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TB 279 (1932)

CORRELATION OF HEREDITARY

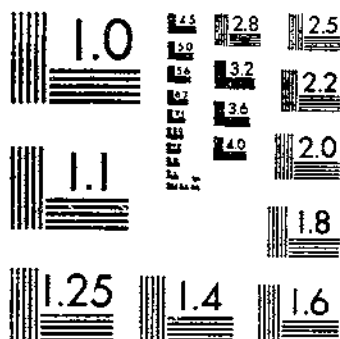
AND OTHER FACTORS AFFECTING
GROWTH IN GUINEA,
EATON, O. N.

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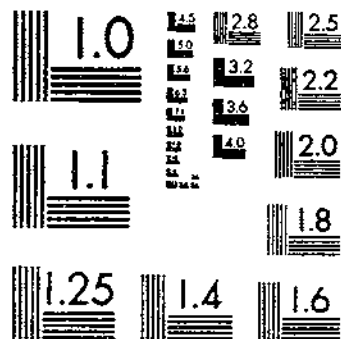
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UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

CORRELATION OF HEREDITARY AND OTHER FACTORS AFFECTING GROWTH IN GUINEA PIGS

By OBSON N. EATON, *Associate Animal Husbandman, Animal Husbandry Division, Bureau of Animal Industry*

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INTRODUCTION

In previous studies of inbreeding in guinea pigs, Wright (17)¹ has discussed its effects on litter size, frequency of litter, weight at birth and weaning, and gain between birth and weaning. He has shown that high correlations exist between litter size and birth weight, birth weight and weaning weight, frequency of litter and litter size, and various other factors. Neither the variations in these correlations among the different inbred and control lines of guinea pigs have been shown, nor the correlations between early weights and gains and those after weaning. This bulletin shows the correlations which exist among several factors influencing birth weight and their relative influence during different parts of the growth period.

In such a study it becomes obvious that factors such as birth weight, early gains, weaning weight, litter size, and gestation period are closely correlated with one another. Heredity, environmental conditions such as feed, certain seasonal changes, and condition of the dam will also be recognized as influencing some or all of these factors.

Conditions affecting the dam would be expected to affect the young directly or indirectly, especially during gestation and for a short period thereafter. The question arises whether as the young approach maturity the effects on growth of the factors named above

¹ Italic numbers in parentheses refer to Literature Cited, p. 34.

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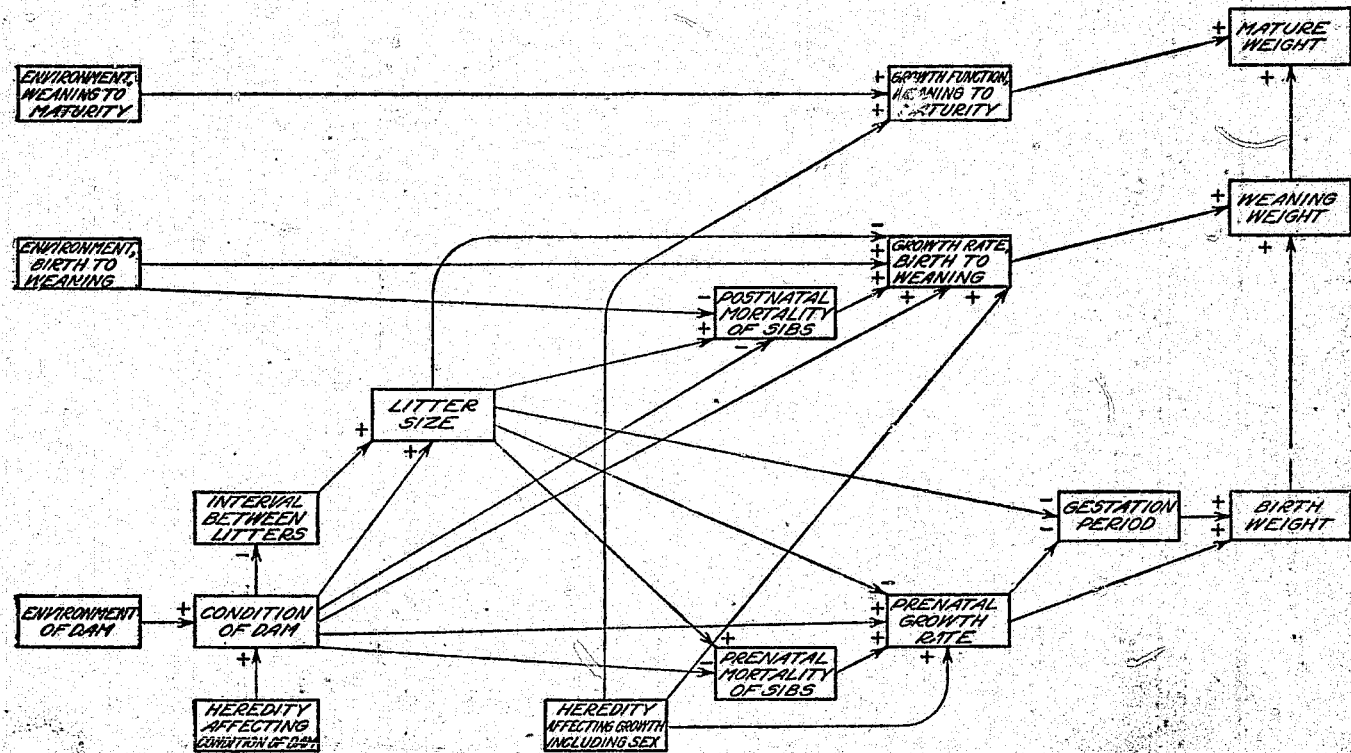


FIGURE 1.—Diagram of the paths of action of the various factors which affect the mature weight of guinea pigs

disappear or have a tendency to persist. Some of these effects, such as litter size, are due almost entirely to the dam, either to her heredity for producing large or small litters, or to some condition which affects the prenatal mortality of the young. The sire's influence on the young would be expected to be very small except for general heredity or influence on size or growth rates.

Mathematical measurement of some of the influences contributing to the growth of the young or the number of young can not be made. For example, the only satisfactory measurements which can be made of condition of dam are age and weight at time of parturition. Within a given line of heredity, females of the same age and breed should have a weight conforming within certain limits to the average weight of females for that age and breed. One which has a marked deficiency in weight would be regarded as being subnormal in general condition. Very young and very old females are not considered to be as good producers as females somewhat midway between these limits.

Effect of feed can be best expressed as a general upward or downward trend of growth and by increased or lessened mortality immediately after a change of feed.

Similarly, seasonal conditions are expressed by trends in the growth and mortality curves. These influences undoubtedly do exert an appreciable effect on some of the factors that can be more definitely measured, and affect, to a certain extent, the real value of the correlations between them.

A diagram showing possible relations between various factors affecting growth is shown in Figure 1. In this diagram the paths and direction of influence are shown by the arrows connecting the various factors represented. Whether the factor concerned exerts a positive or negative influence on another is shown by a plus or minus sign.

The data from which these studies have been made were obtained from the guinea-pig colony maintained by the Bureau of Animal Industry at its experiment farm near Beltsville, Md. Five inbred lines out of 23 lines with which the experiment was begun in 1906 have been kept to the present time by means of brother-sister mating. These are designated as families 2, 13, 32, 35, and 39, the numeral being the identification number of the ancestral female of each line. A control stock, B, with no matings more closely related than second cousins has been maintained for comparison. All have been under like conditions of management and feed; temperature and other conditions are kept as nearly uniform as it is economically possible to do so. Records are kept of the young born, including the day of birth, sex, color, birth weight, weight of sire and dam, and any other facts of interest such as deformities, peculiar spotting, or unusual size. From January, 1916, to June, 1923, weights were taken at the ages of 3, 13, 23, and 33 days, the last being the age at weaning; but since June, 1923, the keeping of weights between birth and weaning has been discontinued. The breeding animals are weighed at 53 days of age and every 30 days thereafter until death or removal from the experiment. By this system it is possible to record the age of sire and dam at the birth of each litter and the interval between succeeding litters.

Green feed throughout the year varies from freshly cut grass or alfalfa in summer to cabbage or kale in the winter. There has been considerable variation in the quality of the green feed at different times during each year. The hay fed has varied from timothy and poor clover to the highest quality alfalfa. The grain ration has consisted exclusively of whole oats.

PREVIOUS WORK

Considerable investigation has been made of the relation to one another of various factors affecting the growth of animals. Eckles (3) finds that in dairy cattle the age of the dam has an important bearing on the vigor of the calves produced, those between 5 and 10 years old producing the most vigorous calves. The length of gestation period and probably the weight of the dam also are correlated with the weight of the calf at birth. Weight of sire has little to do with the birth weight of the calf unless the sire is of a different breed from the dam. The nutrition of the cow during gestation appears to have little influence on the birth weight of the calf. In cattle, breed seems to be the most important factor influencing birth weight. Carmichael and Rice (2) find that in swine litter size increases with age of dam up to a maximum, after which there is a decrease. Investigations of Jones and Rouse (7) show that for multiparous animals the frequency of litters increases with the age of the dam, but this is not definitely determined for uniparous animals. King (8), working with rats, finds that age of dam has an influence on weight of young at birth. The young female is growing and uses energy that would otherwise go into the embryos if she were mature. The female's body weight is determined by her health, age, and other factors, all of which are reflected in the weight of the young. Large litters have a shorter gestation period, and the lactation period of the female affects the length of gestation period for the next litter. First litters are usually smaller and average lighter in weight than following litters. In a later work (9) the same author states that first litters usually are an index of the fertility of the female; if the first litter is large, the others are likely to be large. Litters from very young females are more variable in size and weight than those from older females. The sex of the young is not appreciably affected by age of dam.

