of size of litter as in Figure 1.
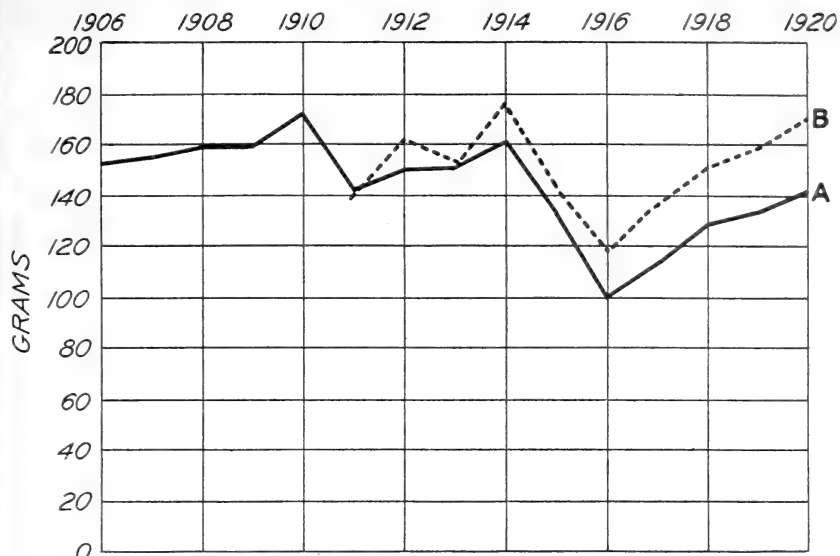
FIG. 6.—The average gain between birth and 33 days. Inbreds (*A*) and controls (*B*), 1906 to 1920. Corrected for effect of size of litter as in Figure 1.
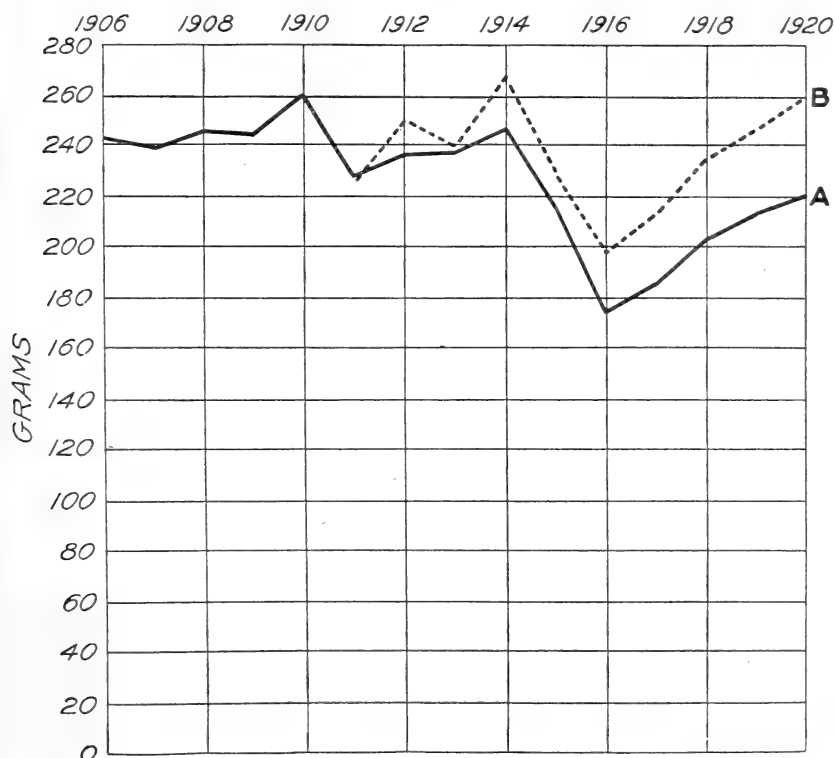
FIG. 7.—The average weight at 33 days. Inbreds (*A*) and controls (*B*), 1906 to 1920. Corrected for effect of size of litter as in Figure 1.

which were derived in part from another source were at least as vigorous as the others, as is shown in Part II. It would thus be a remarkable coincidence if the animals selected to found the control stock happened to have so much more hereditary vigor in every respect than those selected to found the inbred families, especially it will be shown later that vigor in one character is not correlated with vigor in others. It thus seems improbable to the writer that differences can be explained on the grounds of an initial genetic inferiority in the foundation stock of the inbred families.

Another possible explanation of the difference between inbreds and controls is in the greater average age at which the latter were mated. During 1916 and 1917 the differences in vigor were even more marked than previously. During these years the average age of inbred dams was 14.1 months and that of control dams 15.5 months. This difference is altogether too small, considering the slight effects of age in the various characters, to give the controls any appreciable advantage.

The average age of the inbreds at their first litter was 5.9 months. About two-thirds of the controls were immature when mated. Their average age was 5.2 months at the first litter. Most of the remaining control matings were between more or less immature guinea pigs. These considerations, therefore, merely indicate another character in which the controls were more vigorous than inbreds, namely, age of maturity.

The most probable interpretation of the differences between the inbreds and controls, is, therefore, that the inbreds started at about the same level of vigor in all respects as the controls, but declined in the course of time as a direct or indirect result of inbreeding. Here, however, the objection arises that the controls have also declined since 1911, and at almost the same rate as the inbreds. If this decline among the inbreds is genetic, so, it would seem, must be the decline among the controls, while if the latter is due to environmental conditions, so must be the former. The decline among the controls, however, was probably not genetic. It may be urged to the contrary that the rigid system of mating by pedigree prevented selection of animals for vigor as effectually as in the inbreeding experiments. This is true, but the characteristics with which we are concerned depend on heredity to such a slight extent that any selection of individuals should be wholly without appreciable effect, one way or the other, in the short time in which the experiment has been in progress. So far as we know at present, there seems to be no valid reason for assuming any genetic change in the control stock. This being the case, the decline since 1911 in both control and inbreds must be environmental. The excellent record made by both stocks in 1919 and 1920 confirms this view. We thus reach the seemingly paradoxical conclusions that the inbreds were falling off genetically from the
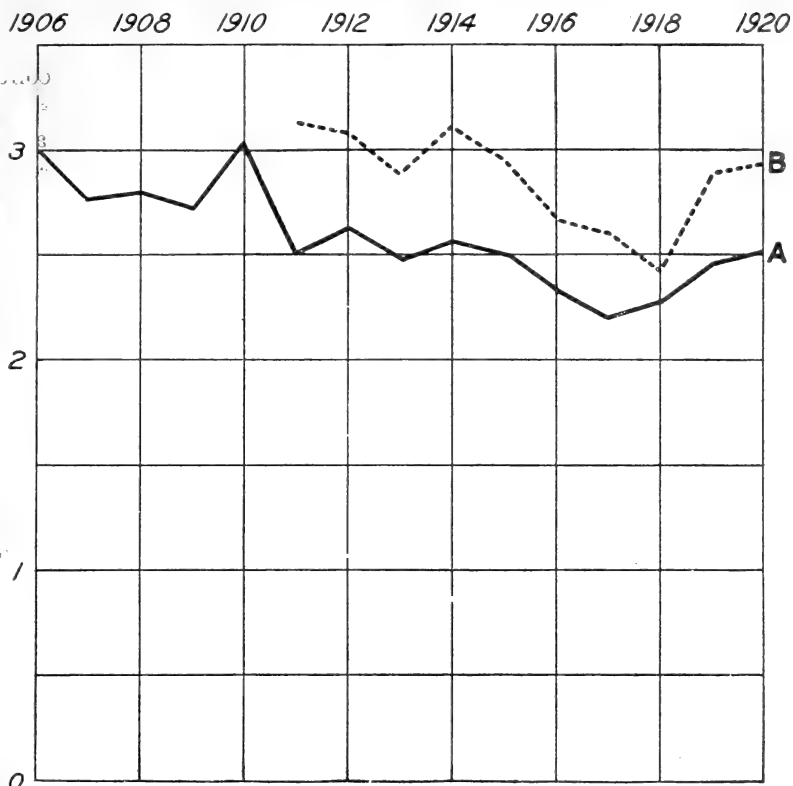
FIG. 8.—The average size of litter. Inbreds (A) and controls (B), 1906 to 1920.
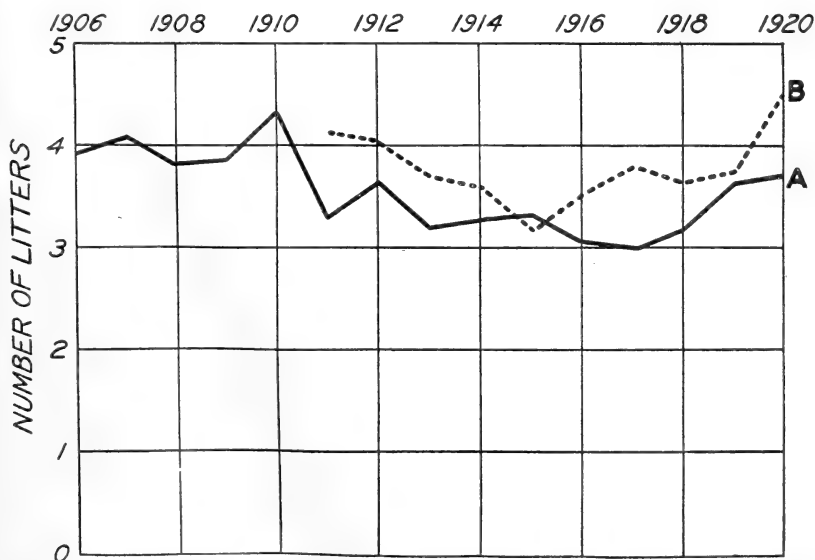
FIG. 9.—The average number of litters produced per year by mature matings. Inbreds (A) and controls (B), 1906 to 1920.

level of the normally bred stock in the years preceding 1911 in which their records show an actual rise, while they were holding their own genetically in the subsequent years in which their records show a marked decline. The situation brings out most strikingly the difficulty in drawing conclusions from results obtained in different years.

The figures which show the changes in the percentage of young raised in the different sizes of litter separately (Tables 8 and 17)
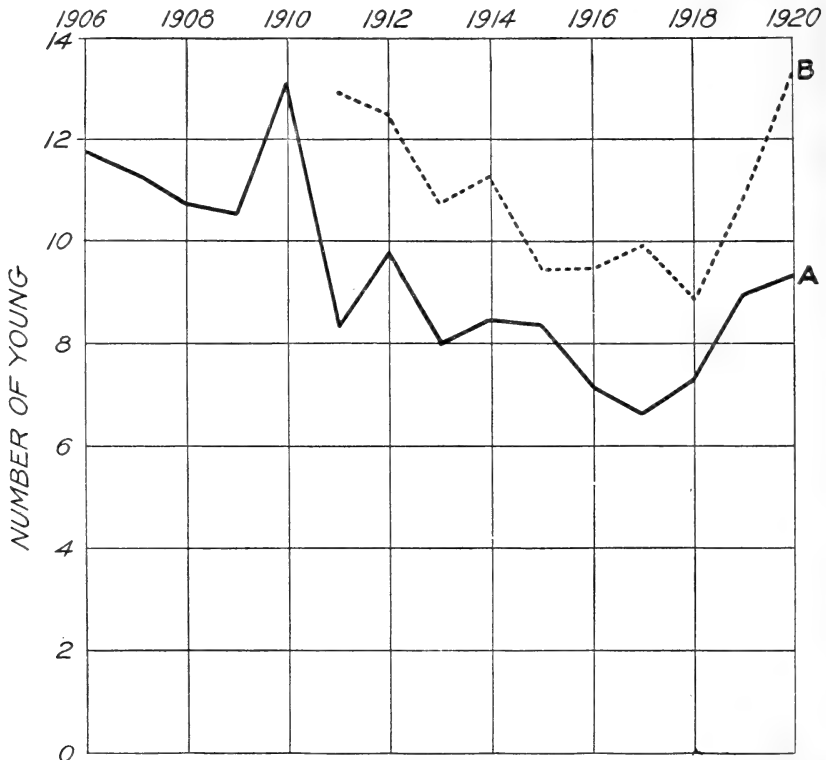
FIG. 10.—The average number of young produced per year by mature matings. Inbreds (*A*) and controls (*B*), 1906 to 1920.

bring out an interesting point, which was touched on earlier in this bulletin (page 15). It will be seen that there was not much difference in the percentages raised in litters of 1 to 5 in the early years. In litters of 1 and 2 there has not been much subsequent decline and the controls do not have much advantage over the inbreds. In litters of 3 the controls begin to show a distinct superiority, which increases in litters of 4 and 5, the decline among the inbreds becoming rapid. Thus it is in the ability to raise large litters that the inbreds show their deterioration most strikingly.

SEX RATIO.

Since the experiment began, there have been no changes in sex ratio which can be relied upon. The number of males per 100 females in different years is given in Table 22. The results are presented graphically in Figure 11. The most interesting point brought out by the figures is the small size of the fluctuations and the absence of any parallelism with those of the other characters. Evidently the favorable conditions of 1910 and 1914 and the unfavorable conditions of 1911, 1916, and 1917 are, like inbreeding itself, without effect on the sex ratio.
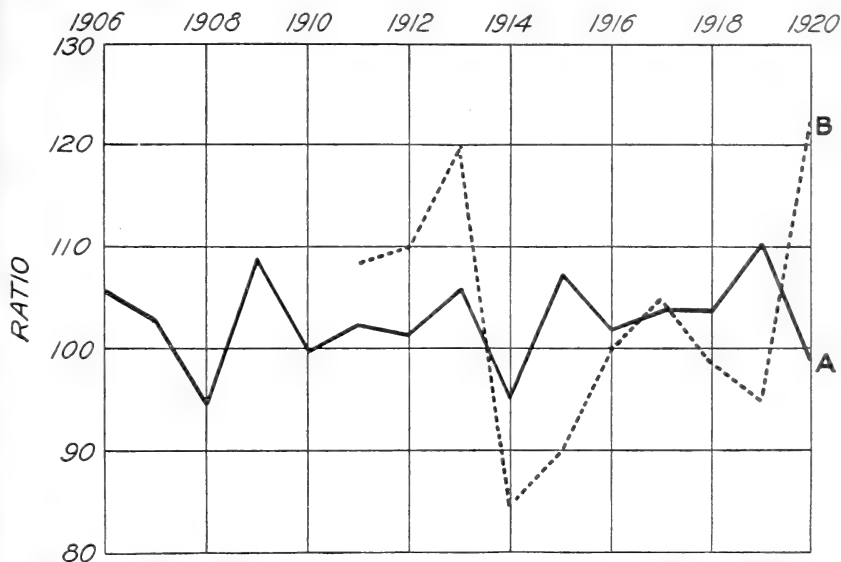
FIG. 11.—Sex ratio. Number of males per 100 females. Inbreds (A) and controls (B), 1906 to 1920.

TESTS FOR DISEASE RESISTANCE.

Tests were made in 1911 on the resistance of inbred and normal guinea pigs to tuberculosis. The methods used and their results are described, as follows, in a report by Dr. E. H. Riley:

The relative susceptibility to disease of inbred and normally bred guinea pigs was tested by inoculating inbred animals as principals and normally bred animals as checks with an equal quantity of material containing tubercle bacilli. This work was done in cooperation with Dr. E. C. Schroeder, Superintendent of the Bureau of Animal Industry Experiment Station, Bethesda, Md. The inoculations were made under his direction, and facilities were supplied by him for the housing and care of the animals during the progress of the disease. The results of the autopsies, which were made at the Experiment Station, for eight different tests are recorded in Table 5.

The principals used in the first two tests were inbred, brother and sister, for six generations, and were selected from the inbreeding experiment. The checks were not inbred, but were selected from the general stock of guinea pigs bred and reared at the experiment station. Aside from having been born and reared in different buildings, they were raised under practically the same conditions of feeding, care,

and management. At the time they were selected for these two tests there was no apparent difference in principals and checks. All were practically the same age and weight when they were inoculated. From two to four weeks before inoculation the animals which were to be inoculated were selected in groups of four, two principals and two checks, all of approximately the same weight, and placed in the cages which they were to occupy after inoculation. This was done so that they could become accustomed to being together and to the conditions of care, feed, and management which they were to receive after inoculation.

The guinea pigs which were used in the remaining six tests here reported were the progeny of selected stock, both the seventh generation inbred and the normally bred individuals. They were kept under exactly the same conditions from the time they were born until they died, so that results obtained from them may be attributed directly to the different methods by which they were bred. When the progeny of this selected stock were large enough—which was when they weighed between 400 and 500 grams—they were selected according to size and age and placed in pens, as indicated in the case of the first two tests, preparatory to inoculation. After inoculation with tubercle bacilli they were kept in the same cages until they died from tuberculosis, or for some other cause which was determined so far as possible by autopsy.

Table 5 shows the relative susceptibility to tuberculosis of normally bred and seventh-generation inbred guinea pigs. It will be seen that there were other causes of death than tuberculosis, the most frequent being pneumonia and inflammation of the bowels. A greater percentage of normally bred than inbred guinea pigs died of generalized tuberculosis. This is accounted for by the fact that a larger percentage of the inbred stock died of other diseases after inoculation, principally pneumonia and inflammation of the bowels. It is probable that their vitality had become diminished to such an extent through inbreeding that they easily succumbed to these diseases. In both tests there were instances where the lesions of tuberculosis were found on autopsy, but death was due to some other cause. The comparative resistance to tuberculosis will be apparent on noting the number of days of life after inoculation with tubercle bacilli. In each of the eight tests the number of days of life after inoculation was greater in the case of guinea pigs that were not inbred. The shortness of the time which the animals in some of the tests lived after inoculation was due to the extreme virulence of the organism used. Considering the average number of days of life after inoculation for each test, it will be noted that the inbred guinea pigs died 12.49 days sooner than the normally bred pigs.

TABLE 5.—*Relative susceptibility of inbred and normally bred guinea pigs to disease as determined by inoculation with tubercle bacilli.*

Test No.	Normally bred.						Inbred.					
	Cause of death.				Lesions of T. B. present, but not cause of death.	Average days of life after injection with tubercle bacilli.	Cause of death.				Lesions of T. B. present, but not cause of death.	Average days of life after injection with tubercle bacilli.
	Generalized tuberculosis.	Pneumonia.	Inflammation of bowels.	Other causes.			Generalized tuberculosis.	Pneumonia.	Inflammation of bowels.	Other causes.		
1.....	99	....	1	1	2	137. 2	79	....	4	10	6	116. 6
2.....	65	5	4	2	2	43. 6	51	6	11	7	1	42. 9
3.....	12	....	....	....	....	77. 2	12	....	....	1	1	74. 7
4.....	21	....	3	....	....	117. 0	25	....	2	....	2	108. 7
5.....	20	2	....	....	1	72. 4	21	....	1	....	1	48. 2
6.....	15	....	....	....	....	121. 3	15	....	....	....	....	104. 7
7.....	8	....	....	....	....	81. 8	8	1	....	....	....	68. 8
8.....	20	1	....	....	1	128. 5	22	3	....	1	4	117. 2
Total	260	8	8	3	6	....	233	10	18	19	15	....
P. ct .	91. 23	2. 81	2. 81	1. 05	2. 10	....	78. 98	3. 39	6. 10	6. 44	5. 09	....
Av...	....	....	....	....	....	101. 47	....	....	....	....	....	88. 98

The results of more recent tests of the resistance to tuberculosis of guinea pigs of the control stock and five of the inbred families have been discussed in a paper by the writer in collaboration with Dr. Paul A. Lewis.[3] In these tests the controls did not live so long on the average as the five inbred families used (2, 13, 32, 35, and 39). These inbred families, however, were markedly differentiated among themselves in resistance and probably do not represent the average of the entire inbred stock as well as did the inbreds of the earlier test, made at a time when most of the families were still on hand.

SUMMARY.

There has been an average decline in vigor in all characteristics during the course of 13 years of inbreeding of guinea pigs, brother with sister. The decline is most marked in the frequency and size of litter, in which it is so great that it would have to be accounted for even though the decline in other respects were assumed to be due wholly to a deterioration in the environmental conditions. The decline is greater in the gains after birth than in the birth weight, and greater in the percentage raised of the young born alive than in the percentage born alive. The ability to raise large litters has fallen off much more than ability to raise small litters.

A comparison of the inbred guinea pigs with a control stock, raised under identical conditions without inbreeding, and derived in the main from the same line-bred stock as the inbred families, indicates that the inbreds have suffered a genetic decline in vigor in all characteristics. The decline in fertility is again shown to be most marked. Experimental inoculation with tuberculosis has shown that the inbreds were inferior on the average to the controls in disease resistance. A study of sex ratio yields results in marked contrast to those obtained in connection with the other characters. There are no significant fluctuations from year to year, no contrast between inbreds and controls, and no indications of change due to inbreeding.

In addition to the points brought out in this bulletin which indicates genetic decline during inbreeding, extensive experiments have been made in which different inbred families have been crossed together. These are described in another paper (Bulletin No. 1121), in which it is shown that crossbred guinea pigs born of unrelated inbred parents are distinctly superior to their inbred relatives in nearly all elements of vigor. A slightly larger percentage are born alive, in small litters at least, and a distinctly larger percentage of those born alive are raised. The young are slightly heavier at birth in a given size of litter and gain much more between birth and wean-

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[3] Wright, S. and Lewis, P. A. 1921. Factors in the resistance of guinea pigs to tuberculosis with especial regard to inbreeding and heredity. Amer. Nat. v. 55, p. 20-50.

ing. They mature earlier, produce larger litters, and produce them more regularly than inbreds. Of the young which they produce a much larger percentage are born alive, especially in large litters, and even more of these are raised than in the first generation. Their young show a further increase in birth weight and in later gains.

Combining the results described in this and in Bulletin No. 1121, there seems no escape from the conclusion that a loss of vigor, especially in fertility, took place as a more or less direct consequence of close inbreeding. The question whether this is an inevitable result of inbreeding, or merely a likely one, as well as other phases of the subject, will be discussed after the presentation of further data.

APPENDIX.

TABLE 6.—*Data on the fertility of the inbred stock by years, 1906 to 1920.*

| Year. | Size of litter. | | | | | | | | Mat-ings. | Num-ber of litters. | Num-ber of young. | Aver-age size of litter. | Litters per year. | Young per year. |
	1	2	3	4	5	6	7	8						
1906	1	4	13	6	.....	.....	.....	.....	6.1	24	72	3.00	3.93	11.80
1907	31	77	79	39	13	6	.....	.....	59.9	245	679	2.77	4.09	11.33
1908	92	173	177	94	46	14	2	.....	155.6	598	1,673	2.80	3.84	10.75
1909	138	308	275	153	54	15	2	1	244.3	946	2,573	2.72	3.87	10.53
1910	145	302	410	254	131	26	7	1	293.4	1,276	3,863	3.03	4.35	13.17
1911	184	303	293	120	32	6	2	.....	284.7	940	2,359	2.51	3.30	8.29
1912	135	271	276	119	39	11	2	.....	231.7	853	2,256	2.64	3.68	9.73
1913	168	274	234	108	27	5	4	.....	256.4	820	2,043	2.49	3.20	7.97
1914	132	234	208	105	25	11	.....	.....	217.2	715	1,835	2.57	3.29	8.45
1915	161	284	288	113	20	6	.....	.....	260.8	872	2,181	2.50	3.34	8.36
1916	164	300	228	70	18	1	.....	.....	254.4	781	1,824	2.34	3.07	7.17
1917	103	196	127	32	1	1	.....	.....	153.5	460	1,015	2.21	3.00	6.61
1918	64	126	89	27	3	.....	.....	.....	96.8	309	706	2.28	3.19	7.29
1919	83	144	136	55	11	2	.....	.....	118.9	431	1,066	2.47	3.63	8.97
1920	87	208	188	67	16	2	.....	.....	152.9	568	1,427	2.51	3.71	9.33

TABLE 7.—*The percentage born alive. Inbred stock by years, 1906 to 1920.*

[The average in litters of each size and an index, litters of 1, 2, 3, and 4 weighted 1, 3, 4, and 2, respectively.]

| Year. | Size of litter. | | | | | | In-dex. | Year. | Size of litter. | | | | | | In-dex. |
	1	2	3	4	5	6			1	2	3	4	5	6	
1906	100.0	100.0	100.0	100.0	.....	.....	100.0	1914	81.1	91.2	89.6	82.4	67.2	77.3	87.8
1907	87.1	90.3	91.6	90.4	89.1	61.1	90.5	1915	86.3	90.0	85.2	79.2	64.0	22.2	85.6
1908	85.9	86.1	86.8	84.3	81.7	69.0	86.0	1916	79.9	80.3	73.8	51.1	37.8	100.0	71.8
1909	89.1	89.0	86.7	80.6	79.3	73.3	86.4	1917	83.5	81.4	72.4	60.2	40.0	0.0	73.8
1910	85.5	90.9	91.6	85.2	79.7	71.2	89.5	1918	82.8	85.3	76.0	71.3	46.7	.....	78.5
1911	77.2	84.7	86.2	74.6	53.8	63.9	82.5	1919	67.5	88.9	89.0	70.4	50.9	.....	83.1
1912	83.7	91.3	86.0	86.6	65.1	51.5	87.5	1920	82.8	89.9	82.8	72.4	77.5	41.7	82.9
1913	80.4	85.9	90.8	78.5	78.5	63.3	85.8								

TABLE 8.—*The percentage raised to 33 days of the young born alive. Inbred stock by years, 1906 to 1920.*

[The average in litters of each size and the index is in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1906	100.0	100.0	97.4	75.0	......	......	94.0	1914	85.0	91.3	89.3	79.2	81.0	68.6	87.5
1907	96.3	94.2	92.6	90.8	87.9	90.9	93.1	1915	84.2	87.5	85.2	80.2	56.2	62.5	84.8
1908	89.9	89.6	90.4	89.6	88.3	86.2	90.0	1916	67.2	72.0	60.6	58.0	38.2	0.0	64.2
1909	84.6	84.8	86.7	87.8	89.2	65.2	86.1	1917	80.2	74.6	63.4	57.1	100.0	......	67.2
1910	91.1	93.1	92.6	89.5	82.2	77.5	92.0	1918	86.8	75.8	68.5	61.0	57.1	......	71.0
1911	83.1	86.4	88.0	77.1	80.2	56.5	84.9	1919	89.3	89.4	84.8	69.0	50.0	......	83.5
1912	85.8	86.5	86.6	82.3	66.1	73.5	85.6	1920	80.6	88.0	84.6	74.7	64.5	100.0	83.2
1913	80.0	81.3	75.4	77.3	75.5	57.9	78.0								

TABLE 9.—*The percentage raised to 33 days of all young born. Inbred stock by years, 1906 to 1920.*

[The average in litters of each size and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1906	100.0	100.0	97.4	75.0	......	......	94.0	1914	68.9	83.3	80.0	65.2	54.4	53.0	76.9
1907	83.9	85.1	84.8	82.0	78.5	55.6	84.2	1915	72.7	78.7	72.6	63.5	36.0	13.9	72.6
1908	77.2	77.2	78.5	75.5	72.2	59.5	77.4	1916	53.7	57.8	44.7	29.6	14.4	0.0	46.5
1909	75.4	75.5	75.2	70.8	70.7	47.8	74.4	1917	67.0	60.7	45.9	34.4	40.0	0.0	50.2
1910	77.9	84.6	84.8	76.3	65.5	55.1	82.3	1918	71.9	64.7	52.1	43.5	26.7	......	56.1
1911	64.1	73.1	75.9	57.5	43.1	36.1	70.1	1919	60.2	79.5	75.5	48.6	25.4	......	69.8
1912	71.8	79.0	74.5	71.2	43.1	37.9	74.9	1920	66.7	79.1	70.0	54.1	50.0	41.7	69.2
1913	64.3	69.9	68.4	60.6	59.2	36.7	66.9								

TABLE 10.—*The average birth weight in grams. Inbred stock by years, 1906 to 1920.*

[The average in litters of each size and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1906	104.5	110.7	81.2	67.4	......	......	89.6	1914	106.5	93.0	80.2	69.3	62.3	57.8	84.5
1907	100.3	89.5	77.1	67.6	61.8	54.1	81.2	1915	97.4	87.4	72.9	63.8	53.5	52.8	77.9
1908	107.4	90.1	78.8	72.0	64.4	58.0	83.7	1916	89.9	75.8	63.9	52.7	46.9	......	67.8
1909	102.4	87.6	76.2	68.6	65.8	55.2	80.7	1917	90.8	72.6	60.9	49.6	54.5	......	65.1
1910	110.9	95.5	81.6	72.3	63.8	60.1	86.8	1918	93.1	75.3	63.3	53.4	53.1	......	67.9
1911	102.7	89.8	76.7	67.3	60.4	54.8	81.4	1919	101.8	87.1	73.1	61.0	50.5	39.5	77.8
1912	102.2	92.7	78.6	69.4	61.6	56.4	83.4	1920	102.4	86.0	70.4	62.5	54.5	48.7	76.7
1913	103.8	89.2	78.3	67.1	62.4	50.6	81.9								

TABLE 11.—*The average birth weight in grams of young raised to 33 days.* **Inbred stock by years, 1906 to 1920.**

[The average in litters of each size and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1906	104.5	110.7	81.1	70.6	......	......	90.2	1914	109.9	94.2	82.0	71.9	67.4	61.6	86.4
1907	101.8	91.8	78.8	69.0	64.3	58.5	83.0	1915	105.3	89.3	76.0	67.1	61.2	60.5	81.1
1908	112.2	92.9	82.2	75.1	67.2	62.9	87.0	1916	99.4	81.5	68.2	59.6	58.3	47.8	73.6
1909	107.5	91.3	80.6	72.6	68.0	58.9	84.9	1917	98.3	77.7	67.0	56.1	59.5	......	71.2
1910	113.0	97.4	83.1	74.2	67.5	63.7	88.6	1918	99.5	81.4	70.3	61.9	79.5	......	74.9
1911	107.4	93.2	79.7	71.9	66.8	58.3	85.0	1919	108.3	87.9	74.7	66.1	60.9	......	80.3
1912	108.1	94.2	81.0	71.7	67.0	64.1	85.8	1920	105.4	87.4	73.5	66.4	60.7	56.5	79.4
1913	109.6	92.4	81.2	70.8	65.9	60.9	85.3								

TABLE 12.—*The average gain in grams between birth and 33 days.* **Inbred stock by years, 1906 to 1920.**