Kopeć (11), working with rabbits, has carried on studies very similar to those of the Bureau of Animal Industry on guinea pigs and has obtained similar results. In another paper (12) he reports effect of litter size, nutrition and age of dam, and length of gestation period on weight at birth and effect of various of these factors on litter size. He finds a correlation of -0.71 ± 0.06 between litter size and birth weight except in an F_2 reciprocal cross where the correlation is -0.52 ± 0.07 . Age of dam affects litter size only in the case of old females which produce larger litters and heavier young than very young females. Length of gestation period and litter size have a correlation of -0.59 ± 0.07 , and weight of young is directly correlated with length of gestation period. In another paper Kopeć (13) states that there is a correlation between the birth weight and all following weights, but that if the animals are grouped according to litter size this correlation disappears.

EXPERIMENTAL DATA

FACTORS AFFECTING LITTER SIZE

CONDITION OF DAM

It has been stated previously that the most satisfactory data available on the dam's condition are her age and weight at time of parturition. These factors were used in this study in measuring the effect of the dam's condition on the various characteristics of the young. In most of the matings made, the male and female are put together at weaning time (33 days of age). A vigorous female is sexually mature at this time, but it is usually a month later before the male reaches sexual maturity. Since the gestation period averages about 67 days, a female's first litter is usually born when the female is between 4 and 5 months old. Her reproductive period extends to about 30 months of age, but litters are frequently produced by females much older.

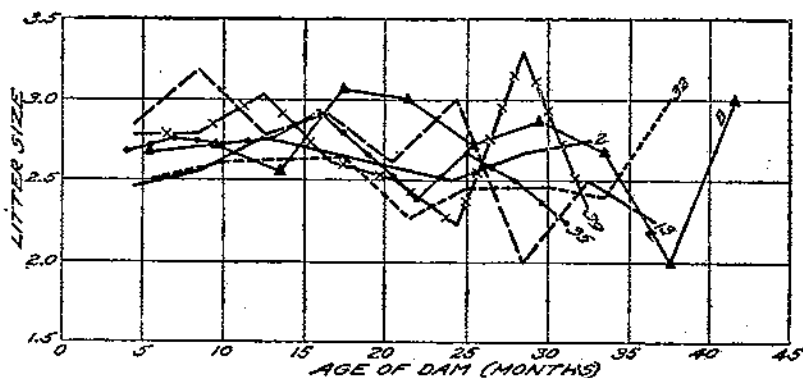


FIGURE 2.—Effect of age of dam on litter size in the five inbred families and control stock of guinea pigs

King (9), Kopeć (12), and Hammond (5) find that the litter size in rats, rabbits, and swine increases to a maximum as the dam's age increases to a certain age, varying for each species, after which the litter size decreases.

There is a slight indication of this for guinea pigs also, but in general there is a great variation for all ages, as shown in Figure 2. The maximum litter size appears in general to occur in inbred stock when the dams are between 12 and 16 months old and in the control stock when the dams are about 18 months old. The reason for the difference between inbred and control stock can not be that the inbreds are mated when slightly younger than the control stock and have produced more litters, for the maximum litter size occurs at about two litter ranks higher in control stock B than in the inbred lines. The reason may be that the inbreds reach their maximum reproductive capacity at an earlier age because of earlier maturity, and that the control stock, maturing later and being more vigorous, retains its high reproductive powers to a greater age.

The relationship between dam's age and litter size is not linear; therefore, the correlation ratio, expressed by the symbol η , is used.

This is computed by the formula $r_{xy} = \frac{\sigma_{xy}}{\sigma_x}$, in which x and y are the two variables, σ_{xy} is the standard deviation of the means of the x arrays, and σ_x is the standard deviation of the x 's. No correction factors have been used in any of the correlation ratios in this bulletin. The values for families 2, 32, and 35 are similar, 0.14, 0.15, and 0.16, respectively, whereas for families 13 and 39 the respective values are 0.25 and 0.27. (Table 1.) The differences, however, are not statistically significant, nor does control stock B, with a value of 0.31, differ significantly from the inbred lines taken separately or from their average value of 0.19, averaged by weighting each family by the number of individuals concerned. This seems to indicate that litter size is more uniform in the inbred lines than in the control stock and, therefore, less influenced by the dam's age.

TABLE 1.—Correlation ratio of age of dam on various factors in guinea pigs

Stock	Number of individuals ¹	Correlation ratio of age of dam to—						
		Length of gestation	Litter size	Birth weight	Gain to 33 days	33-day weight	53-day weight	353-day weight
Inbred:								
Family 2.....	232	0.3089	0.1439	0.1278	0.2296	0.1957	0.2337	0.1693
Family 13.....	215	.1740	.2484	.1467	.2304	.1973	.2159	.1531
Family 32.....	187	.1250	.1503	.2181	.2093	.1745	.2133	.1603
Family 35.....	184	.2838	.1591	.2018	.2791	.2773	.2598	.2315
Family 39.....	128	.1746	.2747	.2537	.4457	.4164	.3185	.2115
Total.....	946	.2319	.1898	.1814	.2642	.2376	.2422	.1707
Control B.....	113	.2545	.3138	.2519	.2893	.2949	.2665	.3074

¹ Numbers given apply to all correlations in this table, except length of gestation period for which the numbers are 673, 468, 293, 251, 121, and 483 for the inbreds and B stock, respectively.

After the birth of a litter the dam's weight bears a higher relationship to litter size than does the dam's age, as shown by the higher correlation ratio values. The real influence is probably not the dam's weight but her general condition of health or vigor, which is expressed in her weight. There is less variation in the correlation values of the different families and control stock than there is in the correlation between age of dam and litter size. The average value of r for the five inbred families is 0.26 and for control stock B 0.34. (Table 2.)

TABLE 2.—Correlation ratio of weight of dam on various factors in guinea pigs

Stock	Number of individuals	Correlation ratio of weight of dam to—					
		Litter size	Birth weight	Gains to 33 days	33-day weight	53-day weight	353-day weight
Inbred:							
Family 2.....	232	0.2057	0.1910	0.1674	0.2021	0.1922	0.2005
Family 13.....	218	.3799	.3922	.2056	.3331	.3497	.2245
Family 32.....	187	.2141	.3032	.4088	.3996	.3820	.2184
Family 35.....	184	.2554	.4628	.2059	.3779	.3865	.3330
Family 39.....	128	.3793	.4820	.4658	.5077	.4523	.4043
Total.....	946	.2574	.3511	.3032	.3464	.3391	.2628
Control B.....	113	.3363	.4417	.3092	.3736	.3183	.3539

LITTER RANK

Litter rank and age of dam are necessarily closely correlated, as litters should be produced at about 69-day intervals after the first litter, provided the sire and dam mate regularly. In some cases one or more oestrus periods of about 16 days are skipped before mating again occurs. In a few other cases old males have been mated to young females or vice versa. These cases are so few, however, that the coefficient of correlation between litter rank and age of dam is 0.91 for the inbred lines and 0.95 for the control stock B.

Various investigators find that litter rank affects litter size. King (9) states that with rats, first litters are the smallest and are also usually an index of the dam's fertility. There is a general tendency for litter size to increase from first litters to the third or fourth and

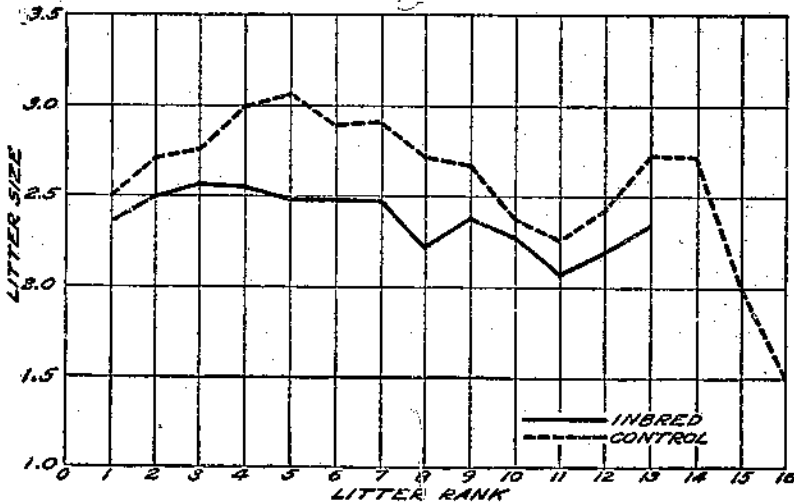


FIGURE 3.—Effect of litter rank on litter size in the average of five inbred families and the control stock of guinea pigs

then gradually to decrease. This is shown in Figure 3. The curve is erratic after the eighth litter in the inbreds and the tenth litter in the control stock because of the few litters involved. The largest litters in control stock B occur at a later birth rank than in the inbreds, a fact which may be due to earlier maturity of the inbreds or to more frequent mating of the controls. The average value of the correlation ratio of litter rank to litter size is 0.18 for the inbred lines and 0.32 for the control stock. (Table 3.) In the individual inbred families the correlation ranges from 0.14 in family 35 to 0.21 in family 32. The high value of the B stock is rather outstanding, but in no case is the difference between this stock and the inbreds statistically significant.

Relation between size of first and later litters was calculated for family 2, which was typical of the inbred families and had a large number of litters, by weighting the number of first litters by the number of later litters produced in a particular mating. This gave 1,110 litters entering into the correlation with an average size of 2.61 for first litters and 2.92 for later litters and 0.10 as the coefficient of correlation between them. This is not a high correlation and could

hardly be interpreted as indicative of the size of later litters. It disagrees with the statement of King (9) that first litters are an index of the dam's fertility, if fertility is considered in terms of litter size.

TABLE 3.—Correlation ratio of litter rank to various other factors in inbred and control stocks of guinea pigs

Stock	Number of individuals	Correlation ratio of litter rank to—		
		Litter size	Birth weight	Gain from birth to weaning
Inbred:				
Family 2.....	232	0.1768	0.2090	0.2007
Family 13.....	215	.1700	.1523	.2631
Family 32.....	187	.2116	.2067	.1892
Family 35.....	184	.1443	.1523	.2333
Family 39.....	128	.1928	.2637	.3057
Total.....	945	.1704	.2024	.2255
Control B.....	113	.3173	.2631	.2224

SEASON OF YEAR

Wright (18) shows that season of the year in which guinea pigs are born has an influence on litter size. King (10) finds this true also with rats and cites many instances from the works of other investigators who have found a seasonal effect on the breeding of various animals. In general, it may be said of guinea pigs that the largest litters are born late in the summer and the smallest in the winter. When litter size in each month is considered separately, there is so much variation that no conclusion can be drawn. The variation among the different families suggests that they respond differently to the same seasonal condition. This is further borne out by the higher death rates in families 32, 35, and 39 during adverse conditions, a matter which is discussed later. Families 2 and 13 seem the easiest to keep alive and propagate. King (10) states that this seasonal effect is an indirect one, acting through the dam. Scarcity of good succulent feed and sudden temperature changes in winter reduce the vitality of the dam, but normal conditions in the spring and summer restore vitality.

The primary seasonal influence on litter size occurs at conception, about 67 days before the birth of the litters. Therefore, it is the seasonal condition at that time and not at birth that affects litter size. Litters born late in the summer, then, are conceived early in the summer or in midsummer, when conditions are favorable, and those born in winter and early in the spring are conceived late in the fall or in the winter, when conditions are not so favorable.

HEREDITY

It has been shown by many investigators with livestock and laboratory animals that breeds differ in conformation, weight, fertility, and other factors. In the guinea pigs from which the data for this bulletin were obtained, Wright (16, 17), Wright and Eaton

(19), and McPhee and Eaton (14) have shown that there are distinct differences in litter size, birth weight, and other characters among the inbred and control stocks. These different lines have as distinctly different characteristics as the breeds of livestock which differ in similar characters. If the sire and dam are of the same breed, they are expected to reproduce breed characteristics in their offspring. Variation in litter size may be considered as characteristic for the different inbred lines, but just how much this has been fixed by heredity may be ascertained from a study of the variability of litter size between the inbred and control stocks.

The coefficient of variability of litter size for the inbred lines is 31.56 and for control stock B is 33.98. The inbreds, therefore, are 87.72 per cent as variable as is the control stock. By squaring this percentage the variance of the inbreds is obtained, which is 76.94 per cent. Subtracting this from 100 per cent, considered as the total variance of a random-bred stock, gives 23.06 per cent as the variance due to genetic factors which has been reduced by inbreeding. This is less than one-fourth the assumed total variability of the stock at the beginning of the experimental breeding. Therefore, heredity does not play so large a part in determining litter size as might at first be expected. King (10) states that among various factors studied in rats, litter size is by far the most constant, a statement which agrees with the data here presented.

FACTORS AFFECTING BIRTH WEIGHT

LITTER SIZE

Litter size is probably the most important factor in determining birth weight of guinea pigs. There is a gradual drop in weight from individuals born in litters of one to those born in larger-sized litters. In previous data Wright (17) has reported the coefficient of correlation between litter size and mean birth weight of litter to be -0.66 . The data presented in this bulletin do not include all young, as did Wright's data, but only males which were mated between 1916 and 1925. The coefficient of correlation is only slightly lower, however, than Wright's, having a value of -0.62 for the average of all inbred lines and -0.60 for the control stock. (Table 4.) The difference among the various inbred families shows a range from -0.52 in family 35 to -0.71 in family 32. The difference between these values is -0.19 ± 0.065 , which is considered significant. This difference is probably due to the fact that birth weight was less variable in family 32, as shown by the coefficient of variability, than in any of the other stock. Litter size in this family was as variable as the average variability for all inbred lines. On the other hand, birth weight was more variable in family 35 than in family 32, whereas litter size was less variable than the average for all inbreds. By decreasing one variable and increasing the other the coefficient of correlation becomes lower.

TABLE 4.—Correlation between litter size and weights at ages indicated in inbred and control stocks of guinea pigs

Stock	Number of individuals	0 days	33 days	53 days	83 days	173 days	263 days	333 days
Inbreds:								
Family 2.....	232	-0.6313	-0.4254	-0.2063	-0.2072	-0.2430	-0.2413	-0.2055
Family 13.....	216	-.6470	-.4368	-.3170	-.2182	-.1825	-.1233	-.1220
Family 32.....	187	-.7004	-.4803	-.3669	-.2335	-.2096	-.2042	-.1818
Family 35.....	164	-.5230	-.3689	-.2138	-.0803	-.0289	+ .0527	+ .0416
Family 39.....	128	-.5828	-.3325	-.1817	-.0600	-.0729	-.0394	-.0925
Total.....	946	-.6221	-.4195	-.2850	-.1703	-.1581	-.1226	-.1185
Control B.....	113	-.6038	-.3292	-.2365	-.1758	-.1566	-.1148	-.1185

Stock	Number of individuals	448 days	533 days	Number of individuals	623 days	713 days
Inbreds:						
Family 2.....	162	-0.1833	-0.2018	112	-0.1721	-0.0748
Family 13.....	145	-.1580	-.2545	102	-.1254	-.0978
Family 32.....	135	-.3071	-.3095	88	-.3189	-.1832
Family 35.....	104	+ .6378	+ .0023	61	-.2098	-.1401
Family 39.....	95	+ .1174	+ .0835	67	+ .0136	-.0096
Total.....	641	-.1245	-.1651	440	-.1712	-.1034
Control B.....	85	-.1118	-.1270	68	-.0550	-.0327

LENGTH OF GESTATION PERIOD

It has often been noticed in the guinea-pig records that young carried longer than the normal gestation period are heavier than those born earlier. This is true of all mammals. The gestation period of the guinea pig varies from 62 to 76 days, with the average about 68 days. No young born in less than 62 days after the preceding litter were alive at birth or survived more than a few hours, and those born later than 76 days afterwards should probably be considered as having been conceived at the second period of oestrus after the previous litter.

The coefficient of correlation between length of gestation period and birth weight averages 0.40 for the inbred lines and 0.44 for the B stock. (Table 5.) Family 13 has the lowest coefficient among the inbreds, with a value of 0.28, which does not, however, differ significantly from the average for all inbred lines. This difference in correlation is due to greater variability in length of gestation period and average variation in birth weight, as explained previously.

TABLE 5.—Coefficient of correlation of length of gestation period to birth weight in inbred and control stocks of guinea pigs

Stock	Number of individuals	Correlation	Stock	Number of individuals	Correlation	
Inbred:						
Family 2.....	1,110	0.4601	Inbred—Continued.			
Family 13.....			161	0.3426		
Family 32.....					2,720	.4040
Family 35.....						
Family 39.....	357	.4770	Control B.....			

Minot (15) states that large litters average less in weight than do small litters, since they are in the uterus a shorter period and as a result have a shorter time in which to develop. Ibsen (6) disagrees with this statement, as the young which he compared in different sizes of litters were in the uterus the same length of time. He believes that difference in weight at birth is due to difference in number in the litter rather than to length of prenatal-growth period. The data in this bulletin seem to indicate that both these conditions are influential factors of birth weight, for small litters have a longer gestation period than large litters (Table 6) and when the number of fetuses is small there is more nourishment available for each from the uterine circulation than when the number of fetuses is large.

TABLE 6.—Length of gestation period in different-sized litters in inbred and control stocks of guinea pigs

[Average size of litter for each family is given in parentheses]

Litter size	Family 2 (2.38)		Family 13 (2.66)		Family 32 (2.15)		Family 35 (2.31)		Family 39 (2.71)		B stock (2.76)	
	Litters	Average gestation period	Litters	Average gestation period	Litters	Average gestation period	Litters	Average gestation period	Litters	Average gestation period	Litters	Average gestation period
	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
1	108	69.83	78	71.44	67	72.23	63	71.06	14	68.93	80	71.08
2	287	68.88	131	70.31	74	70.84	85	70.39	39	69.76	131	70.68
3	189	68.25	129	69.81	66	70.09	70	69.53	42	69.74	129	69.34
4	80	67.78	81	68.61	13	69.12	29	68.47	16	67.44	102	68.53
5	6	66.67	27	68.13	3	67.50	4	70.00	8	67.38	38	68.68
Total or average.	670	68.70	446	69.86	223	70.89	251	70.32	119	68.70	480	69.65

EFFECT OF LITTER SIZE ON LENGTH OF GESTATION PERIOD

The average length of gestation period in families 2 and 39 is 68.7 days; in families 13 and the B stock, 69.8 and 69.6 days, respectively; and in families 32 and 35, 70.9 and 70.3 days, respectively. (Table 6.) This grouping does not correspond with average litter size for these families; length of gestation is, therefore, dependent on some factors aside from this.