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1906	225.0	161.3	152.6	103.3	......	......	152.6	1914	191.0	174.5	155.6	136.4	124.5	111.3	161.0
1907	185.4	166.7	152.3	130.2	116.2	147.0	155.6	1915	163.5	152.9	126.5	102.3	111.1	137.0	133.3
1908	197.3	165.4	151.9	143.8	127.1	113.8	158.9	1916	143.2	114.7	89.9	77.6	76.7	......	100.2
1909	179.5	170.6	153.5	142.8	140.0	121.8	159.1	1917	141.1	123.8	110.8	94.3	140.0	......	114.4
1910	199.2	186.9	165.4	149.9	134.9	129.5	172.1	1918	139.5	134.3	124.4	121.2	130.0	......	128.2
1911	168.5	157.1	133.0	128.3	121.6	112.7	142.8	1919	164.8	143.6	126.0	115.4	112.9	......	133.0
1912	175.8	166.7	145.5	124.1	125.1	107.0	150.6	1920	163.4	155.9	133.6	124.5	129.3	129.0	141.5
1913	182.1	156.3	148.1	137.2	136.6	165.0	151.8								

TABLE 13.—*The average weight in grams at 33 days.* **Inbred stock by years, 1906 to 1920.**

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1906..	329.5	272.0	233.7	173.9	......	......	242.8	1914..	300.9	268.7	237.6	208.3	191.9	172.9	247.4
1907..	287.2	258.5	231.1	199.2	180.5	205.5	238.6	1915..	268.8	242.2	202.5	169.4	172.3	197.5	214.4
1908..	309.5	258.3	234.1	218.9	194.3	176.7	245.9	1916..	242.6	196.2	158.1	137.2	134.1	......	173.8
1909..	287.0	261.9	234.1	215.4	208.0	180.7	244.0	1917..	239.4	201.5	177.8	150.4	199.5	......	185.6
1910..	312.2	284.3	248.5	224.1	202.4	193.2	260.7	1918..	239.0	215.7	194.7	183.1	209.5	......	203.1
1911..	275.9	250.3	212.7	200.2	188.4	171.0	227.8	1919..	273.1	231.5	200.7	181.5	173.8	......	213.3
1912..	283.9	260.9	226.5	195.8	192.1	171.1	236.4	1920..	268.8	243.3	207.1	190.9	190.0	185.5	220.9
1913..	291.7	248.7	229.3	208.0	202.5	225.9	237.1								

TABLE 14.—*Data on the fertility of the control stock (B) by years, 1911 to 1920.*

Year.	Size of litter.									Mat-ings.	Num-ber of litters.	Num-ber of young.	Average size of litter.	Litters per year.	Young per year.
	1	2	3	4	5	6	7	8	9						
1911..	6	20	41	16	9	2	0	1	0	23.0	95	298	3.14	4.13	12.96
1912..	11	31	35	16	7	6	2	0	1	26.9	109	336	3.08	4.05	12.49
1913..	16	37	66	17	9	5	1	0	0	40.7	151	438	2.90	3.71	10.76
1914..	17	51	55	42	18	8	1	0	0	53.0	192	597	3.11	3.62	11.26
1915..	19	31	40	31	13	2	0	0	0	42.5	136	402	2.96	3.21	9.46
1916..	20	56	64	21	7	2	0	0	0	48.0	170	455	2.68	3.54	9.48
1917..	22	51	59	24	2	0	1	0	0	41.8	159	414	2.60	3.81	9.90
1918..	28	50	43	17	1	1	0	0	0	35.6	130	316	2.43	3.65	8.88
1919..	11	41	46	16	11	4	0	0	0	34.3	129	374	2.90	3.76	10.90
1920..	23	35	50	34	11	4	1	0	0	34.7	158	465	2.94	4.55	13.44

TABLE 15.—*The percentage born alive. Control stock by years, 1911 to 1920.*

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1911..	100.0	87.5	81.3	87.5	86.7	91.7	86.3	1916..	90.0	92.0	88.5	73.8	80.0	16.7	86.8
1912..	81.8	90.3	92.4	96.9	91.4	77.8	91.6	1917..	72.7	91.2	84.2	84.4	90.0	......	85.2
1913..	87.5	87.8	92.9	86.8	88.9	63.3	89.6	1918..	85.7	87.5	79.8	79.4	40.0	......	82.6
1914..	82.3	86.3	93.3	86.9	85.6	81.2	88.8	1919..	90.9	92.7	87.7	87.5	83.6	83.3	89.5
1915..	73.7	87.1	92.5	92.8	84.6	50.0	89.1	1920..	78.3	88.6	84.7	81.6	85.4	70.8	84.6

TABLE 16.—*The percentage raised to 33 days of the young born alive. Control stock by years, 1911 to 1920.*

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1911..	66.7	91.4	92.0	75.0	87.2	72.7	85.9	1916..	83.3	86.4	82.4	77.4	42.9	100.0	82.7
1912..	88.9	92.8	89.7	83.9	100.0	82.2	89.4	1917..	87.5	86.0	78.5	75.3	77.8	......	81.0
1913..	85.7	81.5	85.3	57.6	75.0	68.4	78.7	1918..	87.5	84.3	84.5	85.2	......	......	84.9
1914..	85.7	94.3	90.9	84.2	93.5	79.5	90.0	1919..	70.0	88.2	86.8	83.9	82.6	45.0	85.0
1915..	64.3	87.0	89.2	88.7	78.2	66.7	86.0	1920..	88.9	93.5	91.3	80.2	66.0	52.9	89.5

TABLE 17.—*The percentage raised to 33 days of all young born. Control stock by years, 1911 to 1920.*

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1911..	66.7	80.0	74.8	65.6	75.6	66.7	73.7	1916..	75.0	79.5	72.9	57.1	34.3	16.7	71.8
1912..	72.7	83.9	82.9	81.2	91.4	63.9	81.9	1917..	63.6	78.4	66.1	63.5	70.0	......	69.0
1913..	75.0	71.6	79.3	50.0	66.7	43.3	70.5	1918..	75.0	73.7	67.4	67.6	0.0	......	70.1
1914..	70.6	81.4	84.8	73.2	80.0	64.6	79.9	1919..	63.6	81.7	76.1	73.4	69.1	37.5	76.0
1915..	47.4	75.8	82.5	82.2	66.2	33.3	76.6	1920..	69.6	82.9	77.3	65.4	56.4	37.5	75.8

TABLE 18.—*The average birth weight in grams. Control stock by years, 1911 to 1920.*

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1911..	92.8	89.8	77.1	64.8	64.3	57.8	80.0	1916..	89.2	85.0	70.1	56.8	48.6	50.3	73.8
1912..	115.4	94.8	85.9	72.9	67.0	60.0	88.9	1917..	99.5	83.4	69.5	57.8	62.5	......	74.3
1913..	110.2	90.6	81.1	70.2	60.5	53.5	84.7	1918..	109.5	85.6	68.2	65.8	48.3	47.8	77.1
1914..	105.1	101.1	83.6	73.6	69.3	58.9	89.0	1919..	105.4	95.3	80.5	69.5	62.2	58.7	85.2
1915..	98.2	94.2	83.4	68.7	61.3	47.0	85.2	1920..	118.0	90.4	80.8	69.2	59.2	45.8	85.1

TABLE 19.—*The average birth weight in grams of young raised to 33 days.   Control stock by years, 1911 to 1920.*

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1911..	99.5	93.6	80.2	69.3	65.1	62.0	84.0	1916..	108.5	88.7	73.1	64.5	53.7	59.5	79.6
1912..	110.7	96.2	88.5	73.7	67.9	63.6	90.1	1917..	105.2	86.8	73.0	63.5	64.5	......	78.5
1913..	111.2	96.6	83.0	70.1	64.2	63.0	87.3	1918..	117.4	91.3	73.8	71.9	......	......	83.0
1914..	117.8	103.7	85.5	77.8	72.7	63.2	92.7	1919..	113.1	97.9	80.9	72.2	65.6	60.1	87.5
1915..	100.1	95.1	84.5	69.8	64.5	59.5	86.3	1920..	118.9	95.9	83.4	72.1	63.2	51.2	88.4

TABLE 20.—*The average gain between birth and 33 days, in grams.   Control stock by years, 1911 to 1920.*

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1911..	195.0	141.5	136.7	127.8	92.6	120.0	142.2	1916..	173.0	137.2	102.0	96.6	102.5	130.0	118.6
1912..	168.8	178.3	164.4	120.4	139.7	112.9	160.2	1917..	170.0	152.7	129.8	98.1	90.7	......	134.3
1913..	190.0	175.5	135.9	128.8	109.3	103.4	151.8	1918..	193.0	168.7	135.0	139.8	......	......	151.9
1914..	198.4	201.5	167.9	143.2	114.0	130.8	176.0	1919..	185.0	180.6	147.8	133.5	112.8	113.8	158.5
1915..	160.5	171.0	131.1	114.4	94.8	95.0	142.7	1920..	218.1	182.2	161.3	147.1	123.7	120.5	170.4

TABLE 21.—*The average weight at 33 days, in grams.   Control stock by years, 1911 to 1920.*

[The average in each size of litter and the index, as in Table 7.]

Year.	Size of litter.						In-dex.	Year.	Size of litter.						In-dex.
	1	2	3	4	5	6			1	2	3	4	5	6	
1911..	294.5	235.1	216.9	197.1	157.7	182.0	226.2	1916..	281.5	225.9	175.1	161.1	156.2	189.5	198.2
1912..	279.5	274.5	252.9	194.1	207.6	176.5	250.3	1917..	275.2	239.5	202.8	161.6	155.2	......	212.8
1913..	301.2	272.1	218.9	198.9	173.5	166.4	239.1	1918..	310.4	260.0	208.8	211.7	......	......	234.9
1914..	316.2	305.2	253.4	221.0	186.7	194.0	268.7	1919..	298.1	278.5	228.7	205.7	178.4	173.9	246.0
1915..	260.6	266.1	215.6	184.2	159.3	154.5	229.0	1920..	337.0	278.1	244.7	219.2	186.9	171.7	258.9

TABLE 22.—*The number of males and females and the sex ratio (males per 100 females).*

[Inbred and control stocks by years, 1906 to 1920.]

Year.	Inbred stock.			Control stock.			Year.	Inbred stock.			Control stock.		
	Males.	Females.	Males per 100 females.	Males.	Females.	Males per 100 females.		Males.	Females.	Males per 100 females.	Males.	Females.	Males per 100 females.
1906........	37	35	105.7	......	......	......	1015........	1,129	1,051	107.4	191	211	90.5
1907........	343	333	103.0	......	......	......	1916........	894	879	101.7	223	223	100.0
1908........	806	855	94.3	......	......	......	1917........	498	480	103.8	209	199	105.0
1909........	1,335	1,223	109.2	......	......	......	1918........	341	329	103.6	151	153	98.7
1910........	1,919	1,922	99.8	......	......	......	1919........	556	504	110.3	178	187	95.2
1911........	1,188	1,158	102.6	155	143	108.5	1920........	704	711	99.0	255	209	122.0
1912........	1,135	1,119	101.4	176	160	110.0							
1913........	1,051	991	106.0	239	199	120.1	Total....	12,831	12,529	102.4	2,051	2,007	102.2
1914........	895	939	95.3	274	323	84.8							

II. DIFFERENTIATION AMONG INBRED FAMILIES.

The first part of this bulletin gives a description of an inbreeding experiment with guinea pigs begun in 1906 by the Bureau of Animal Industry. An account is given of the origin of 23 families, descended from 23 females and 9 males by matings exclusively of brother with sister. It is shown that the inbred stock as a whole suffered a decline in vigor in all characteristics studied, but most markedly in fertility. This decline was not, however, a rapid one, the relatively high vigor after more than a dozen generations of the closest inbreeding being, perhaps, as noteworthy a result as the fact of a slow average decline. In this part of the bulletin the different families will be considered separately, in order to determine how far differentiation has taken place among them and how far inbreeding has affected them alike.

DIFFERENTIATION IN COLOR.

A differentiation among the families in color has been obvious. The original stock contained both intense and dilute agoutis, blacks with red, yellow or cream spotting, reds, and albinos. All grades of the piebald and tortoise-shell patterns were found. Each of the families produced a variety of colors in the early generations. As time went on, however, different colors automatically became fixed in different lines, and as the families became more homogeneous through the elimination of early branches from the main line of descent most of them came to be characterized by a particular color. The mode of inheritance of the main color varieties is thoroughly understood, and as their automatic fixation through inbreeding is a well-known consequence of their mode of inheritance, it will not be necessary to go into the rather complex details.

Of greater interest is the fixation of those color variations and patterns whose heredity has not yet been analyzed as Mendelian and which appear to follow a blending mode of inheritance. Among these characters are the minor variations in intensity of color, and the minor variations in the extent and localization of the piebald and tortoise-shell patterns. Among the minor differences in intensity come interesting contrasts between Families 38 and 32 and between Families 18 and 35. All four of these families have red or yellow spotting. The red in Family 32 is always a remarkably intense mahogany color, like that of no other guinea pigs which the writer has seen. Family 38 has pale red or yellow, impossible to confound with the red of Family 32, but rather similar to the pale red or yellow of Family 18. The young of Family 18 are usually classified as light red when born, appearing slightly more intense than the young in Family 38, but changing to a typical yellow when older. Family 35 shows a typical yellow at all ages. When these 4 families are crossed

with albinos ($c^a c^a$), it at once becomes apparent that Families 32 and 38 alike have the intensity factor (C), the crossbred young (Cc^a) showing a red spotting which is less intense than that of Family 32 but more intense than in Family 38. Families 18 and 35, on the other hand, are proved unmistakably to possess an intermediate factor in the albino series (c^k) the young in both cases having the cream-colored spots typical of heterozygous dilutes ($c^k c^a$).

In quantity of white spotting, the families have also become markedly differentiated from each other. At one extreme are Families 38 and 39 with only about 20 per cent white on the average, and at the other are Families 13 and 31, with about 90 per cent of white. The remaining families are scattered between these limits. Similarly, grades of yellow spotting have also become fixed. This subject will be treated in detail in another paper. Here it is enough to note that the 23 families, most of them descended from the same line-bred stock and the rest of them half descended from it, have automatically become so differentiated from each other in kind of color, in intensity of color, and in pattern that a new litter could usually be recognized at a glance as belonging to its particular family.

ABNORMALITIES.

Another kind of variation in which differentiation among the families is clearly shown is polydactylism. Guinea pigs normally have only three toes on the hind feet. It is not uncommon, however, to find a vestigial fourth toe hanging loosely beside the others. Castle [4] has shown that this condition is hereditary although not following any simple Mendelian scheme. He produced by selection a stock in which the fourth toe was regularly as well developed as the other toes. This abnormal fourth toe, it may be noted in passing, is interesting from an evolutionary standpoint as a true vestigial organ, representing a toe which is present in most rodents but which cavies have nearly lost. It is of a different kind from the extra toes occasionally found in cats and man, which are due to a symmetrical reduplication. The extra toe of guinea pigs is not placed symmetrically with respect to any of the other toes.