Average length of gestation period for litters of one in all the inbred lines is 70.9 days, whereas for litters of five the average is 67.9 days. The coefficient of correlation between gestation period and litter size averages -0.37 for the inbred lines and -0.43 for the control stock.

The reason for gestation period varying for different sized litters has not been satisfactorily explained. It can not be a matter of weight of the fetuses, for there are numerous cases in which a litter of 1 or 2, although it exceeded in weight that of a litter of 4 or 5, was carried 73 to 75 days whereas the litter of 4 or 5 was expelled at about 65 days. Hammond (5) lists several theories of the causes of birth taken from Williams's Veterinary Obstetrics. Among those seeming most likely, from the observations on guinea pigs, are in-

creasing size of the fetus and consequent increasing distension and irritability of the uterus, and the possibility of the action of hormones.

EFFECT OF AGE OF DAM ON LENGTH OF GESTATION PERIOD

Age of dam seems to have an effect on the length of the gestation period of guinea pigs (fig. 4), the younger females having the shorter period. This is true for all the inbred lines, but there is considerable variation among them. Families 2, 35, and 39 have a very perceptible rise in length of gestation period for increase in age of the dam, bearing almost a linear relationship. The drop or rise at or near the end of the graphs is due to but one litter at these ages of the female. The gestation periods of families 13 and 32 seem to be less affected by dam's age. The difference in length of gestation period in the first 3 families named varies more than a day for females at 4 months of age and those at 30 months of age; for the last 2 families the

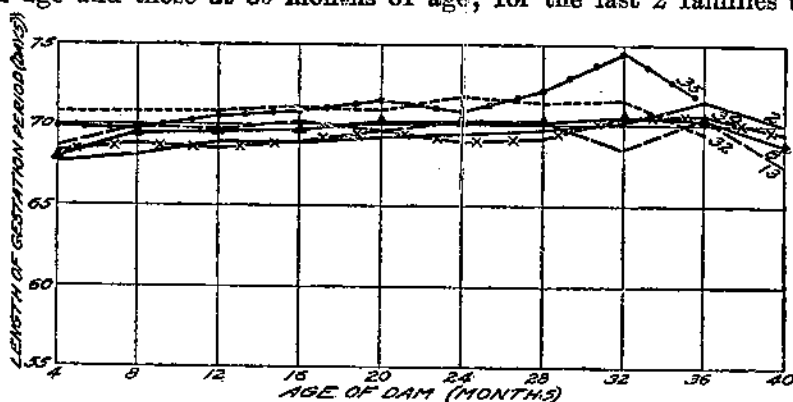


FIGURE 4.—Effect of age of dam on length of gestation period in inbred families and the control stock of guinea pigs

difference is only about half a day for the same age differences. Stock B has a gradual rise in length of gestation period from females 4 months old to 32 months old and then a decline, but the length of gestation period is nearly a day greater for females 40 months old than for those 4 months old and the maximum gestation period at 32 months of age is slightly more than $1\frac{1}{2}$ days longer than at 4 months. The value of γ for the five inbred lines is 0.23 and for B 0.25. (Table 1.)

These results appear to contradict the fact that litter size also rises with age of dam; consequently, length of gestation period should drop. The rise in litter size, however, is not so great as the difference in days of gestation, and after the maximum litter size is reached at about the twelfth to sixteenth month of the dam's age, litter size decreases. A possible explanation of the increase in gestation period in older females, which are producing on an average slightly larger litters, is found in the theory of parturition because of irritation and distension of the uterus. Since the birth weight and consequently the number of pigs in first litters are only very slightly smaller than in later litters, and since the uterus of the young female and the female herself as an organism have not reached their maximum physical

development, less distension and irritation of the uterus are necessary to cause parturition in a young female than in an older one which has reached maximum physical development, and therefore a young female will expel the fetuses earlier.

CONDITION OF DAM

Since the condition of the dam, as expressed by age and weight, has been found to influence litter size to a certain extent, it is to be expected that weight at birth will be influenced also by these factors. King (9) working with rats, Kopeć (11) with rabbits, Eckles (3) with cattle, and Carmichael and Rice (2) with swine, have found this relationship between age of dam and birth weight of

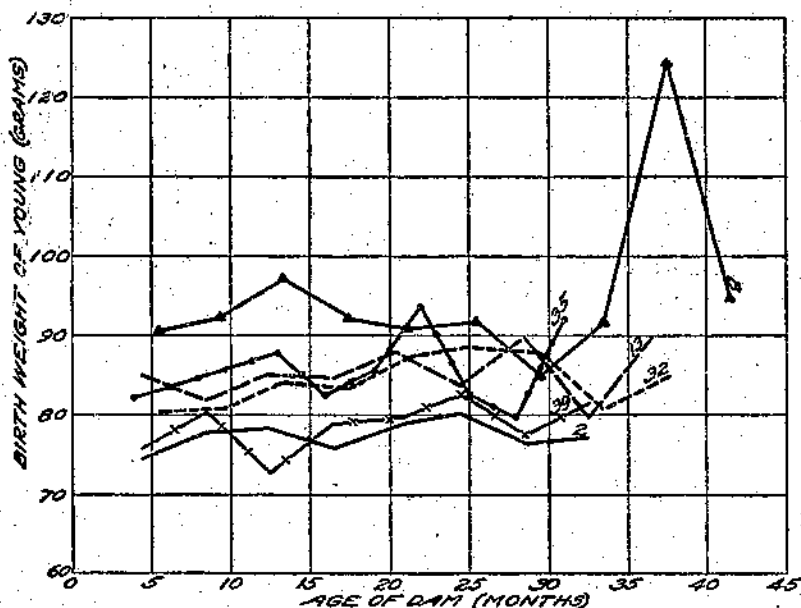


FIGURE 5.—Effect of age of dam on birth weight of young in five inbred families and the control stock of guinea pigs

young to exist. In all cases the young from mature dams were heavier than those from young females. In guinea pigs this is also true to a slight degree, as shown by Figure 5. Not much weight is to be placed on results after 30 months, as only a few females bore young after this age. The value of the correlation ratio of age of dam to birth weight of young was 0.13 and 0.15 for families 2 and 13, respectively, and 0.22, 0.20, 0.25, and 0.25 for families 32, 35, 39, and B. The differences in these values are in no case statistically significant. The average value for all the inbred lines is 0.18. (Table 1.)

Since weight of dam is more of an indication of the dam's health and vigor than is age, a closer relationship to the birth weight of the young would be expected. This is shown in higher correlations between these factors. All inbred families except family 2 have a correlation ratio of more than 0.3. (Table 2.) The low value of 0.19 for family 2 appears to be due to greater variability of the birth

weight of the young in the data from which these figures are calculated than in the other inbred lines. The average correlation ratio of weight of dam to birth weight of young is 0.35 for the inbred lines and 0.44 for the control stock. The difference is not statistically significant.

When the young are classified as to size of litter in which they were born, the correlation between the dam's weight and the birth weight of the young increases as the litter size increases. The averages for the 5 inbred families are 0.56, 0.57, 0.58, and 0.61 for litters of 1 to 4, respectively. (Table 7.) Family 13 has the lowest correlations, which range from 0.45 for litters of 1 to 0.58 for litters of 4. There is considerable variation among the families as to the highest correlation in different litter sizes, but family 39 appears to be more consistently high than the other families, ranging from 0.56 for litters of 1 to 0.74 for litters of 4. It will be noted that these correlations are considerably higher than the correlation for all-sized litters taken together. This shows that weight of dam does not vary much, regardless of the size of litter she produces. Weight of young varies greatly from litters of 1 to litters of 4, but within a litter of given size, the variation in the weight of the young is much less, as would be expected.

TABLE 7.—Correlation ratio of weight of dam to birth weight of young born alive in different litter sizes in inbred and control stocks of guinea pigs

Stock	Litter size of—							
	1		2		3		4	
	Number of individuals	Ratio	Number of individuals	Ratio	Number of individuals	Ratio	Number of individuals	Ratio
Inbred:								
Family 2.....	147	0.6315	802	0.5460	918	0.5592	268	0.5837
Family 13.....	149	.4467	556	.5471	723	.5139	320	.5769
Family 32.....	184	.5578	588	.5640	477	.5871	104	.6748
Family 35.....	121	.5352	508	.6354	509	.6119	168	.8151
Family 39.....	55	.5598	206	.5897	284	.6793	98	.7430
Total.....	658	.5503	2,600	.5704	2,991	.5767	955	.6128
Control B.....	122	.4452	504	.5876	786	.6646	436	.5967

In the B stock the correlation does not differ greatly from that in the inbred lines, being 0.45, 0.59, 0.59, and 0.60 for litters of one to four, respectively. This is more variable, however, than the correlations in the inbred stock and is due probably to greater variability among the weights of different litter sizes.

LITTER RANK

The effect of litter rank on birth weight is small, as shown by a correlation ratio of only 0.20 for the average of all inbred lines and 0.25 for the control stock. (Table 3.) There was a marked variation from these values in family 39, in which the value of η was 0.29, but the difference between this family and the other inbreds is not statistically significant and may be due to the fact that fewer numbers enter into this calculation than enter into the others except in control stock B.

The average birth weight for first and later litters of family 2 was computed in the same way as explained for litter size in first and later litters. First litters averaged 70.5 grams in weight and later litters 71.1 grams, with a coefficient of correlation between them of 0.06. It must be remembered, however, that the average size of litters after the first was 0.31 larger than the first litter. This should result in a smaller birth weight of young in litters after the first than in the first litter; therefore, the real difference in average weight between young born in first litters and later litters is considerably more than 0.6 gram when corrected to constant litter size. However, this does not give a significant correlation between the birth weight in first and later litters.

SEX

It has long been recognized that the weight at birth and maturity and growth rates of animals of the two sexes differ. In most mammals the male is the heavier. Male guinea pigs average 3 grams heavier at birth and 8 grams heavier at weaning than female guinea pigs, according to a study made by Haines (4). According to unpublished data the present author finds that the difference in weight between males and females at maturity varies from 70 to 120 grams according to the families to which they belong. Therefore, in studying weight relations in guinea pigs it is important to consider the sexes separately, especially in the later weights where the differences become greater. Birth-weight correlations would not be affected to such a great extent. Correlations involving the litter as a unit necessarily disregard sex.

HEREDITY

Part of the correlation between birth weight of the young and dam's weight may be due to heredity, for Wright (17) has shown that the inbred lines are differentiated with regard to their weight at birth and weaning and that these differences have become practically fixed characters for the families concerned. McPhee and Eaton (14) have shown that not only the birth and weaning weights but also the mature weights of the different inbred lines have become fixed. This being the case and birth weight in guinea pigs being about one-tenth of mature weight, a relation must exist between dam's weight and birth weight of the young.

Computed by means of variability coefficients, the average of all the inbred lines is 53 per cent of the variance of birth weight of the control stock, leaving 47 per cent of the variability of the inbreds genetic and bred out by close inbreeding. This being the case, heredity is a larger factor in determining birth weight, where nearly 50 per cent of variability has been bred out, than in determining litter size, where less than 25 per cent of variability has been bred out.

CHANGES IN TEMPERATURE AND FEED

Guinea pigs are very sensitive to sudden changes of temperature and feed. In the guinea-pig colony from which these data are derived, an effort is made to keep conditions as nearly uniform as possible, but there is of necessity wide variations in temperature and in feed from season to season. In the summer, temperature runs

to above 90° F. at times. In the winter an attempt is made to maintain a temperature of 70°, but in severe weather it frequently drops to 50°. Sudden changes of temperature are usually followed by colds, pneumonia, and death, both of young and old. Through the winter cabbage or kale is fed, and early in the spring before fresh green feed can be cut it often becomes very inferior in quality. The green feed late in the spring, through the summer, and early in the autumn includes lawn clippings, good alfalfa, Sudan grass, soybeans, and rye. The last three feeds do not seem to be satisfactory for guinea pigs. The kind of hay varies from timothy and poor clover to the highest quality alfalfa. These variations are reflected in low gains and high mortality. The grain fed consists exclusively of unground oats.

Unlike the seasonal effect on litter size occurring primarily a little more than two months before the birth of a litter, seasonal effect on birth weight continues over the whole period from conception to birth. The influence is wholly through the dam and affects the young less than might be expected because nourishment of the fetus is entirely from the blood stream of the dam and, as Eckles (3) states, there is a strong tendency for the composition of the blood to remain constant, even under adverse conditions of nutrition. In case of food shortage during gestation, the dam, not the fetus, suffers. In inbred families 2, 32, and 39 the heaviest pigs were born during the 3-month period, October to December. In family 13 the heaviest pigs were born during April to June and in family 35, during January to March. In the inbred lines as a whole the heaviest young were born during October to December. Among the control stock the heaviest were born during January to March. When the birth weights by individual months are considered, there is so great variation that no conclusion can be drawn. The lightest young were born in general during July to September. This is the period during which the largest litters occurred; therefore, the relationship here may be due to litter size rather than to season, for litter size is an important factor in the determination of birth weight, as was shown previously.

MORTALITY

Mortality, both prenatal and postnatal, has an indirect relation to growth. Prenatal mortality is expressed as percentage of young born alive, the difference between 100 per cent and this percentage being the percentage dying before birth. This may not represent the actual prenatal death rate, however, for some of the young reported dead at birth may actually have been alive when born but may have died before they were found, as 14 hours sometimes elapse between actual birth and the time the young are found by the caretaker. Haines² found by comparing the number of corpora lutea with the number of fetuses in females killed shortly before parturition that there was an excess of corpora lutea, a fact which showed that some of the fetuses develop for a short period, then die, and become resorbed. Several fetuses were found in process of resorption

²HAINES, G. H. A STATISTICAL STUDY OF THE RELATION BETWEEN VARIOUS EXPRESSIONS OF FERTILITY AND VIGOR IN THE GUINEA PIG. 1929. (Unpublished part of thesis, Ph. D. Univ. Md.)

during this investigation. Thus the true percentage of prenatal mortality may be greater or less than actually reported as young born alive. Data presented in Table 8 and Figure 6 show that litters of 4 and 5 and litters of 1 have greater prenatal mortality than litters of 2 and 3. Haines (4) found also that the young raised to weaning average about 14 grams heavier at birth than those born dead. This difference may be due to more available nutrition from the blood stream of the dam after the death of the sibs took place. The number of young dead at birth may also give a clue to the dam's general condition.

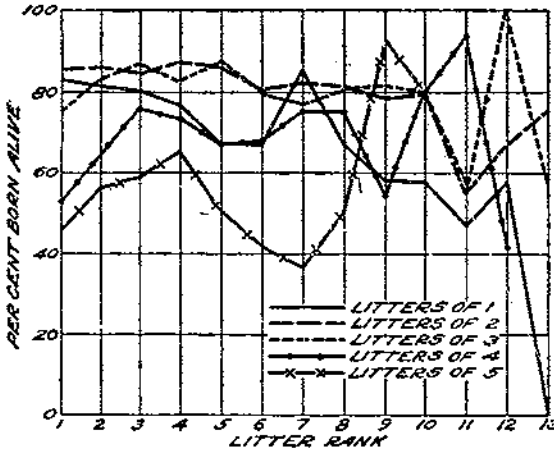


FIGURE 6.—Percentage of young born alive in the different litter sizes and ranks for the average of five inbred lines of guinea pigs

TABLE 8.—Percentage of young born alive and percentage raised of those born alive in different litter sizes and ranks (average of inbred lines)

PERCENTAGE BORN ALIVE

Litter size	Litter rank of--												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1	82.89	81.25	80.37	79.77	67.37	67.12	85.00	66.67	58.06	57.89	46.67	67.14	0
2	85.55	86.08	84.35	87.23	86.13	80.31	82.48	81.44	78.57	79.27	54.54	66.67	75.00
3	74.85	82.77	80.53	82.51	87.37	80.00	77.38	80.25	81.63	79.30	58.87	100.00	68.33
4	52.43	84.01	75.95	73.73	67.10	67.67	75.00	75.00	64.64	80.00	93.76	41.67	
5	45.71	56.00	58.95	65.00	50.00	42.00	30.67	50.00	93.33	80.00			
Total	75.20	77.02	80.34	80.83	78.95	74.01	77.30	78.28	75.66	77.61	60.04	69.56	61.90

PERCENTAGE RAISED OF THOSE BORN ALIVE

1	74.60	75.21	80.23	75.00	82.81	75.51	76.47	89.28	83.33	81.82	71.43	50.00	
2	73.82	79.48	81.69	81.93	80.62	83.33	82.38	84.81	77.92	80.00	66.67	100.00	83.33
3	77.50	78.68	81.91	85.00	76.12	80.30	78.46	80.00	77.50	68.00	52.04	46.67	85.71
4	62.25	69.53	69.28	72.10	60.78	64.97	73.33	69.23	66.67	71.88	40.00	40.00	
5	68.75	61.43	50.90	57.69	60.00	57.14	63.64	80.00	35.71	75.00			
Total	74.23	76.30	77.24	78.70	73.97	76.68	78.44	81.67	75.10	74.69	57.14	69.38	84.62

Postnatal mortality is expressed as percentage raised of those born alive. The influence of this factor on growth is brought about probably during the nursing period of the young, which is probably not more than two weeks in a guinea pig, and the young even before this time are able to eat and thus are not entirely dependent on the dam for food. In large litters, the young derive less nourishment

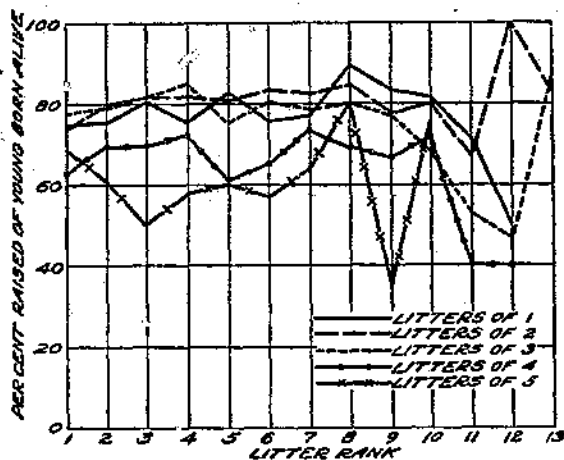


FIGURE 7.—Percentage raised of young born alive in the different litter sizes and ranks for the average of five inbred lines of guinea pigs