Extra toes were occasionally to be found in the stock from which the inbreeding experiments were started. Four cases were recorded in the control stock (B) between 1911 and 1915. Among the inbred families, 1906 to 1915, the distribution of extra toes has been irregular. There were 181 cases recorded in Family 35, 152 in Family 31, 59 in Family 38, 26 in Family 36, 25 in Family 11, and 19 in Family 24, while 12 were scattered among Families 2, 7, 14, 17, and 39. None were recorded in Families 1, 3, 13, 15, 18, 19, 20, 21, 23, 32, and 34.

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[4] Castle, W. E. 1906. The origin of a polydactylous race of guinea pigs. Carnegie Inst. Wash. Pub. No. 49.

The genetic differentiation among the families is obvious. It is further interesting to note that there was segregation in this respect among the lines of descent within the families.

The history of Family 31 is especially interesting. The original pair were both normal as to toes and produced only normal young. Two matings were made in the next generation, neither of which produced any four-toed young. Sixty-six matings were made among the descendants of one of them. Among the numerous young only 2 are recorded as four-toed. One of these came in the fourth generation, the other in the twelfth. The two matings which produced the four-toed young also produced 11 normal young. Evidently the vestigial toe was almost below the threshold of appearance in this line. A mating of 2 normals derived from the other mating in the first generation produced 11 normals but also 4 four-toed young. Two matings made in the next generation left numerous descendants. The two lines derived from these two matings and thus diverging in the third generation were remarkably different from each other in respect to heredity of polydactylism. One line starting from a mating of normal with normal contained 18 matings, of which only 5 produced four-toed young. These 5 matings produced 23 normal young and 6 four-toed young. The other line, starting from a mating of 2 four-toed animals, contained 27 matings, of which 25 produced 139 four-toed to 70 normal young. A large percentage of the four-toed young in this line had four well-developed toes on both hind feet.

There are similar evidences of segregation within Family 35. In this case three out of four lines starting from matings in the second generation produced numerous four-toed young. The other line, containing 43 matings, produced none. The segregation among the family lines is so sharp that it is probable that a careful investigation of polydactylism would yield Mendelian results, though much non-genetic variation must be present. The differentiation among the families and among the lines of descent within families is obviously very similar to that found in the case of the color characters.

Of more interest from the standpoint of inbreeding are abnormalities which are not merely reappearances of formerly normal characters. It has often been held that inbreeding has a specific tendency to cause physical malformations to appear. The array of bottles of preserved specimens of abnormalities which have appeared in the present experiments is indeed rather imposing. The total number of young born, however, has been so great that the sum of all of the abnormalities (excluding polydactylism) forms really an insignificant proportion.

Most of the types of abnormalities have appeared also in the control stock, showing that inbreeding can not be the prime cause of their appearance. Moreover, a study of their distribution among the fami-

lies shows a situation similar to that found with color, pattern, and polydactylism.

Three of the families (1, 9, and 20) produced no abnormalities of any kind. It will be shown later that Family 1 was one of the two poorest families in regard to vigor. It was the second family to become extinct, doubtless because of its deterioration in both fertility and ability to raise such young as were born. The other poorest family, No. 15, produced only two abnormalities. One was no more serious than a tuft of long hair or "mustache" on the right side of the muzzle. The other was an animal in which the legs were rudimentary.

Turning to the family which was unquestionably the most vigorous between 1906 and 1915, namely, Family 13, we find a considerable number of abnormalities. Aside from 7 animals with "mustaches," 1 with an abnormally small left eye, 1 with the neck twisted to the right, 1 with a hole in the skull through which the brain protruded, and one with the front legs bent back against the body, there were 11 of the well-known cyclopean type of monster. Another cyclops was a crossbred, three-fourths of whose ancestry came from Family 13. All of the other inbred families combined produced only 23 of these monsters. Five came from Family 19, 9 from Family 32, 3 from Family 35, and the rest from Families 7, 11, 17, and 18. Here again we find evidences of family differentiation, the family most productive in cyclopean monsters happening to be the most vigorous in other respects.

The distribution of the cyclopeans within Family 13 is interesting. All were descended from a single mating in the second generation. All but two (uncle and niece) were descended from a single mating in the seventh generation. Two were sisters.

As the 11 cyclopeans in Family 13 had 162 normal brothers and sisters, the variation can not be a simple Mendelian recessive. Nevertheless it seems clear that a tendency to produce it is hereditary, segregating out in particular lines of particular families, and that this tendency has nothing to do with the vigor of the stock. One cyclopean monster of an extreme type was produced by the control stock.

In another type of monster the body was undersized (which was not the case in the cyclopean monsters) and the legs were rudimentary. In extreme cases a leg would be represented externally merely by a single claw to be found only by feeling in the fur. One such case, as already noted, was produced by Family 15. There were 5 in Family 24 and possibly 1 in Family 39. Two of those in Family 24 were born in different litters from a single mating in the eighth generation. This mating also produced 16 normal young. Three matings were made among the normal young. Two produced only normals

(6 and 24, respectively).   The other produced the 3 other abnormals as well as 10 normals.   These abnormals again all came in different litters.   Each of the five litters containing an abnormal also contained normals.   Only one mating was made in the next generation from this line, and only 3 normal young were produced.   The abnormality is evidently hereditary and the data consistent with the view that it is due to a recessive Mendelian factor.   The matings of normal to normal produced 26 normals to 5 abnormals.   It is quite probable that the abnormality arose as a mutation sometime during the course of the experiment, as it is hardly likely that it would have failed to appear in others of the many lines in this family if the factor had been present in the original pair.   Even in this case, however, it is clear that we are dealing with a definite hereditary factor or factors, not with a specific effect of inbreeding.

The same conclusion applies to another abnormality, the absence of one or both eyeballs.   There were 4 of these animals in the control experiment and 11 among the inbreds.   Eight were produced by Family 38, 2 by Family 7, and 1 by Family 32.   Five individuals, one in each of the Families 3, 11, 13, 31, and 36, were recorded as having one eye smaller than the other.

The remaining abnormalities were well scattered among the families.   There were nine with various malformations of the jaws or muzzle.   One described as having a "bulldog face with no upper incisors" appeared among the controls.   There were 23 with deformed legs of various kinds besides those with miniature legs, noted above.   Three of this kind appeared among the controls.   Ten were described as having a hole in the skull, through which the brain protruded.   Three had abnormally large heads.   There were 2 in which toes were fused, a variation which also appeared among the controls.   Twenty-nine individuals had "mustaches," besides 2 among the controls.   The inheritance of many of these variations is, is, of course, very doubtful.

The general conclusion which is suggested by a survey of these abnormalities is the same as that advanced in connection with color, pattern, and vestigial toes.   Inbreeding per se has nothing to do with their origin.   We find a cyclops, several eyeless pigs, and several head and leg abnormalities among the controls.   Whether an abnormality appears in an inbred family depends mainly on its initial heredity in that particular respect.   One family, as it happens the most vigorous, has the greatest tendency toward producing cyclopean monsters.   Another family produces most of the eyeless animals.   Another produces monsters with miniature legs.   The two weakest families, in most respects, produce few or no abnormalities.   Thus inbreeding can not be considered to be a cause of the origin of abnor-

malities.   At the most it merely brings out more frequently variations
which depend on recessive factors, which factors are either already
in the stock or which arise from time to time as mutations.

DIFFERENTIATION IN VIGOR.

These results raise the question as to whether the inbred families
have become differentiated in a similar manner in the less tangible
traits connected with vigor, such as fertility, rate of growth, and
ability to raise the young successfully.

The characters of this kind which have been used in the present
work were defined in the first part of this bulletin.   Their relations to
each other and their variation under the influence of external con-
ditions were discussed there at some length.   Under the heading of
fertility are considered the average size of litter, the number of litters
produced per year by mature parents, and the product of these
factors, the number of young produced per year.   The rate of growth
is studied in the birth weight, in the gain between birth and weaning
at 33 days of age, and in the sum of these weights, the weight at 33
days.   The percentage of the young born alive, the percentage of
these raised to weaning, and the product, the percentage of all of the
young raised to weaning, measure the vitality of the young and the
capacity of the females for raising them.

Averages for each of these characters have been calculated in each
inbred family for two periods, 1906 to 1910, and 1911 to 1915.   In
the former period most of the families were composed of several lines
of descent, connected with each other only in the first generation of
inbreeding.   Many of the lines had been eliminated before the
second period, in which, therefore, the families might be expected to
be more homogeneous.   The figures on mortality among the young
and also the weights were calculated separately for each size of litter.
Indexes were obtained, as previously, by weighting the averages for
litters of 1, 2, 3, and 4, in the ratio 1:3:4:2.   The results are given in
Tables 7 to 15.

Examination of the tables reveals considerable differences be-
tween the families.   Table 1 shows the extremes in the period from
1911 to 1915.

TABLE 1.—*Families with extreme records in the period from 1911 to 1915.*

Character.	Best family.	Poorest family.
Size of litter	No. 11 (2.90)	No. 1 (1.74).
Litters per year	No. 23 (3.80)	No. 38 (2.46).
Young per year	No. 35 (10.34)	No. 1 (4.68).
Percentage born alive	No. 39 (91.5 per cent)	No. 3 (76.5 per cent).
Percentage raised of those born alive	No. 2 (89.3 per cent)	No. 3 (76.1 per cent).
Percentage raised	No. 20 (78.5 per cent)	No. 3 (57.7 per cent).
Birth weight of young raised	No. 13 (91.5 grams)	No. 2 (75.6 grams).
Gain from birth to 33 days	No. 11 (169.1 grams)	No. 2 (122.2 grams).
Weight at 33 days	No. 11 (260.2 grams)	No. 2 (197.8 grams).

A certain amount of difference between families from 1911 to 1915 would be expected to occur simply by chance, owing to the limited number of observations. It is important to determine whether the actual differences are greater than those expected by chance. The actual differences can best be measured by considering the families as units and finding the standard deviation in the group of family means, with respect to each character. The reliability of each family mean can be estimated by calculating its standard deviation (σ_m). The average of these standard deviations gives the standard deviation in the group of family means which might be expected by chance, and may be compared with the figures actually found.

The expected standard deviation in each family in the cases of the percentage born alive, the percentage raised of those born alive, and the total percentage raised, can be calculated by the formula

$$\sigma_{100\,p} = 100\sqrt{\frac{p(1-p)}{n}}$$ where 100 p is the percentage in question and n is the number of cases. In the case of the size of litter, the formula for the standard deviation of the mean is $\frac{\sigma}{\sqrt{n}}$ where σ is the standard deviation within a family (about 1.14) and n is the number of litters. In the cases of the weights the same formula applies, but the use of indexes somewhat complicates the matter. The indexes for the standard deviations of the weight at birth of the young raised to 33 days, the gain, and the weight at 33 days are approximately 11.0, 34.0, and 39.4 grams. These figures were derived from the total inbred families in 1916 and 1917. The figures within a single family would be slightly smaller, but these results are sufficiently accurate for the present purpose. For the reasons given in the discussion of the indexes in Part I of this bulletin this should be a compromise between the number of litters of 1 to 4 and the number of individuals in these litters. A standard deviation of means based on litters is about 60 per cent larger than one based on individuals. A reduction of 23 per cent from the figure based on a number of litters is in accordance with the assumptions involved in the indexes and is used here. In the cases of the number of litters and number of young produced per year the writer has not attempted to calculate the standard deviation to be expected by chance, and the reality of the differentiation among the families must be established by other means.

Having found the standard deviation of the mean in each family, the unweighted average in the 22 families has been used to measure the standard deviation to be expected by chance in the population of family means. Table 2 gives the comparison of these expected figures with the standard deviations actually found. It will be seen that in every case the actual variation is much the greater. The

difference is greatest among the weights, but is great enough in the other cases to make it reasonably certain that there are significant differences among the families, differences which might be expected to persist, even though so many young were raised in each family that the standard deviation of each family mean became practically zero.

TABLE 2.—*The differentiation among the inbred families.*

[The mean and standard deviation of the 22 family means relative to each of the characteristics studied is given for the two periods 1906 to 1910 and 1911 to 1915 (columns 2, 3, 5, and 6). The standard deviation of family means expected from random sampling (columns 4 and 7) may be compared with the actual standard deviations (columns 3 and 6). The yearly rate of decline in each element of vigor is estimated, taking either the family (column 8) or the individual (column 9) as the unit.]

Character.	1906–1910.			1911–1915.			Yearly decline.	
	Mean of family means.	σ of means.		Mean of family means.	σ of means.		Fami-ly the unit.	Indi-vidual the unit.
		Actual.	Due to chance.		Actual.	Due to chance.		
Size of litter	2.820	0.235	0.116	2.492	0.268	0.094	0.085	0.043
Litters per year	4.090	.321	....	3.303	.383	....	.203	.110
Young per year	11.536	1.302	....	8.227	1.226	....	.853	.450
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*
Percentage born alive	88.55	3.92	2.50	85.00	3.99	2.03	0.92	0.29
Percentage raised of those born alive	89.36	3.80	2.42	82.95	4.24	1.96	1.65	1.04
Percentage raised	79.14	4.96	3.20	70.64	5.38	2.59	2.19	1.16
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Birth weight of all young	83.95	3.88	....	81.82	4.19	....	0.55	0.19
Birth weight of young raised	86.86	3.57	0.87	85.00	4.57	0.70	.48	1.19
Gain to 33 days	165.18	9.26	2.67	146.55	11.75	2.16	4.80	1.96
Weight at 33 days	252.04	12.17	3.10	231.55	15.02	2.51	5.28	2.15

It will be noticed that, with one exception, the actual variation among family means is greater in the second period than in the first, in spite of the fact that the larger numbers born in the second period have reduced the variation due to random sampling. In the case of the one apparent exception, the number of young produced per year, the standard deviation is slightly smaller in the second period, but the coefficient of variation is much greater, owing to the smaller mean. It can thus be said with safety that there has been a pronounced increase in the differentiation among the families in every respect between the first and second periods. This increase in differentiation is a natural consequence of the increasing homogeneity in each family.

The unweighted average of the family means was calculated for each character in each period, and a consideration of the results brings out some interesting points. In every case the second period shows a marked decline compared with the first. This is in harmony with the results described in Part I. It is to be noted, however, that in the present figures the family is the unit, so that changes in relative importance among the families have no effect on the results. In order to make a comparison with the results obtained when all families were combined we must calculate the average difference

in time between the two periods. The average date of birth for the first period comes out 1909.04 or 1909.07, depending on whether the years are weighted by the number of litters born or the number of individuals. The average for the second period is 1912.93 in both cases. The periods may thus be considered as 3.88 years apart on the average. The yearly rate of decline in each character on this basis is given in the next to the last column of Table 2. The last column gives the rate of decline found, as described in Part I, by fitting the best straight line to the yearly averages for all inbred young born between 1907 and 1915. It appears that the decline within an average family has been about twice as rapid as that in the inbred stock as a whole. The reason is easy to understand. The vigorous families expanded at the expense of the families in which hereditary weaknesses had become fixed, and this expansion to some extent obscured the decline within the families.

DETAILED STUDY OF FAMILY CHARACTERS.

The existence of a significant degree of differentiation among the families would lead us to expect a correlation between the average of a character in the first period and its average in the second. Inspection of Tables 7 to 15 in fact soon shows that families which were high in rank in one period tended to be above the average in the other, and conversely. Among the extreme families listed in Table 1, Family 1 produced the smallest litters from 1906 to 1910 as well as from 1911 to 1915. Family 3 had the smallest percentage born alive in both periods excepting Family 15, which became extinct in 1911, while Family 13 led in birth weight in both periods, and Family 2 made the poorest gains.