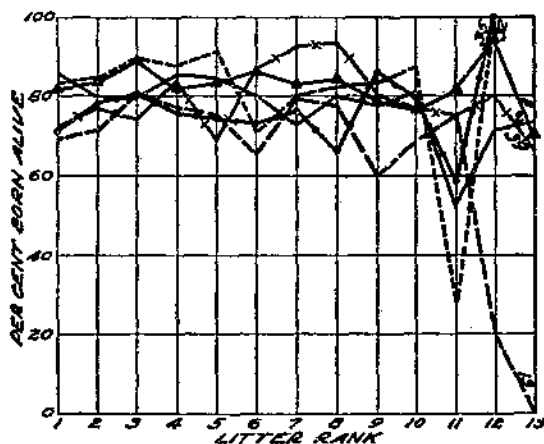


FIGURE 8.—Percentage of young born alive in all-sized and successive litters of the five inbred lines and control stock of guinea pigs

from the dam during the nursing period than the young in small litters. This may slow up the early growth rate and result in a lower weaning weight than if some of the young died during the first two weeks and made more nourishment available for the surviving young. The postnatal mortality is lowest in litters of two and three. (Table 8 and fig. 7.) The different inbred families and control stock vary in the percentages of young born alive and in the percentage raised of those born alive. (Table 9 and figs. 8 and 9.)

The ranking of the families in prenatal mortality is practically the same as their rank in weight at birth, indicating possibly a rather close relationship, but the ranking in postnatal mortality and weaning weight shows practically no agreement, indicating little or no relation.



FIGURE 9.—Percentage raised of young born alive in allized and successive litters of the five inbred lines and control stock of guinea pigs

TABLE 9.—Percentage of young born alive and percentages raised of young born alive in different stocks and ranks (average of all litter sizes)

Stock	Litter rank of—												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Inbred:													
Family 2.....	85.50	79.92	79.02	85.12	84.26	80.00	72.61	79.58	77.85	80.44	52.17	70.97	73.33
Family 13.....	68.97	71.00	79.72	77.14	75.64	65.17	79.36	77.56	59.74	68.63	75.00	20.60	0
Family 32.....	83.03	84.29	82.47	87.83	90.91	70.87	79.80	82.26	83.33	87.50	22.57	100.00	-----
Family 35.....	71.14	78.45	80.48	75.69	74.13	73.33	76.38	66.23	86.05	79.17	83.33	100.00	-----
Family 39.....	72.06	76.92	74.12	83.33	68.27	86.67	92.50	93.75	80.00	76.92	75.00	80.00	63.67
Total.....	75.20	77.02	80.34	80.83	78.95	74.01	77.30	78.26	76.66	77.51	60.00	69.56	61.90
Control B.....	81.55	83.30	88.91	82.10	83.56	86.44	82.44	84.43	78.57	76.22	81.43	94.12	70.00

PERCENTAGE RAISED OF YOUNG BORN ALIVE

Inbred:													
Family 2.....	79.80	77.95	85.1	84.91	85.81	82.33	90.86	85.93	87.07	89.19	79.17	72.73	81.82
Family 13.....	80.68	74.82	75.53	78.63	69.29	71.26	65.33	79.67	43.48	45.71	23.33	100.00	-----
Family 32.....	65.25	77.02	75.94	72.29	70.77	84.44	78.48	80.39	71.43	50.00	0	0	-----
Family 35.....	76.23	79.93	74.85	78.86	68.75	77.68	85.57	84.31	75.68	84.21	28.57	25.00	-----
Family 39.....	69.18	66.67	67.46	66.67	63.33	61.54	64.05	66.67	83.33	80.00	75.00	25.00	100.00
Total.....	74.23	76.30	77.24	78.70	73.97	76.69	78.44	81.67	75.19	74.69	57.14	59.38	84.62
Control B.....	82.12	79.12	80.26	66.29	79.34	81.96	72.68	83.24	85.61	76.40	73.68	79.17	63.67

WEIGHTS AND GAINS BEFORE WEANING

Since the age and weight of the dam had so little effect on birth weight, it is necessary to mention only the correlation between these factors and weight at weaning (33 days of age). The correlation

ratio between age of dam and weaning weight is 0.24 for the inbred lines and 0.29 for the B stock. (Table 1.) For age of dam and gain between birth and weaning the correlation ratio is 0.26 for the inbreds and 0.29 for the B stock, practically the same as the correlations for weaning weight. These correlations are somewhat higher than those between age of dam and birth weight. This may be due to the fact that older dams are better able to furnish the proper amount of nourishment for the young during the early period between birth and weaning, thus assuring good gains through the entire period to weaning. The nourishment which the young receive during the prenatal period is more uniform, as it comes from the blood stream, and is not affected so much by the dam's vigor, as the blood composition remains fairly constant. This point is noted by Eckles (3) in his study of dairy calves. He says that if conditions are adverse the dam rather than the fetus suffers during the prenatal period, but a poor condition of the dam after parturition retards the growth of the nursing calf. In explaining the effect of immaturity of the dam on birth weight of young, King (8) states that young rats are growing and use energy that would otherwise go into the fetuses, and the birth weight is, therefore, dependent on the dam's age. With guinea pigs, the condition seems to agree more closely with that found in cattle.

The correlation ratio of weight of dam to gain between birth and weaning is 0.30 for the inbreds and 0.31 for B stock. (Table 2.) The correlation ratio of weight of dam to weaning weight of the young is 0.35 for the inbred lines and 0.37 for B stock. These values are only slightly higher than the correlation of dam's age with birth weight and gain from birth to weaning. Correlations of 0.3 are considered significant and in the cases here presented are more than $4\frac{1}{2}$ times their probable error.

The correlation ratio of litter rank to gain from birth to weaning is 0.22 for both inbred and control stocks. (Table 3.) This correlation was not calculated for weaning weight since it was found of so little significance for birth weight.

The effect of litter size on weights from birth to weaning is still important. In family 2 the coefficient of correlation was calculated for litter size and weight at 3, 13, 23, and 33 days and found to be -0.64, -0.56, -0.46, and -0.42, respectively. These values differ but slightly from the average of the inbreds; in fact, the average correlation at 33 days is -0.42 for the latter also. (Table 4.) In the different inbred families this correlation agrees very closely and in no cases are the differences significant. For the B stock the coefficient of correlation between litter size and weaning weight is -0.33.

The effect of litter size on gains from birth to weaning seems to be operative for only a short period, as shown by the correlation values. The average correlation between litter size and gain between birth and weaning for the five inbred families is -0.31 and for B -0.19. The gain is dependent on the food supply and on the individual's ability to assimilate it rather than on litter size. In family 2, for which several gains between birth and weaning were recorded, the correlation between litter size and the first 3 days' gain was very low, -0.03; it rose for the next 10 days' gain to -0.30; and gradually decreased for each 10 days' gain thereafter till weaning. This indicates either practically equal gains by all young, re-

ardless of how many there are in the litter, or practically no gain. The latter condition probably results, as the correlation between litter size and birth weight was but slightly higher than that between litter size and weight at 3 days of age, a fact which shows that the relationship of weights remained practically unchanged from that at birth. The records show that in some litters the weight at 3 days of age was actually less than at birth.

The coefficient of correlation between weight at birth and at 3 days of age averages 0.94 for the five inbred families and 0.96 for B stock. (Tables 10 and 11.) There is very little variation among the inbred families in this correlation, the lowest being 0.92, in family 39, and the highest 0.95, in family 2. The correlation between weight at birth and at 13 days of age averages 0.82 for the inbreds and 0.87 for the B stock. Here the variation between the families is greater than in the previous correlation, ranging from 0.77, in family 2, to 0.89, in family 35. The correlations continue to decrease as length of time from birth increases and the variation among the different families becomes greater. The correlation between weaning weight and birth weight has decreased to 0.71.

TABLE 10.—Average correlations between weights and between gains of young at ages indicated for the inbred lines of guinea pigs¹

CORRELATIONS BETWEEN WEIGHTS (DAYS)

Age	3	13	23	33	53	83	173	263	353	443	533	623	713
Birth.....	0.94	0.82	0.77	0.71	0.60	0.49	0.44	0.41	0.35				
3.....		.88	.82	.71	.64	.53	.43	.40	.35				
13.....			.94	.87	.76	.64	.54	.48	.41				
23.....				.85	.85	.71	.58	.50	.43				
33.....					.89	.76	.60	.60	.47	0.44	0.40	0.43	0.31
53.....						.90	.69	.55	.50	.47	.41	.37	.38
83.....							.76	.60	.53	.52	.42	.40	.38

CORRELATIONS BETWEEN GAINS (DAYS)

Period of gain	3	13	23	33	53	83	173	263	353	443	533	623	713
0-3.....	0.48	0.46	0.41	0.36	0.37	0.33	0.21	0.19	0.18				
3-13.....		.89	.84	.78	.69	.59	.50	.42	.36				
13-23.....			.78	.72	.68	.53	.43	.36	.31				
23-33.....				.59	.64	.50	.39	.27	.23				

¹ Correlations given were made on 946 guinea pigs for all ages through 353 days, 641 for 443 and 533 days, and 440 for 623 and 713 days.