More conclusive evidence can be obtained by calculating the coefficients of correlation between the averages in the two periods. This has been done for each character, using the product-moment method (Table 3). It will be seen that all of the correlations are positive and the lowest is +0.25. Unfortunately, the probable errors are also rather high, owing to the small number of families (22) on which the correlations are based. Nevertheless, a pronounced and lasting differentiation among the families is demonstrated in most of the cases. In regard to rate of growth, we find correlations of +0.65, +0.64, and +0.68 for birth weight, gain, and weight at 33 days, respectively, with a probable error of only ±0.08 in each case. The permanent differentiation in size of litter is of similar degree, with a correlation of +0.65 ±0.08 between the periods. In regard to the other element in fertility, the frequency of litters, the correlation of +0.25 ±0.13 can merely be said to be consistent with a genetic differentiation. Total fertility, as measured by the number

of young produced per year by mature matings, shows a probably significant correlation of $+0.41 \pm 0.12$. Hereditary differences in the ability to bear the young alive are demonstrated by the correlation of $+0.51 \pm 0.11$, while hereditary differences in the percentage raised of the young born alive are at least indicated by the correlation of $+0.32 \pm 0.13$. The correlation in the case of percentage raised of all the young is of course a compromise between these figures, $+0.36 \pm 0.13$.

In considering these results it must be carefully noted that a significant degree of genetic differentiation among the families during a given period of time does not necessarily imply a significant degree of correlation between different periods. It is to be expected that there will be a certain amount of differentiation among the lines of descent, which diverged in the early generations within a family. The lines of descent which are most important in the first period are not always most important in the second. A striking example of a change in the character of a family, No. 35, brought about by the rapid displacement of one set of lines of descent by the expansion of a hitherto insignificant line, is discussed later. If this family and another one, Family 2, which also changed its character to a very marked extent in the course of the experiment, were omitted from the tables, the correlations would be increased.

TABLE 3.—*Correlations between the family averages for each character, 1906 to 1910, and those for the same character 1911 to 1915.*

[The positive correlations indicate heredity.   Based on 22 families.]

Vitality:
  Per cent born alive.. $+0.51$
  Per cent raised of those born alive.. $+.32$
  Per cent raised.. $+.36$
Growth:
  Birth weight... $+.65$
  Gain... $+.64$
  33-day weight.. $+.68$
Fertility:
  Size of litter... $+.65$
  Litters per year... $+.25$
  Young per year... $+.41$

TABLE 4.—*Correlation between the family averages for various pairs of characters. Calculated separately for 1906 to 1910 and 1911 to 1915.*

[Significant correlations indicate physiological interrelation. Effect of size of litter on mortality and growth eliminated from consideration by use of indexes.]

		1906–10.	1911–15.
Vitality	Per cent born alive with per cent raised (BA)[1]	+0.03	+0.30
Growth	Birth weight with gain	+ .75	+ .59
Fertility	Size of litter with litters per year	+ .04	− .03
Vitality with growth	Per cent born alive with birth weight	− .08	+ .01
	Per cent born alive with gain	+ .03	− .28
	Per cent raised (BA)[1] with birth weight	+ .07	− .21
	Per cent raised (BA)[1] with gain	+ .02	− .23
	Per cent raised with 33 days' weight	− .04	− .31
Vitality with fertility	Per cent born alive with size of litter	− .10	+ .12
	Per cent born alive with litters per year	+ .04	+ .01
	Per cent raised (BA)[1] with size of litter	+ .28	+ .17
	Per cent raised (BA)[1] with litters per year	.00	+ .23
	Per cent raised with young per year	+ .03	+ .29
Fertility with growth	Size of litter with birth weight	+ .26	+ .62
	Size of litter with gain	+ .37	+ .62
	Litters per year with birth weight	− .05	− .34
	Litters per year with gain	+ .09	− .22
	Young per year with 33 days' weight	+ .21	+ .22

[1] Per cent raised of those born alive.

The demonstration of significant differences among the families in rate of growth, fertility, and mortality among the young, raises the question as to whether the variations in these characters are inherited independently of each other, or are merely so many manifestations of a differentiation in general vigor. Such a differentiation, if present, might be due to the transmission of disease in families as well as to genetic causes. To settle this point, the various characters were correlated with each other in each period, again using the product-moment method. The results are given in Table 4.

Before examining these results in detail it will be well to point out that if the differentiation among the families were merely in general vigor we should expect to find even higher correlations than where the families were compared at different periods of time with respect to a given character. In the present case we are comparing characters of the very same animals.

The results, however, contain few correlations which are at all significant, remembering that only values above 0.40 can be looked on as definitely significant, while values below 0.30 can be given little weight. Among the 36 correlations, only 4 are above +0.40, and only 2 more are between +0.30 and +0.40. The latter are balanced by two correlations between −0.30 and −0.40. This, of course, is directly antagonistic to the hypothesis of a differentiation in general vigor, genetic or otherwise.

Two of the four significant correlations are between birth weight and gain—namely, +0.75 ±0.06, and +0.59 ±0.09 in the two

periods.   There are evidently genetic factors which act alike on the rate of growth before and after birth.   It would, indeed, be surprising if it were otherwise.   The correlation between the family means for weight at birth and weight at a year, of males born in litters of three, was given as +0.63 in an earlier paper.   (Wright, 1917)[5]. The difference between the undersized guinea pigs of such a family as No. 2 and the large ones of such a family as No. 13, is in fact even more marked among the adults than among the young.   The demonstration of factors which affect the rate of growth at all ages has, however, no bearing on differentiation in general vigor.

The other two significant correlations connect size of litter with birth weight and gain, respectively, in the period from 1911 to 1915. Each of these correlations was +0.62 ±0.08.   The correlations, in the period from 1906 to 1910, were not certainly significant, although relatively high (+0.26 and +0.37 respectively).   Because of the close connection between birth weight and gain, it is evident that we are really dealing with a single correlation, one between size of litter and rate of growth (for a given size of litter).   There is an indication of an interrelation here, although, as will be shown later, there is another possible explanation which must be considered.

In opposition to the hypothesis of a differentiation in general vigor, we have the evidence of the remaining 30 correlations, only 1 of which is as high as +0.30, and 11 of which are negative.   The low correlations in certain cases are especially noteworthy.   The percentage born alive, and the percentage of those raised to weaning, show virtually no correlation in the first period (+0.03), and only a doubtful one in the second (+0.30).   It would appear that these depend, to a large extent, on independent hereditary factors.   There is evidence which is brought out in Bulletin 1121 that the percentage born alive depends more on the vigor of the dam, while the percentage raised of those born alive depends more on the vigor of the young themselves.   There must, of course, be important factors in common, but the effects of these seem to be neutralized by the tendency toward negative correlation which independent factors would have in this case.   Factors which tend to remove the less vigorous young at or before birth tend thereby to increase the percentage raised of those born alive, if they do not also prejudice the chances of the young after birth.

But even though there may be factors in common, the differences among the families in vigor in these respects is in marked contrast to the differences between stocks of guinea pigs raised under different environmental conditions.   Under unfavorable conditions both the percentage born alive and the percentage raised of those born alive tend to decline.

[5] See footnote 2.

The lack of correlation between the two elements in fertility, size and frequency of litters (+0.04 and −0.03 in the two periods) is also surprising. Here again the hereditary factors must be largely independent of each other. A small amount of common heredity may be obscured by a tendency toward negative correlation due to independent factors. Within inbred stock large litters tend to be followed by a long delay, and fertilization immediately after the birth of a litter tends to result in a small litter. These tendencies are not very important, however, as was shown in the first part of this bulletin.

The correlations between average weight and ability to bear and raise the young successfully have more tendency to be negative than positive. The lack of correlation between percentage born alive and birth weight or gain is noteworthy because genetic differentiation with respect to these characters is beyond question. The absence of significant correlation between the percentage born alive and size of litter is important for the same reason. The other correlations which connect vitality and fertility agree in giving no significant indications of heredity of general vigor. There is finally a tendency toward negative correlation between body size and frequency of litters.

It will be seen that in general the differences among the families are of a different kind from those which distinguish individuals in a given stock or similar stocks raised under different conditions. In the latter cases we are undoubtedly dealing largely with differences n general condition. In summer and fall litters are both larger and more frequent, larger percentages of the young are born alive and also raised among those born alive, and growth is more rapid, than in winter and spring. Inspection of the yearly fluctuations in the averages of the various characters (given in Part I) shows that if the year were made the unit very high positive correlations would be obtained in all cases instead of the insignificant ones of Table 4, got by making the family the unit. This would be true even though the downward trend of all characters were eliminated. The conclusion which is forced on us by these considerations is that there is little or no differentiation among the families in general vigor, but instead a fixing in each family of particular traits in some particular combination.

A detailed study of the combinations of characters actually found in the 22 families is instructive. For this purpose it is convenient to arrange the families in the order of excellence in each character in each period of years. A division into five groups makes the relations more easy to grasp. In Table 5 the best three families in any respect are given rank A; the next five, rank B; the middle six,

rank C; the next five, rank D; and the poorest three, rank E. Family 15, which produced too few young in the second period to give significant results, is assigned ranks in the first period but is not counted in assigning ranks to the other families.

TABLE 5.—*Ranks of the families during years 1906 to 1910, and 1911 to 1915.*

[The best three are given rank A; the next five, rank B; the middle six, rank C; the next five, rank D; and the poorest three, rank E. Family 15 is given a rank in the first period only and is not counted in assigning ranks to the others. The ranks for 1906–1910 and 1911–1915 are given in succession. For example, EC means among the poorest three in 1906–1910 and middling in 1911–1915. Great changes in rank are indicated by stars.]

Family.	Per cent born alive.	Per cent raised of those born alive.	Per cent raised.	Birth weight (those raised).	Gain to 33 days.	Weight at 33 days.	Size of litter.	Litters per year.	Young per year.
1	CC	EE	ED	ED	DE	EE	EE	DE	EE
2	EC*	CA*	DB*	CE*	EE	EE	DD	EA***	EB**
3	EE	CE*	EE	BC	BA	BB	BC	DB*	CB
7	DD	DB*	EC*	DC	CC	CB	BC	CC	BB
9	DD	CC	DD	AB	AA	AA	BA	CD	BC
11	DC	EE	DE	BA	BA	BA	AA	DD	BC
13	CB	CB	CB	AA	AB	AA	AB	CC	BA
14	EE	CD	DD	CC	CB	CB	CC	CE*	CE*
15	E	B	E	C	E	D	E	D	E
17	AB	AB	AA	ED	ED	ED	DD	DC	DC
18	BB	DD	BC	BB	CC	CC	CC	BB	CC
19	DD	BD*	CD	CB	DD	DC	BB	BB	BA
20	DB*	DA**	DA**	CC	CD	CD	EC*	CD	DD
21	BD*	DB*	CC	AD**	BC	AC*	EE	BB	DD
23	AA	ED	CC	BC	BD*	BE**	BD*	AA	AB
24	CE*	BD*	BE**	DE	DC	DC	CE*	AB	AD**
31	AD**	BA	AB	CC	DC	CC	CB	ED	DD
32	BC	CC	BD*	DD	ED	DD	CD	BC	CC
34	CB	AC*	BC	BB	BE**	BD*	DD	CD	CD
35	BC	DB*	CB	DB*	DB*	DB*	DA**	DA**	DA**
36	CC	BC	BC	DD	CB	CC	AC*	BC	AC*
38	BA	AC*	AB	CA*	AB	BB	CB	EE	EE
39	CA*	BC	CA*	EE	CC	DD	DB*	AC*	CB

Inspection of Table 5 brings out clearly the tendency of the families to hold their rank with respect to each character. Changes of rank of more than one grade are indicated by stars. A shift of two grades is shown by one star, of three grades by two stars, and one case in which there was a change from E to A by three stars. There was the greatest shifting of places in the percentage raised among those born alive, but even here 12 of the 22 held their rank or changed by only one grade. The correlation between successive periods was rather low in this case, being only + 0.32. In the cases of the other characters, there were from 16 to 19 of the 22 families which held their place in the sense given above or changed only one grade. The case of the frequency of litters is especially interesting, since the coefficient of correlation between successive periods (+ 0.25) did not appear to be significant. It is therefore surprising to find that eight of the families were of the same grade in both periods and that nine changed by only one grade, leaving only five which made conspicuous changes in rank. The low correlation is evidently due to the remarkable change in character of two families, namely, Nos. 2 and 35.

Family 2 was the poorest family in producing litters between 1906 and 1910, but tied with Family 23 for the first place in the second period. The change was nearly as great in Family 35. The correlation becomes +0.66 if these two families are omitted.

Looking through the table, we find that Families 35 and 2 made conspicuous changes in rank in several other respects. A few other families also made numerous changes. In fact, a majority of the marked cases of relative improvement or deterioration are found in Families 35, 2, 24, 20, and 21, and these include 10 of the 13 cases in which there were changes of more than two grades. There were, on the other hand, six families (1, 9, 11, 13, 17, and 18) which made no important changes and eight more with only one or two changes. We are thus led to look into the history of the families to see why it is that certain of them have changed in many respects while others have remained constant,

Careful study of the pedigrees shows that there has been a much greater revolution in the predominant lines of descent in Family 35 than in any other family. A single mating was made in the first generation of this family, but four were made in the second generation, which may be looked upon as founding four subfamilies. The smallest of these subfamilies, which during the first seven generations included only 17 per cent of the matings, suddenly began to expand at this time and produced 65 per cent of the matings made between the eighth and twelfth generations. All of these were descended from a single mating in the seventh generation. By the end of 1917 the entire family, which was one of the largest in the stock, was descended from a single mating in the twelfth generation and had reached the most advanced generation of inbreeding in any family.

With this history, it can hardly be a coincidence that Family 35 has changed in character more than any other family. It will be seen from Table 5 that Family 35 made poor records during the first period in birth weight, gain, and weight at 33 days, in size and frequency of litter, and hence in total fertility, and finally in the percentage raised of those born alive. During the second period the birth weight, gain, and weight at weaning were good; size and frequency of litters and total fertility were among the best, and the percentage born alive and the total percentage raised were good. A decline from rank B to C in the percentage born alive meant merely a change from eighth to ninth among the 22 families. Following the second period, i. e., since 1915, the relative improvement continued in every respect and the family became on the whole the most vigorous in the stock, displacing Family 13, which had previously held this position. Family 35 evidently started with relatively inferior heredity for most elements of vigor. Apparently,

however, a remarkably fortunate combination of genetic factors segregated out in one line, and this line ultimately displaced all other lines.

Family 2 had a somewhat similar history. There were many lines in the early generations, but after the seventh generation all of the matings traced back to a single pair in the fourth generation. The family began as one of the weakest in nearly every way and was absolutely the poorest in rate of gain and in frequency of litters. The successful line continued to produce small litters of undersized animals, and held the record for smallness of gains in the second period, as well as in the first. The percentage born alive, however, increased from very poor to medium, and the percentage raised of those born alive increased from medium to the very best. The most remarkable change was from the lowest in litters per year in the first period to a tie with Family 23 for the highest record in the second. Since 1915 small litters and very light weight have remained characteristic, but also frequent litters and great success in raising the young born alive. In spite of its defects it is one of the easiest families to maintain. Its ability to raise the young which are born alive seems to be correlated with high vitality thereafter.

Study of the pedigrees indicates that Family 24 must probably be considered as next to Family 35 in the extent to which there has been a shifting in the importance of lines of descent. Table 5 shows that it stands third in change of characteristics. In this case, however, the change was for the worse in most respects. Apparently a number of fairly vigorous lines were superseded by an inferior one. This would seem hardly as likely to happen as the expansion of a good line, noted in Families 35 and 2, but it is not impossible. It must be remembered that the characters of a line of descent can be determined only from the average of many individuals. At a given time the genetically inferior line might well happen to be represented by the more vigorous individuals.

Among the remaining families, Nos. 20, 21, and probably also 34, were ones in which the rather important changes in character may also well have been due to the expansion of particular lines of descent. The changes in 23 and 39 can not be explained so satisfactorily in this way. In certain cases families remained fairly true to type, even though the predominant lines of descent altered considerably. This was true of Families 1, 9, 13, 19, and 38. This, however, is not surprising. In the remaining families the original lines of descent run parallel to each other through both periods and there were few important changes in the family characteristics.

A consideration of these family histories, especially those of Families 35, 2, and 24, strengthens the argument for the inheritance of characters in which the coefficient of correlation between the suc-

cessive periods was too low to be certainly significant. The low correlation in regard to litters per year (+0.25) is, as already noted, largely due to the remarkable change from one extreme to the other in Family 2, and the only slightly less remarkable change in Family 35. But in view of the likelihood that a real genetic change took place in these families, through segregation in the early generations and expansion of one line of descent at the expense of the others, the changes in these families must not be weighed too heavily against the absence of important changes in rank in 17 other families. Similarly, in the case of the percentage raised of those born alive, and the percentage raised of all young, the changes in Families 35, 2, and 24 play a large part in making the correlations low (+0.32, +0.36).

If we attempt to arrange the families in order with respect to general vigor, there would be little hesitation in picking out Family 13 as the best. It is the only family which was average or better than average in every character in both periods. It was easily among the best families in weight and fertility, and changed from medium to good in the ability to raise the young. At the other extreme come Families 1 and 15. Family 1 was among the poorest families in the majority of characters in both periods. Family 15 was similarly poor during the first period and it is not surprising that it was the first family to become extinct, in spite of all efforts to maintain it, and that it was followed to extinction by Family 1.

Even in these families, however, we are not dealing merely with differences in general vigor. Family 13 is relatively lower in its ability to raise its young than in growth and fertility, and Families 1 and 15 each have a redeeming trait. In both the earlier and later period slightly more than the average percentage of the young were born alive in Family 1, an advantage lost through inability to rear them successfully. The situation was reversed in Family 15, which lost a larger percentage of the young at birth than any other family, but was well above the average in the percentage raised of those born alive.

When we consider the remaining families, the impossibility of ranking them in general vigor becomes at once apparent. Family 38 would be placed second to Family 13 in general vigor but for the fact that it produced litters less frequently than any other family. Owing probably to this defect, it was always a small family. Families 11 and 9 are two similar families which have a remarkable combination of vigor and weakness in different characters. They were among the best three families in both size of litter and weight, yet both of them produced litters irregularly and were unsuccessful in raising the young. The contrast was especially marked in Family 11, which led all of the families during the second period in size of litter, gain, and weight at 33 days, but was one of the three poorest families in the

percentage of young which reached weaning. Family 3 agrees with Families 9 and 11 in combining rapid growth with inability to raise the young successfully. It was doubtless this poor success in raising the young which caused Families 3 and 11 to be among the five families which were extinct at the end of 1915.

Family 2, during the second period, had a combination of characters the opposite of that in Families 9 and 11. With the smallest weight and small litters it combined the greatest regularity in producing litters and the best record in raising the young which were born alive. Family 17 was consistently of this type in most respects. During both periods it produced small litters and small pigs, but pigs which were easily raised. This combination seemed to be more fortunate than that of Families 9, 11, and 3, since Family 2 became the most numerous of all the families after 1915, and Family 17 was a large family, while, as noted above, Families 3 and 11 were among the first to become extinct and Family 9 was always a small family.

It was shown earlier that the only significant correlations between the different groups of characters were those between birth weight or gain and size of litter ($+0.26$ and $+0.37$ in the first period, both $+0.62$ in the second). The impossibility of considering these correlations as an indication of heredity of general vigor may be seen by comparing Families 9, 11, and 3 with Families 2 and 17. As we have just seen, the latter families appeared to be the more successful, in spite of their great inferiority in size of litter and weight.

There is a possible cause of correlation between characters which should be mentioned. It will be remembered that the experiment started with 23 different females, but only 9 males. If one of the male ancestors of several families happened to transmit two of the characters in an extreme degree, it would tend to bring about a correlation in these characters among the families, which would have no significance as an indication of inheritance of general vigor or of a common physiological factor. It may not be a coincidence that the three families which traced back in all lines (Families 9 and 11) or in the principal line (Family 13) to a certain foundation male ancestor (Male 3) should be the three leading families in both size of litter and weight. Again, two of the four families descended from Male 1 (Families 1 and 2 in the group 1, 2, 3, and 7) are characterized by remarkably small litters and light weight. If we suppose that Male 3 transmitted both large size of litter and great weight in a remarkable degree, and perhaps that the converse was true of Male 1, we can account for the correlation between these characters observed in the present data.

The other groups of families with common male ancestors, namely, Families 17 to 24, 31 and 32, 35 and 36, were not clearly differentiated, but it may well have been that Males 3, 9, and 11 were medioc-

rities genetically, heterozygous in many respects, among whose descendants any trait was likely to segregate out. That one or two of the males transmitted extreme degrees of two characters is a mere coincidence on the view suggested above and would not be expected to happen with other characters.

The absence of correlation between the characters finds extreme illustrations in most cases. Compare, for example, Family 23, in which the young were born alive with great success, but died in unusually large numbers before weaning, with Family 13, in which the reverse was true. Families 17 and 3 have already been noted as families which were successful or failed in both respects. Families 11, 21, 19, and 1 show extremes of size and frequency of litters, combined in four different ways. Even in the case of birth weight and gain, some independence may be noted. In Family 39 the young made better gains in both periods than their birth weights indicated as most likely, while the opposite was true of Family 19.

RECORDS OF FIVE FAMILIES IN RECENT YEARS.

As already noted, most of the inbred families have been disposed of since 1915 to make room for a more intensive study of the five which have been retained, Nos. 2, 13, 32, 35, and 39, and for experiments on crossbreeding. The data for years 1916 to 1919 is presented in Bulletin 1121. It is desirable here, however, to compare the standing of the above-mentioned five families in 1916–19 with their standing in the earlier periods. This is especially true because two of these families, Nos. 2 and 35, were the ones among the original 22 which showed the greatest change in character from the first to the second period. The rank in various characters of the five remaining families is shown in Table 6 for the three periods together with rank in longevity of the males and females (1915–1918) and resistance to tuberculosis during 1919–20. The resistance to tuberculosis has been obtained in experiments in cooperation with Dr. Paul A. Lewis, of the Henry Phipps Institute. (Wright and Lewis, 1921.)[6]

The correlation between the ranks in the first and second, the first and third, and the second and third periods are shown in the last three lines of Table 6. A single correlation based on five entries does not, of course, have much significance by itself. It will be seen, however, that while the correlation between standing in the first period and the second or third is negative in almost as many cases as it is positive, all of the correlations between the second and third periods are positive, and most of them are high. Their average is +0.75, where +0.04 and +0.01 are the averages in the cases of the correlation of first with second and third period respectively. The

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[6] See footnote 3.

absence of appreciable correlation between first and second periods among the five families in contrast with the significant correlation found in dealing with all 22 families (Table 3) is of course due to the large part played by Families 2 and 35 among the 5 families. It strengthens the evidence for inheritance to find that even these families became fairly well settled in relation to the other families during the second period.

Considering the separate characters the evidence for differentiation in weight is most consistent. There is close agreement between rank in weight at all ages and in both sexes. The only important exception is that Family 32 appears to produce heavy young relative to its adult weight.

The rank of the families in both size and frequency of litters appears to have become fairly well settled in the second period. Because of the negative correlation present in the five families between these elements of fertility there is not much differentiation in the product, the number of young produced per year. The perfect correlation in 1916–1919 between adult weight and size of litter is noteworthy. It will be remembered that significant correlations were found among the 22 families between birth weight or gain and size of litter in the second period. The possible explanation suggested in that case, namely that the three best families in both weight and size of litter were all derived from one male ancestor, has no application among the five families considered here. There is undoubtedly an indication of a direct physiological relation between weight and size of litter, apart, of course, from the direct (negative) effect of size of litter on the early weights, for which due correction is made by the use of indexes.

There is good evidence for differentiation in both percentage born alive and percentage raised of those born alive. Just as in the case of the two elements of fertility, there happens to be a negative correlation between the two characters among the five families, with the consequence that there is no very clear-cut differentiation in their product, the percentage raised of all births.

The longevity of the males and females born 1915–1918 was obtained by taking each interval of three months in age separately and finding the death rate among those not disposed of during the period in question. The most noteworthy feature is the marked superiority of Family 2 shown by both sexes. There was not much differentiation among the other families.

A comparison of ranks in different characters during the third period confirms the conclusion drawn from study of the 22 families in the earlier periods, namely, that there is not differentiation in general vigor, but differentiation in each characteristic separately. The number of young raised per year by a mating is perhaps the best single

measure of the efficiency of the families. There is good evidence for differentiation in this in the second and third periods. There is also rather close agreement with rank in resistance to tuberculosis. There is not, however, agreement with longevity or with weight.

TABLE 6.—*The rank of five inbred families in various characteristics in three successive periods, 1906 to 1910, 1911 to 1915, 1916 to 1919.*

[The correlations between these ranks in the first and second, the first and third, and the second and third periods are shown below. The ranks of the families in longevity of males and females, born from 1915 to 1918, and in resistance to tuberculosis (1919–1920) are shown in the three columns at the right.]

Family.	Percentage born alive.	Percentage raised of those born alive.	Percentage raised.	Birth weight of those raised.	Gain to 33 days.	Adult weight.		Size of litters.	Litters per year.	Young per year.	Young raised per year.	Longevity.		Resistance to tuberculosis.
						Males.	Females.					Males.	Females.	
2	5-5-5	4-1-2	5-4-2	2-5-5	5-5-5	2-5-4	5-5-5	4-4-4	5-1-1	5-4-2	5-3-2	-1	-1	-2
13	4-2-4	2-2-3	4-2-4	1-1-1	1-1-1	1-1-1	1-2-1	1-2-1	3-3-4	1-2-3	1-2-3	-3	-2	-4
32	1-4-2	3-5-5	1-5-5	3-3-3	4-4-3	4-4-5	3-4-4	2-5-5	2-4-3	2-5-4	2-5-4	-2	-3	-3
35	2-3-3	5-3-1	3-3-1	4-2-2	3-2-2	3-2-2	4-1-2	3-1-2	4-2-2	4-1-1	4-1-1	-4	-4	-1
39	3-1-1	1-4-4	2-1-3	5-4-4	2-3-4	5-3-3	2-3-3	5-3-3	1-5-5	3-3-5	3-4-5	-5	-5	-5
Correlations.														
1st-2d	+0.10	-0.30	-0.10	+0.30	+0.90	+0.30	+0.40	+0.10	-1.00	0.00	-0.20			
1st-3d	+.70	-.70	-.50	+.30	+.70	+.50	+.70	+.30	-.90	-.50	-.50			
2d-3d	+.60	+.70	+.20	+1.00	+.90	+.90	+.90	+.90	+.90	+.50	+.80			

SUMMARY.

Part II deals with the differences found among 23 inbred families, derived wholly or in part from the same original line-bred stock.

It is found that a certain color and pattern tended to become fixed automatically in each line of descent. In certain cases an entire family came to breed true to a given color and pattern. In other cases subfamilies derived from different matings in the early generations of a family each developed a characteristic color and type of pattern to which they came to breed true.

In a similar way, certain subfamilies became differentiated from other subfamilies and from other families by developing a strong tendency toward reappearance of an ancestral fourth toe on the hind feet.

Relatively few monstrosities were produced either by the inbred families or by the controls. The tendency to produce a given type of monstrosity has been characteristic of certain families. Such a tendency has had no connection with the vigor of the family in other respects. The two feeblest families gave few or no pronounced abnormalities, while about 30 per cent of the cyclopean monsters were produced by the most vigorous family. Another family produced most of the eyeless young and another had several defective young with rudimentary legs. There was evidence of heredity within the families, of the tendency to produce these abnormalities. There was no evidence that inbreeding has any specific causal connection with

the origin of the monsters.   Inbreeding seems merely to have brought to light genetic traits in the original stock.

Although most of the families came from the same line-bred stock, a striking differentiation with respect to traits connected with vigor was found among them.   These traits included size and frequency of litters, percentage born alive and raised of those born alive, birth weight, and gain to 33 days.   The differences between the families were greater than could be due to chance, and increased as the inbreeding progressed and the families became more homogeneous through the elimination of early branches from the main lines of descent.   The families tended to keep the same rank with respect to each character.   The correlation between the average grades in the early and later histories of the families was high in respect to size of litter, birth weight, and gain.   It was high enough to be significant in the case of the percentage born alive.   The correlations were positive but of doubtful significance for the percentage raised of the young born alive and for the frequency of litters.   A detailed study of the individual families, however, showed that the correlations would have been higher and all would have been significant but for two or three families in which there had been reversal of relative importance among the subfamilies and in which therefore a change in rank in all or many respects was not surprising.   Recent evidence indicates that even these families have now become fixed in their characteristics.   The conclusion seems warranted that there was heredity of all of the traits studied.

There did not, however, appear to be heredity of general vigor. The average vigor of a family in one respect was found to be in the main independent of its vigor in other respects.   Thus the average success of the families in raising their young was not correlated with weight or with size or frequency of litters.   Neither was weight correlated with regularity in producing litters.   There was not even a significant correlation between the percentage born alive and the percentage of those raised, although success or failure in each separaately was undoubtedly characteristic of families.   Similarly there was no correlation between the average size of litter and litter frequency. The only apparent exception, outside of high correlations between birth weight, gain, and year weight, was in a high correlation between weight and size of litter, for which there is undoubtedly some indication of a physiological interrelation.

The study of the individual families brought out interesting examples of extreme vigor throughout the history of a family in certain respects, associated with extreme weakness in others, as well as cases in which all kinds of vigor or all kinds of weakness were combined.

While the characteristics of a family probably reflected to a considerable extent simply the average of the genetic factors in the original pair, there was considerable evidence of segregation in the early generations in characters associated with vigor, just as in the cases of color, pattern, polydactylism, and tendency to produce monstrosities. In one family which was very weak in most respects in the early generations, a single line of descent began to expand in the eighth generation until it composed the entire family. This line revealed itself as the most vigorous in nearly all respects in the entire stock of inbred families. There were other less extreme cases of this sort.

The study brought out a striking contrast between the effects on vigor of hereditary and environmental factors. Favorable or unfavorable conditions affect alike growth, mortality among the young, and fertility, in all their aspects. On the other hand, hereditary factors which affect each character by itself appear to be much more important than ones which affect general vigor.