TABLE 11.—Average correlation between weights and between gains of young at ages indicated for the control stock of guinea pigs¹

CORRELATIONS BETWEEN WEIGHTS (DAYS)

Age	3	13	23	33	53	83	173	263	353	443	533	623	713
Birth.....	0.96	0.87	0.79	0.72	0.70	0.54	0.50	0.48	0.47				
3.....		.91	.83	.78	.67	.55	.51	.49	.62				
13.....			.93	.89	.77	.64	.56	.53	.63				
23.....				.94	.83	.70	.62	.55	.56				
33.....					.81	.73	.65	.66	.66	0.61	0.62	0.68	0.66
53.....						.78	.67	.63	.62	.57	.56	.56	.57
83.....							.82	.69	.65	.57	.55	.49	.51

¹ Correlations were made on 73 guinea pigs through 33 days, 113 from 53 through 353 days, 85 for 443 and 533 days, and 68 for 623 and 713 days.

TABLE 11.—Average correlation between weights and between gains of young at ages indicated for the control stock of guinea pigs—Continued

CORRELATIONS BETWEEN GAINS (DAYS)

Period of gain	3	13	23	33	53	83	173	263	353	443	633	623	713
0-3	0.51	0.48	0.51	0.47	0.34	0.28	0.29	0.35	0.39				
3-13		.89	.86	.81	.70	.60	.49	.42	.40				
13-23			.58	.57	.59	.58	.45	.38	.40				
23-33				.49	.44	.49	.36	.32	.35				

Correlations between weights at 3 days of age and at later periods show a similar decrease. The correlation between weights at 3 days and at 13 days is somewhat higher than that between weight at birth and at 13 days, averaging 0.88 for the 5 inbred families. The correlations of the weights at 13 days and at 23 days with the weights 10 days later are higher than the correlation between the weight at 3 days and at 10 days later, as the correlation is 0.94 between weights at 13 days and 23 days and 0.95 between 23 days and 33 days.

It has been stated previously that weight at any time is dependent on the preceding gains. Therefore, there should be a certain amount of correlation between a given gain and the weights following it for a considerable period. The gain is variable at 3 days of age; in some cases there has been a loss in weight, in others a gain of several grams. This variability does not seem to depend on the birth weight of the young, but may occur in heavy as well as light animals at birth. The average coefficient of correlation for gain during the first three days and weight at three days is 0.48 (Table 10), and it gradually decreases for the later weights. In the B stock the correlations are higher, being 0.51 between gain from birth to 3 days of age and weight at 3 days of age and correspondingly higher for the other weights.

The gain between 3 and 13 days of age is more uniform than that between birth and 3 days of age and shows a higher correlation in all cases with the weights which follow than the gain between birth and 3 days shows with its following weights. The correlation of gain between 3 and 13 days with weight at 13 days is 0.89.

The gain during the next 10-day period, from 13 to 23 days of age, does not determine to such an extent the future weights of a guinea pig as the gain during the preceding 10-day period but still is very important. The correlation between gain from 13 to 23 days of age and weight at 23 days is 0.73.

The correlation of gain between 23 and 33 days of age and with weight at 33 days averages 0.59 for the inbred families and 0.49 for B stock.

In numerous data collected by Brody (1) on the growth of various animals, it is shown that growth progresses at a rather uniform but decreasing rate as maturity is approached. In the present data the correlation of gain during the first three days to gain during the next 10 days averages 0.32 for the inbred families and 0.34 for B stock. For the gain from 13 to 23 days the correlation decreases to 0.17 for the inbreds but remains rather high for B stock, with a value of 0.27. In the period from 23 to 33 days the correlation is 0.15 for the inbreds but has decreased to -0.02 for the B stock.

The correlation of gain between 3 and 13 days with gain between 13 and 23 days is 0.43 for the inbreds and 0.27 for B stock, and for the period 23 to 33 days it is 0.19 and 0.20 for the inbreds and B stock, respectively. The correlation of gain from 13 to 23 days with gain from 23 to 33 days is 0.29 for the inbreds and 0.14 for B stock.

WEIGHTS AND GAINS AFTER WEANING

The correlation ratios between age and weight of dam and weights of young after weaning change very little from what they were for the earlier weights. This probably indicates that what little influence these two factors do exert on weight does not change much, even throughout the lifetime of the offspring, or, in other words, the weights of offspring at no time are more variable than the weights of their dam. For the inbred lines the correlation ratio between

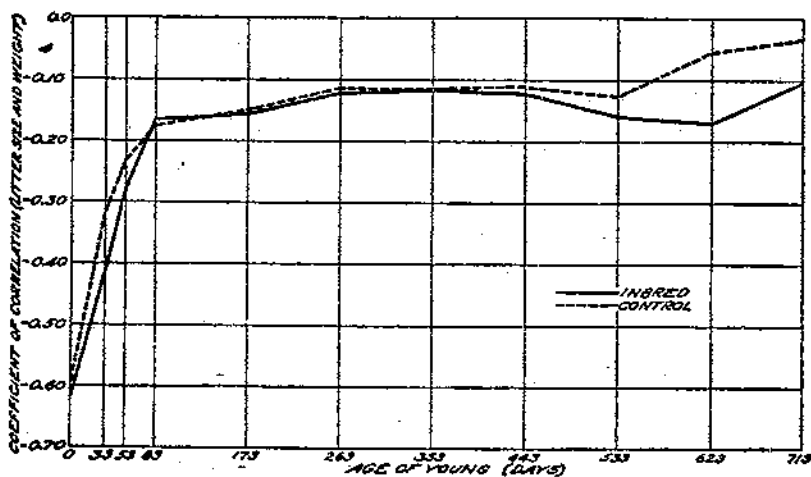


FIGURE 10.—Coefficient of correlation between litter size and weight at different periods for the average of five inbred lines and the control stock of guinea pigs

age of dam and weight of offspring at 53 days of age averages 0.24, and at 353 days, or approximately 1 year of age, 0.18. (Table 1.) The correlation values between weight of dam and weight of offspring at the same periods are 0.34 and 0.26, respectively. (Table 2.) For B stock the correlation of age of dam to weight at 53 days is 0.26 and to weight at 353 days 0.40. For B stock the correlation of weight of dam to weight of offspring at these same periods are 0.32 and 0.35, respectively. The differences between none of these values are significant.

Correlation between litter size and weight of young continues to drop after weaning. (Table 4 and fig. 10.) Among the inbreds at 83 days the coefficient of correlation is -0.17 , and at 713 days, or approximately 2 years of age, it is -0.10 . For B stock at 713 days the correlation is -0.03 . None of these differences are statistically significant.

These correlations show that litter size has a strong influence in determining the weight of guinea pigs at birth and that this influence persists appreciably even to 53 days of age. As the young grow

there is a tendency to overcome the effects of litter size on weight, but there is some influence even to 1 year of age or beyond. This was shown by McPhee and Eaton (14) in growth curves of guinea pigs born in litters of different sizes.

After 33 days each succeeding weight, as shown in Figure 11 and Table 10, has about the same correlation with the weight immediately following, and these correlations decrease as the interval between weights increases. It can thus be seen that there is a correlation among all weights, and even at 2 years of age there is still a correlation of 0.31 with the weight at weaning.

One interesting observation is that between any weight selected after 53 days of age and the next 30-day weight there is a correlation of approximately 0.92. The weights selected for this determina-

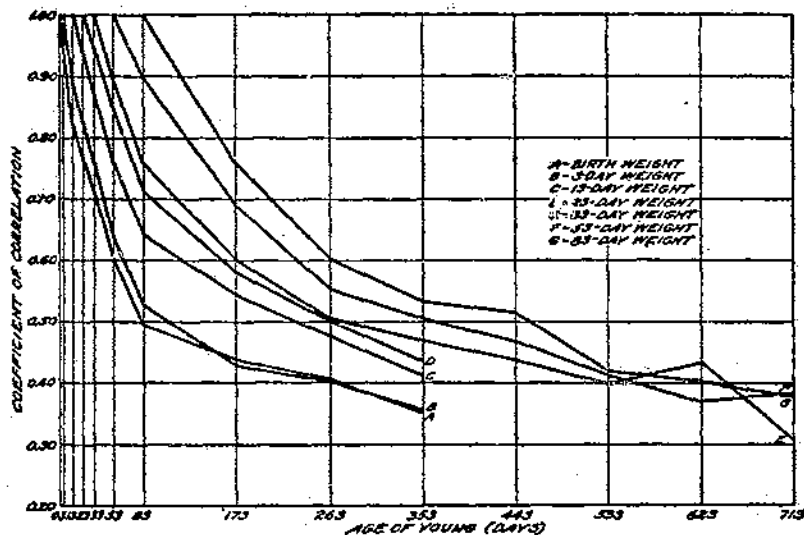


FIGURE 11.—Coefficient of correlation between weights of guinea pigs in the five inbred families at birth, 3, 13, 23, 33, 53, and 83 days of age and the following weights in each case

tion were those at 53, 147, 233, 417, and 593 days and the following weight in each case. When an interval of two 30-day periods, or 60 days, was taken, the correlation between that weight and the weight 60 days later averaged 0.84. For a 90-day interval, the correlation averaged 0.80, and for 120 days the average was 0.75. These correlations show a fairly constant relationship between any weight and its next 30-day, 60-day, 90-day, or 120-day weight, except that the correlation is lower as more time elapses between weights. Another point of interest is that the correlations are higher when taken near maturity than when taken earlier. Thus the correlation between weight at 53 days and 113 days is 0.82, between 83 days and 143 days it is 0.83, and between 443 and 503 days 0.86. This rise is general whether intervals of 2, 3, or 4 months are taken. The probable reason for this is that as maturity is approached the variability in weights and gains becomes less, and any weight near maturity bears a higher relation to the following weight, or even to its third

or fourth succeeding weight, than an earlier weight would bear to its succeeding or third or fourth following weight, where the differences in weight are greater. Also the gains are a proportionately smaller part of the following weight as maturity is reached.