Finally the study illustrates what is one of the most important results of inbreeding, namely, the bringing to light and fixing of characters in a family. In the case of color the mechanism of heredity is thoroughly understood and the automatic fixation of type is a necessary consequence of this mechanism. The similarity of the phenomena in the other characters makes it probable that the mechanism is essentially the same in all cases.

APPENDIX.

TABLE 7.—*Data on the fertility of the different inbred families, 1906 to 1910.*

Family.	Size of litter.								Number of mating-years.	Number of litters.	Number of young.	Average size of litter.	Litters per year.	Young per year.
	1	2	3	4	5	6	7	8						
1....	11	13	15	3	1	....	....	....	10.9	43	99	2.30	3.94	9.08
2....	22	40	28	20	7	2	....	....	37.8	119	313	2.63	3.15	8.28
3....	13	41	45	29	8	5	1	....	35.0	142	423	2.98	4.06	12.09
7....	14	47	57	38	11	3	2	....	40.9	172	518	3.01	4.21	12.67
9....	13	21	33	26	8	3	....	....	25.6	104	316	3.04	4.06	12.34
11....	17	45	76	56	21	5	1	....	56.2	221	701	3.17	3.93	12.47
13....	19	71	61	38	37	5	....	....	56.8	231	711	3.08	4.07	12.52
14....	19	41	41	27	9	1	2	....	33.4	140	397	2.83	4.19	11.89
15....	12	28	25	8	1	....	....	....	18.9	74	180	2.43	3.92	9.52
17....	25	52	31	19	14	3	1	....	35.7	145	393	2.71	4.06	11.01
18....	14	31	31	18	7	5	....	....	24.9	106	306	2.89	4.26	12.29
19....	11	11	22	10	5	0	1	1	14.4	61	179	2.93	4.24	12.43
20....	20	35	16	9	4	3	....	....	20.6	87	212	2.44	4.22	10.29
21....	12	25	23	9	2	....	....	....	16.6	71	177	2.49	4.28	10.66
23....	11	14	16	11	7	2	....	....	14.0	61	178	2.92	4.36	12.71
24....	46	65	90	45	22	6	1	....	60.9	275	779	2.83	4.52	12.79
31....	19	30	36	28	7	2	1	....	34.4	123	353	2.87	3.58	10.26
32....	43	109	121	63	28	3	....	....	86.3	367	1,034	2.82	4.25	11.98
34....	2	20	15	4	4	....	....	....	10.7	45	123	2.73	4.21	11.50
35....	23	43	50	23	10	5	....	....	38.6	154	431	2.80	3.99	11.17
36....	15	35	61	34	21	5	1	1	40.0	173	554	3.20	4.33	13.85
38....	15	31	44	21	9	2	....	....	34.9	122	350	2.87	3.50	10.03
39....	11	16	17	7	1	1	....	....	11.6	53	133	2.51	4.57	11.47

TABLE 8.—*Data on the fertility of the different inbred families, 1911 to 1915.*

Family.	Size of litter. 1	2	3	4	5	6	7	Number of mating-years.	Number of litters.	Number of young.	Average size of litter.	Litters per year.	Young per year.
1....	16	11	7	.....	.....	.....	.....	12.6	34	59	1.74	2.70	4.68
2....	42	97	83	16	8	.....	.....	64.7	246	589	2.39	3.80	9.10
3....	19	30	33	6	4	1	1	25.9	94	235	2.50	3.63	9.07
7....	49	67	70	33	11	3	1	67.6	234	605	2.58	3.46	8.95
9....	26	46	58	30	7	5	.....	55.2	172	477	2.77	3.12	8.64
11....	17	38	54	36	9	1	.....	53.8	155	450	2.90	2.88	8.36
13....	42	96	134	63	12	3	.....	100.7	350	966	2.76	3.48	9.59
14....	12	21	26	7	.....	.....	.....	25.9	66	160	2.42	2.55	6.18
15....	.....	2	1	.....	.....	.....	.....	1.2	3	7	.....	.....	.....
17....	71	117	72	38	6	1	1	88.3	306	716	2.34	3.47	8.11
18....	32	72	46	23	6	2	1	51.8	182	455	2.50	3.51	8.78
19....	24	35	41	23	5	3	.....	37.5	131	352	2.69	3.49	9.39
20....	27	61	52	15	6	.....	1	51.2	162	402	2.48	3.16	7.85
21....	49	61	28	8	2	.....	.....	41.2	148	297	2.01	3.59	7.21
23....	41	47	43	14	6	.....	.....	39.7	151	350	2.32	3.80	8.82
24....	49	55	39	15	4	.....	1	46.1	163	363	2.23	3.54	7.87
31....	33	39	52	28	8	5	.....	56.9	165	449	2.72	2.90	7.89
32....	50	107	84	26	6	1	.....	78.9	274	656	2.39	3.47	8.31
34....	20	31	22	13	2	.....	.....	28.7	88	210	2.39	3.07	7.32
35....	49	90	97	64	15	9	1	87.2	325	912	2.81	3.73	10.48
36....	50	107	88	42	6	3	.....	86.1	296	744	2.51	3.44	8.64
38....	25	45	59	21	6	2	.....	62.6	154	418	2.71	2.46	6.68
39....	37	91	110	44	14	.....	1	87.0	297	802	2.70	3.41	9.22

TABLE 9.—*The percentage born alive in the different inbred families.*

[The average in litters of each size and an index (litters of 1, 2, 3, and 4, weighted 1, 3, 4, and 2 respectively), 1906 to 1910 and 1911 to 1915.]

Family.	Size of litter, 1906–1910. 1	2	3	4	5	6	Index.	Size of litter, 1911–1915. 1	2	3	4	5	6	Index.
	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.		Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	
1....	100.0	76.9	95.6	91.7	100.0	.....	89.7	68.8	95.5	85.7	.....	.....	.....	85.9
2....	72.7	82.5	88.1	75.0	94.3	82.3	82.3	81.0	90.2	84.3	76.6	72.5	.....	84.2
3....	76.9	79.3	83.7	81.0	95.0	43.3	81.2	84.2	83.3	82.8	50.0	20.0	00.0	76.5
7....	85.7	85.1	87.7	77.0	70.9	50.0	84.6	81.6	83.6	81.4	83.3	72.7	61.1	82.5
9....	84.6	90.5	84.8	81.7	85.0	94.4	85.9	80.8	84.8	78.7	83.3	77.2	50.0	81.7
11....	70.6	90.2	88.2	84.4	78.1	63.3	86.3	76.5	89.5	88.3	66.7	48.9	83.3	83.2
13....	79.0	88.7	88.5	88.2	86.0	73.3	87.6	90.5	87.5	89.8	85.3	78.3	94.4	88.3
14....	84.2	80.5	87.0	82.4	82.2	33.3	83.9	83.3	90.5	76.9	67.9	.....	.....	79.8
15....	83.3	78.6	77.3	78.1	00.0	.....	78.5	.....	50.0	66.7	.....	.....	.....	.....
17....	96.0	95.2	92.5	92.1	95.7	61.1	93.6	83.1	93.6	89.4	82.9	50.0	83.3	88.7
18....	85.7	90.3	96.8	95.8	77.2	90.0	93.5	75.0	90.3	92.0	87.0	53.3	33.3	88.8
19....	90.9	77.3	87.9	85.0	92.0	.....	84.4	91.7	94.3	77.2	60.9	80.0	61.1	80.5
20....	85.0	84.3	85.4	86.1	90.0	61.1	85.2	85.2	85.2	89.1	93.3	83.3	.....	88.4
21....	100.0	88.0	91.3	94.4	70.0	.....	91.8	75.5	82.8	85.7	71.0	10.0	.....	81.1
23....	81.8	96.4	93.8	95.5	88.6	66.7	93.7	80.5	87.2	93.8	92.9	90.0	.....	90.3
24....	87.0	90.0	89.3	85.0	78.2	91.7	88.4	67.4	75.5	82.9	78.3	40.0	.....	78.2
31....	94.7	96.7	93.5	93.8	71.4	41.7	94.6	66.7	89.8	78.2	91.1	95.0	83.3	83.1
32....	95.4	92.7	90.6	84.9	72.2	66.7	90.6	94.0	85.5	89.7	71.2	56.7	16.7	85.2
34....	50.0	95.0	93.3	93.8	75.0	.....	89.6	75.0	90.3	90.9	84.6	40.0	.....	87.9
35....	82.6	98.8	93.3	75.0	60.0	70.0	90.2	71.4	88.9	91.7	83.2	64.0	46.2	87.1
36....	93.3	94.3	86.9	78.0	81.9	90.0	88.0	92.0	91.6	87.9	73.2	60.0	55.6	86.5
38....	93.3	93.6	97.0	84.5	86.7	83.3	93.1	88.0	93.3	92.7	77.4	53.3	50.0	89.4
39....	90.9	94.8	84.3	85.7	0.0	0.0	88.4	94.6	94.0	91.8	85.8	64.3	.....	91.5

TABLE 10.—*The percentage raised to 33 days of the young born alive in the different inbred families.*

[The average in litters of each size and the index (see Table 9), 1906 to 1910 and 1911 to 1915.]

Family.	Size of litter, 1906–1910.						Index.	Size of litter, 1911–1915.						Index.
	1	2	3	4	5	6		1	2	3	4	5	6	
	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.		Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	
1....	81.8	80.0	86.0	63.6	100.0	......	79.3	72.7	81.0	77.8	......	65.5	......	77.1
2....	100.0	90.9	85.1	88.3	93.9	80.0	89.0	97.0	90.6	86.2	89.8	65.5	......	89.3
3....	90.0	84.6	92.0	89.4	78.9	76.9	89.1	62.5	78.0	74.4	83.3	100.0	......	76.1
7....	83.3	85.0	86.0	89.7	71.8	88.9	86.2	80.0	90.2	89.5	80.9	80.0	81.8	87.0
9....	100.0	89.5	88.1	88.2	79.4	41.2	89.7	76.2	89.7	81.0	87.0	66.7	53.3	84.3
11....	83.3	80.2	90.0	88.3	86.6	68.4	86.1	84.6	79.4	76.9	65.6	63.6	60.0	76.2
13....	73.3	88.1	95.1	93.3	85.5	81.8	90.5	78.9	82.8	90.8	85.6	66.0	88.2	86.2
14....	81.2	90.9	92.5	91.0	91.9	100.0	90.6	100.0	84.2	73.3	78.9	......	......	80.4
15....	100.0	90.9	89.6	88.0	......	......	90.7	......	100.0	50.0	......	......	......	......
17....	95.8	96.0	97.7	97.1	85.6	90.9	96.9	89.8	88.1	89.6	76.2	40.0	60.0	86.5
18....	66.7	94.6	90.0	85.5	88.9	77.8	88.2	87.5	91.5	76.4	72.5	93.8	0.0	81.3
19....	100.0	88.2	93.1	97.0	69.6	......	93.1	68.2	77.3	91.6	73.2	65.0	54.5	81.3
20....	94.1	86.4	90.2	83.9	94.4	90.9	88.2	91.3	91.3	87.0	87.5	80.0	......	88.8
21....	75.0	95.4	87.3	79.4	85.7	......	86.9	91.9	91.1	87.5	82.6	100.0	......	88.0
23....	88.9	88.9	73.3	90.5	83.9	87.5	83.0	87.9	73.2	81.8	78.8	74.1	......	79.2
24....	85.0	92.3	92.5	90.2	91.8	90.9	91.2	78.8	79.5	76.3	74.5	87.5	......	77.2
31....	88.9	94.8	91.1	89.5	88.0	60.0	91.7	90.9	87.1	91.0	83.3	73.7	68.0	88.2
32....	97.6	88.6	91.5	86.4	81.2	100.0	90.2	85.1	85.8	85.4	73.0	58.8	0.0	83.0
34....	100.0	86.8	97.6	93.3	80.0	......	93.7	86.7	73.2	86.7	84.1	100.0	......	82.1
35....	78.9	89.4	87.1	92.8	90.0	71.4	88.1	80.0	88.9	87.3	81.2	79.2	60.0	85.8
36....	100.0	93.9	88.0	86.8	84.9	70.4	90.7	78.3	86.7	83.2	78.7	88.9	90.0	83.1
38....	82.9	93.1	94.5	85.9	84.6	60.0	92.2	81.8	84.5	80.5	81.5	62.5	66.7	82.0
39....	90.0	86.7	97.7	83.3	......	......	90.8	77.1	92.4	85.5	70.8	68.9	......	83.8

TABLE 11.—*The percentage raised to 33 days of all young (born dead or alive) in the different inbred families.*

[The average in litters of each size and the index (see Table 9), 1906 to 1910 and 1911 to 1915.]

Family.	Size of litter, 1906–1910.						Index.	Size of litter, 1911–1915.						Index.
	1	2	3	4	5	6		1	2	3	4	5	6	
	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.		Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	
1....	81.8	61.5	82.2	58.3	100.0	......	71.2	50.0	77.3	66.7	......	......	......	66.6
2....	72.7	75.0	75.0	66.2	88.6	66.7	73.0	78.6	81.9	72.7	68.8	47.5	......	75.3
3....	69.2	67.1	77.0	72.4	75.0	33.3	72.3	52.6	65.0	61.6	41.7	20.0	0.0	57.7
7....	71.4	72.3	75.4	69.1	50.9	44.4	72.8	65.3	75.4	72.8	67.4	58.2	50.0	71.8
9....	84.6	81.0	74.7	72.1	67.5	38.9	77.1	61.5	76.1	63.8	72.5	51.4	26.7	69.0
11....	58.8	72.2	79.4	74.6	67.6	43.3	74.2	64.7	71.0	67.9	43.8	31.1	50.0	63.7
13....	57.9	78.2	84.2	82.2	73.5	60.0	79.4	71.4	72.4	81.6	73.0	51.7	83.3	76.1
14....	68.4	73.2	80.5	75.0	75.6	33.3	76.0	83.3	76.2	56.4	53.6	......	......	64.2
15....	83.3	71.4	69.3	68.8	0.0	......	71.2	......	50.0	33.3	......	......	......	......
17....	92.0	91.3	90.4	89.5	82.8	55.6	90.7	74.6	82.5	80.1	63.2	20.0	50.0	76.9
18....	57.1	85.5	87.1	81.9	68.6	70.0	82.6	65.6	82.6	70.3	63.0	50.0	0.0	72.1
19....	90.9	68.2	81.8	82.5	64.0	......	78.8	62.5	72.8	70.7	44.6	52.0	33.3	65.3
20....	80.0	72.8	77.1	72.2	85.0	55.6	75.1	77.8	77.9	77.6	81.7	66.7	......	78.5
21....	75.0	84.0	79.7	75.0	60.0	......	79.6	69.4	75.4	75.0	59.4	10.0	......	71.4
23....	72.7	85.6	68.8	86.4	74.3	58.3	77.8	70.7	63.8	76.7	73.2	66.7	......	71.5
24....	73.9	83.1	82.6	76.7	71.8	83.3	80.7	53.1	60.0	63.2	58.3	35.0	......	60.3
31....	84.2	91.7	85.2	83.9	62.8	25.0	86.8	60.6	78.2	71.2	75.9	70.0	56.7	73.2
32....	93.0	82.1	82.9	73.4	58.5	66.7	81.8	80.0	73.3	76.6	51.9	33.3	0.0	71.0
34....	50.0	82.3	91.1	87.5	60.0	......	83.7	65.0	78.1	78.8	71.2	40.0	......	72.1
35....	65.2	88.4	81.3	69.6	54.0	50.0	79.5	57.1	80.0	80.1	67.6	50.7	27.8	75.3
36....	93.3	88.6	76.5	67.6	69.5	63.3	80.0	72.0	79.4	73.1	58.3	53.3	50.0	71.9
38....	86.7	87.1	91.7	72.6	73.3	50.0	86.0	72.0	78.9	74.6	63.1	33.3	33.3	73.3
39....	81.8	81.2	82.4	71.4	0.0	0.0	79.8	73.0	86.8	78.5	60.8	44.3	......	76.9

TABLE 12.—*The average birth weight of all young born (dead or alive) in the different inbred families.*

[The average in litters of each size and the index (see Table 9), 1906 to 1910 and 1911 to 1915.]

Family.	Size of litter, 1906–1910.						Index.	Size of litter, 1911–1915.						Index.
	1	2	3	4	5	6		1	2	3	4	5	6	
	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.		Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	Per c't.	
1....	99.1	78.7	72.1	59.5	72.5	......	74.3	103.9	89.9	65.9	......	......	......	76.3
2....	108.1	86.3	79.1	71.1	63.6	58.7	82.6	97.8	82.9	67.1	59.4	60.5	......	73.4
3....	111.4	91.7	79.5	70.8	67.1	57.6	84.6	104.5	88.7	73.1	67.0	49.5	27.8	79.7
7....	100.9	91.3	78.5	67.0	67.1	58.7	82.3	103.5	90.5	78.6	69.0	59.8	56.7	82.7
9....	107.6	99.7	82.2	76.0	65.0	64.5	88.8	107.6	94.2	79.3	75.3	64.5	55.5	85.5
11....	105.7	90.6	81.0	74.6	63.2	57.2	85.1	108.6	95.3	83.5	67.7	59.2	59.5	86.4
13....	107.7	101.2	83.0	76.0	71.1	64.1	89.5	113.5	96.5	82.7	71.7	64.0	61.2	87.7
14....	100.8	88.5	80.9	69.0	67.8	66.2	82.8	103.7	93.3	74.3	69.1	......	......	81.9
15....	122.8	90.5	83.0	68.4	40.5	......	86.3	......	94.5	91.2	......	......	......	
17....	105.7	86.4	74.1	68.6	63.2	55.1	79.9	101.0	88.1	72.3	62.4	53.8	59.5	77.9
18....	112.4	95.3	85.0	71.0	69.9	56.2	88.0	110.1	95.3	83.2	70.7	69.0	47.0	87.0
19....	110.1	85.5	78.7	75.9	68.9	......	83.3	112.8	97.1	80.6	65.4	71.3	62.8	85.5
20....	109.5	85.3	77.6	72.5	62.0	59.5	82.1	102.3	94.0	78.0	69.5	62.8	......	83.5
21....	112.0	96.7	82.2	76.2	60.5	......	88.3	96.1	87.8	75.8	65.4	57.5	......	79.4
23....	103.6	96.6	83.0	73.4	67.7	64.5	87.2	105.3	91.2	78.8	64.0	58.5	......	82.2
24....	103.8	89.2	77.8	67.2	62.9	59.8	81.7	100.1	81.6	71.1	62.2	59.0	......	75.4
31....	111.9	95.3	82.3	69.3	61.3	52.8	86.6	107.0	91.9	74.4	67.5	59.5	54.5	81.5
32....	105.0	90.0	75.8	68.9	57.5	50.6	81.6	103.1	85.5	74.8	62.1	56.8	47.8	78.3
34....	94.5	93.3	86.9	83.3	65.0	......	88.9	96.5	91.6	81.3	73.0	58.5	......	84.3
35....	104.5	90.1	76.0	69.0	59.2	55.1	81.7	97.6	94.8	81.0	70.0	63.8	54.3	84.6
36....	107.4	88.9	77.9	70.2	63.2	55.5	82.6	105.3	91.2	74.1	63.0	62.1	53.4	80.1
38....	107.2	91.1	81.5	71.0	63.2	57.0	84.9	118.5	98.4	81.9	69.6	62.2	63.7	88.1
39....	95.4	83.9	74.1	65.6	48.5	44.5	77.5	96.9	83.8	74.8	63.5	53.5	......	77.5

TABLE 13.—*The average birth weight of young raised to 33 days in the different inbred families.*

[The average in litters of each size and the index (see Table 9), 1906 to 1910 and 1911 to 1915.]

Family.	Size of litter, 1906–1910.						Index	Size of litter, 1911–1915.						Index
	1	2	3	4	5	6		1	2	3	4	5	6	
	Grams.	Grams.	Grams	Grams.	Grams	Grams.		Grms.	Grms.	Grms.	Grms.	Grms.	Grms.	
1....	104.5	88.9	74.8	65.9	72.5	......	80.2	112.0	95.1	69.5	......	......	......	81.1
2....	110.7	93.2	81.2	73.9	64.8	60.7	86.3	102.1	83.4	70.3	61.1	64.5	......	75.6
3....	121.2	97.4	82.4	72.1	71.7	61.5	88.7	114.5	96.8	77.9	75.5	74.5	......	86.8
7....	106.5	95.5	81.3	71.1	68.8	63.3	86.0	109.2	92.8	81.8	71.9	64.8	57.8	85.9
9....	110.9	101.6	85.9	78.9	66.9	73.1	91.7	120.1	98.1	83.8	76.9	67.8	62.0	90.3
11....	114.5	95.6	83.0	77.8	67.9	63.7	88.9	117.1	99.3	86.8	74.3	72.4	57.8	89.3
13....	119.0	105.4	86.3	77.9	73.5	64.5	93.6	119.2	102.0	85.7	73.7	71.9	63.2	91.5
14....	112.2	90.0	83.7	72.8	71.0	79.5	86.3	105.5	96.1	79.7	74.5	......	......	86.2
15....	124.5	90.7	85.7	69.0	......	......	87.7	......	114.5	84.5	......	......	......	
17....	107.1	87.3	76.3	69.9	64.7	65.5	81.4	103.6	89.6	74.3	65.9	67.8	61.2	80.1
18....	112.0	97.7	87.1	74.0	72.8	57.8	90.1	112.6	97.1	86.6	74.0	77.8	......	89.8
19....	113.5	92.5	83.4	75.7	70.7	......	87.6	120.5	99.2	83.6	74.7	81.4	66.2	90.2
20....	110.7	89.4	83.1	78.7	63.3	64.5	86.9	105.5	93.9	79.6	69.8	65.5	......	84.5
21....	118.9	97.3	84.1	77.5	67.8	......	90.2	98.3	88.1	75.8	66.1	44.5	......	79.8
23....	112.0	96.6	86.3	74.8	69.9	68.8	89.7	109.3	94.0	80.0	65.7	63.5	......	84.3
24....	105.4	91.5	79.3	70.7	65.8	60.8	83.9	100.7	83.3	75.5	66.2	57.4	......	78.5
31....	113.3	96.5	84.2	71.1	66.3	64.5	88.2	110.5	95.3	78.7	68.9	61.3	58.0	84.9
32....	107.7	93.0	78.3	70.3	59.5	53.7	84.1	106.7	88.5	77.0	67.1	60.5	......	81.4
34....	84.5	95.7	89.1	83.1	70.3	......	89.4	102.2	94.7	84.9	78.4	59.5	......	87.6
35....	107.8	89.9	78.7	73.3	61.9	58.5	83.9	107.0	97.0	82.1	72.2	65.8	61.8	87.5
36....	107.4	91.7	82.3	72.3	65.3	60.1	85.6	108.7	92.6	76.0	66.9	63.3	66.7	82.4
38....	107.6	93.4	82.4	76.1	66.6	61.2	87.0	124.5	99.7	83.9	75.3	74.5	64.5	91.0
39....	97.8	88.3	75.7	72.0	......	......	81.0	96.7	85.7	76.9	66.2	56.7	......	79.4

TABLE 14.—*The average gain between birth and 33 days, in the different inbred families.*

[The average in litters of each size and the index (see Table 9), 1906 to 1910 and 1911 to 1915.]

Family.	Size of litter, 1906–1910.						Index	Size of litter, 1911–1915.						Index
	1	2	3	4	5	6		1	2	3	4	5	6	
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*		*Grms.*	*Grms.*	*Grms.*	*Grms.*	*Grms.*	*Grms.*	
1.....	207.2	158.1	144.4	152.2	173.0	......	156.4	162.5	157.9	102.9	......	......	......	126.2
2.....	158.8	162.6	144.8	142.4	95.0	101.3	151.1	134.1	137.5	118.1	101.6	112.4	......	122.2
3.....	208.3	187.7	161.5	138.8	130.5	138.0	169.5	189.0	173.2	156.5	154.0	155.0	......	164.2
7.....	181.0	179.0	150.7	145.1	140.0	116.2	161.1	160.9	161.5	148.0	121.6	129.7	142.8	148.0
9.....	229.6	189.7	179.3	153.8	158.2	127.8	182.4	215.6	186.8	148.0	134.5	140.6	130.0	163.7
11.....	205.0	191.7	154.3	159.5	125.0	119.6	171.6	201.4	194.3	157.1	139.0	132.8	158.4	169.1
13.....	212.3	206.8	169.6	161.2	138.6	127.2	183.4	207.0	178.7	150.9	133.3	129.9	93.0	161.4
14.....	217.3	178.2	167.0	136.7	139.7	170.0	169.3	192.0	164.0	140.7	121.7	......	......	149.0
15.....	225.0	165.3	147.3	125.9	......	......	156.2	......	115.0	165.0	......	......	......	......
17.....	163.3	158.8	159.6	124.3	120.3	114.0	152.7	175.3	155.4	131.8	118.8	121.7	115.0	140.7
18.....	187.5	177.5	161.2	153.5	140.0	123.1	167.1	169.3	151.7	139.8	127.5	167.7	......	143.9
19.....	212.0	154.3	157.6	131.4	121.3	......	156.8	153.0	160.9	127.5	122.1	101.9	93.3	139.0
20.....	182.6	167.7	158.3	147.7	114.4	131.0	161.4	169.7	155.8	129.1	100.9	98.0	......	135.6
21.....	217.2	192.7	166.8	153.5	151.7	......	177.0	190.0	161.6	137.2	123.4	145.0	......	147.0
23.. ..	215.0	185.4	165.0	132.1	137.3	123.6	169.5	176.8	155.8	124.3	102.8	125.0	......	134.7
24.....	172.3	169.1	153.5	135.8	135.6	111.4	156.5	171.1	153.5	146.4	131.3	72.1	......	148.0
31.....	201.2	167.9	156.6	135.8	139.6	131.7	160.3	171.0	162.7	145.8	118.5	117.5	143.3	147.9
32.....	180.3	168.2	149.3	137.0	128.0	132.5	155.6	165.8	159.7	131.1	129.4	139.0	......	142.9
34.....	165.0	169.0	172.6	180.7	147.5	......	172.4	116.5	139.2	133.8	137.9	100.0	......	134.5
35.....	184.4	164.9	151.4	138.9	147.6	141.7	156.2	162.5	161.9	143.8	129.9	131.6	129.0	148.3
36.....	192.1	165.5	163.1	140.9	136.5	143.1	162.3	188.6	159.5	141.9	132.2	146.2	76.1	149.9
38.....	200.4	175.4	178.3	168.8	127.3	125.0	177.7	223.9	170.1	152.1	131.2	123.0	95.0	160.5
39.....	185.0	184.3	150.5	152.5	......	......	164.1	181.0	160.3	144.3	112.3	117.3	......	146.4

TABLE 15.—*The average weight at 33 days in the different inbred families.*

[The average in litters of each size and the index (see Table 9), 1906 to 1910 and 1911 to 1915.]

Family.	Size of litter, 1906–1910.						Index	Size of litter, 1911–1915.						Index
	1	2	3	4	5	6		1	2	3	4	5	6	
	Grams.	*Grams.*	*Grams.*	*Grams*	*Grams*	*Grams.*		*Grms.*	*Grms.*	*Grms.*	*Grms.*	*Grms.*	*Grms.*	
1.....	311.7	247.0	219.2	218.1	245.5	......	236.6	274.5	253.0	172.4	......	......	......	207.3
2.....	269.5	255.8	226.0	216.3	159.8	162.0	237.4	236.2	220.9	188.4	162.7	176.9	......	197.8
3.....	329.5	285.1	243.9	210.9	202.2	199.5	258.2	303.5	270.0	234.4	229.5	229.5	......	251.0
7.....	287.5	274.5	232.0	216.2	208.8	179.5	247.1	270.1	254.3	239.8	197.5	194.5	200.6	233.9
9.....	-340.5	291.3	265.2	232.7	225.1	200.9	274.1	335.7	284.9	231.8	211.3	208.4	192.0	254.0
11.....	319.5	287.3	237.3	237.3	192.9	183.3	260.5	318.6	293.6	243.9	213.3	205.2	216.2	260.2
13.....	331.3	312.2	255.9	239.1	212.1	191.7	277.0	326.2	280.7	236.6	207.0	201.8	156.2	252.9
14.....	329.5	268.2	250.7	209.5	210.7	249.5	255.6	297.5	260.1	220.4	196.2	......	......	235.2
15.....	349.5	256.0	233.0	194.9	......	......	243.9	......	229.5	249.5	......	......	......	......
17.....	270.4	246.1	235.9	194.2	185.0	179.5	234.1	278.9	245.0	206.1	184.7	189.5	176.2	220.8
18.....	299.5	275.2	248.3	227.5	212.8	180.9	257.3	281.9	248.8	226.4	201.5	245.5	......	233.7
19.....	325.5	246.8	241.0	207.1	192.0	......	244.4	273.5	260.1	211.1	196.8	183.3	159.5	229.2
20.....	293.3	257.1	241.4	226.4	177.7	195.5	248.3	275.2	249.7	208.7	170.7	163.5	......	220.1
21.....	336.2	290.0	250.9	231.0	219.5	......	267.2	288.3	249.7	213.0	189.5	189.5	......	226.8
23.....	327.0	282.0	251.3	206.9	207.2	192.4	259.2	286.1	249.8	204.3	168.5	188.5	......	219.0
24.....	277.7	260.6	232.8	206.5	201.4	172.2	240.4	271.8	236.8	221.9	197.5	129.5	......	226.5
31.....	314.5	264.4	240.8	206.9	205.9	196.2	248.5	281.5	258.0	224.5	187.4	178.8	201.3	232.8
32.....	288.0	261.2	227.6	207.3	187.5	186.2	239.7	272.5	248.2	208.1	196.5	199.5	......	224.3
34.....	249.5	264.7	261.7	263.8	217.8	......	261.8	218.7	233.9	218.7	212.7	159.5	......	222.1
35.....	292.2	254.8	230.1	212.2	209.5	200.2	240.1	269.5	258.9	225.9	202.1	197.4	190.8	235.4
36.....	299.5	257.2	245.4	213.2	201.8	203.2	247.9	297.3	252.1	217.9	199.1	209.5	142.8	232.3
38.....	308.0	268.8	260.7	244.9	203.4	186.2	264.7	348.4	269.8	236.0	206.5	197.5	159.5	251.5
39.....	282.8	272.6	226.2	224.5	......	......	245.4	277.7	246.0	221.2	178.5	174.0	......	225.8