RELATION OF WEIGHTS AND GAINS BEFORE WEANING TO WEIGHTS AND GAINS AFTER WEANING

For the inbreds the coefficient of correlation between the weight at 173 days, or approximately 6 months, and the birth weight is 0.44, and between weight at 353 days or approximately 1 year, and the birth weight the correlation is 0.35. For the B stock the corresponding correlations are 0.50 and 0.47, respectively. (Tables 10 and 11.) The correlation of the weight at 3 days with weight at 353 days is 0.35 for the inbred lines. This value is equal to the birth-weight correlation probably for the reason that there is so little change between weights at birth and 3 days, as previously noted. The correlations of 13-day and 23-day weights with weights after weaning gradually decrease, as in the previous cases, but are higher at 353 days as the length of time from this weight and the weight in question decreases. Thus weight at 23 days has a higher correlation with weight at 353 days than weight at 13 days has, for the length of time is shorter between 23 and 353 days than between 13 and 353 days. The coefficient of correlation between gain from birth to 3 days and weight at 53 days is 0.37. At 263 days a constant relationship apparently has been reached, for at this age the correlation is 0.19 and at 353 days is 0.18.

For the inbreds the coefficient of correlation between gain from 3 to 13 days and weight at 53 days is 0.69 and is 0.36 at 353 days weight. The values for stock B are almost identical for these correlations, being 0.70 and 0.40, respectively. From the high value of these correlations, it appears that in a guinea pig gain between 3 and 13 days of age has an important bearing on practically all its future weights. Interpreting it in another way, one can say that in order to have a vigorous animal as measured by weight, it is essential that it grow well soon after birth. In swine this period would correspond approximately to the first three weeks, and in a Jersey calf to about the first two months. The correlation between gain during the next 10-day period, from 13 to 23 days, and later weights is not so high but is still important. At 53 days the correlation is 0.68 and at 353 days 0.31 in the inbred lines and 0.59 and 0.40, respectively in the control stock. At 353 days the correlation with gain between 23 and 33 days is 0.23 in the inbred stock and 0.35 in the control stock.

For the inbreds the coefficient of correlation between total gain from birth to 33 days and monthly weights from 33 days to 353 days gradually decreases from 0.95 at 33 days to 0.42 at 353 days and 0.33 at 713 days, or approximately 2 years of age. For B stock the correlation at 33 days is also 0.95, but for weights after 113 days the correlations are somewhat higher than in the inbreds. (Table 12 and fig. 12.) The correlations discussed are shown graphically in Figures 11 and 13.

After 83 days there is a lack of correlation among early and later gains, as the correlations fluctuate between low plus values

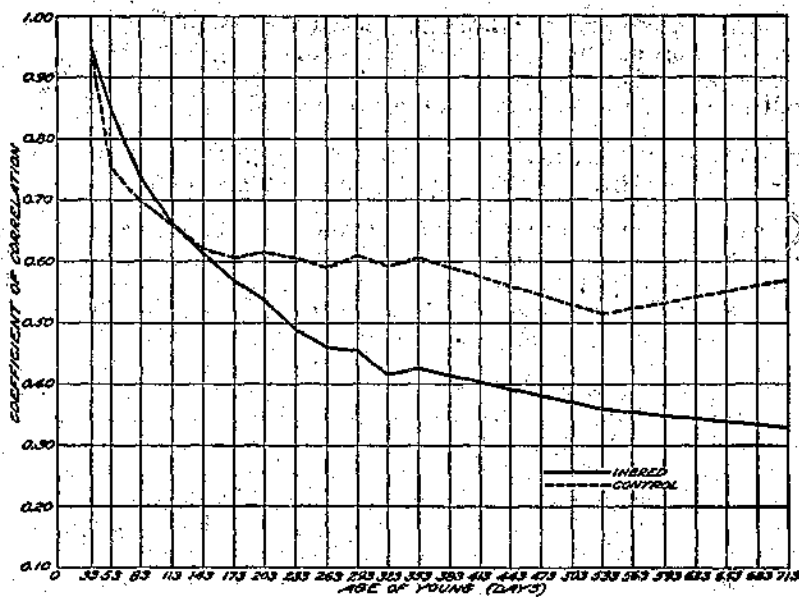


FIGURE 12.—Coefficient of correlation between gain from birth to 33 days and weights at later ages in the average of five inbred families and the control stock of guinea pigs

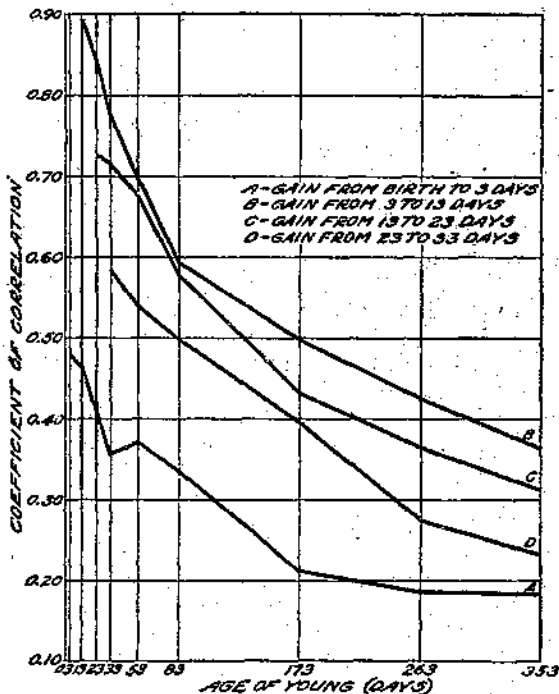


FIGURE 13.—Coefficient of correlation between gains at different periods, with weights at the ages indicated in the average of five inbred lines of guinea pigs

and minus values. There is little or no correlation between gains from birth to weaning and gains after 53 days. (Table 13.) The foregoing results show that up to about 2 months of age there is an appreciable correlation among gains, but there is no assurance that a guinea pig which gains well up to weaning will continue to make good gains to maturity.

TABLE 12.—Correlation of gain from birth to 33 days of age with weights at ages indicated

Age (days)	Inbred stock (946 animals)	Control stock (113 animals)	Age (days)	Inbred stock (946 animals)	Control stock (113 animals)	Age (days)	Inbred stock (946 animals)	Control stock (113 animals)
33	+0.35	+0.65	173	+0.57	+0.60	323	+0.41	+0.50
33	.35	.76	233	.54	.61	333	.42	.50
83	.74	.70	238	.40	.59	533	1.35	1.51
113	.86	.53	293	.46	.59	713	3.33	4.57
143	.01	.63	293	.45	.61			

1 641 animals used. 2 85 animals used. 3 440 animals used. 4 63 animals used.

TABLE 13.—Correlation of gain from birth to 33 days of age with gains at periods indicated

Period of gain (days)	Inbred stock (946 animals)	Control stock (113 animals)	Period of gain (days)	Inbred stock (641 animals)	Control stock (85 animals)	Period of gain (days)	Inbred stock (440 animals)	Control stock (68 animals)
33-33	+0.30	+0.21	353-383	-0.03	+0.01	533-563	-0.02	0.00
33-83	.00	+0.14	383-413	+0.04	-.27	563-593	-.03	-.02
83-113	-.14	-.09	413-443	-.09	+0.02	593-623	+0.03	+0.29
113-143	-.18	-.03	443-473	-.02	-.05	623-653	+0.03	-.13
143-173	-.11	+0.07	473-503	-.07	+0.02	653-683	+0.02	-.06
173-203	-.03	+0.07	503-533	+0.02	-.11	683-713	-.07	+0.35
203-233	-.10	-.04						
233-263	-.03	.00						
263-293	-.01	-.04						
293-323	-.03	+0.06						
323-353	-.02	+0.05						

In a comparison of the values of η and r in the correlations between gains and following weights, it was found that the values agree very closely to about 1 year of age, after which they differ considerably but continue to run approximately parallel. These comparisons were made for gain from birth to 33 days, 33 days to 53 days, and 53 days to 83 days and the weights taken at later dates in families 2, 13, 35, and in stock B. There is very little difference in any of these groups. This shows that a nearly linear relationship exists between the gains made during the three periods named above and the later weights. The test for linearity is denoted by ζ where

$$\zeta = \eta^2 - r^2. \text{ The significance of this value is expressed by } \sigma\zeta = 2 \sqrt{\frac{\zeta}{N}}, \text{ in}$$

which N is the number of individuals entering into the correlations. Only those cases were tested in which the graphs showed the widest departure, and in none of the inbreds was ζ found to be significant, the values of $\sigma\zeta$ being not more than twice the value of ζ . In B stock the differences were larger, but even there the values of $\sigma\zeta$ did not

exceed three times the value of ζ . Comparisons of η and r values for family 2, which is representative of the other families, are shown in Figure 14.

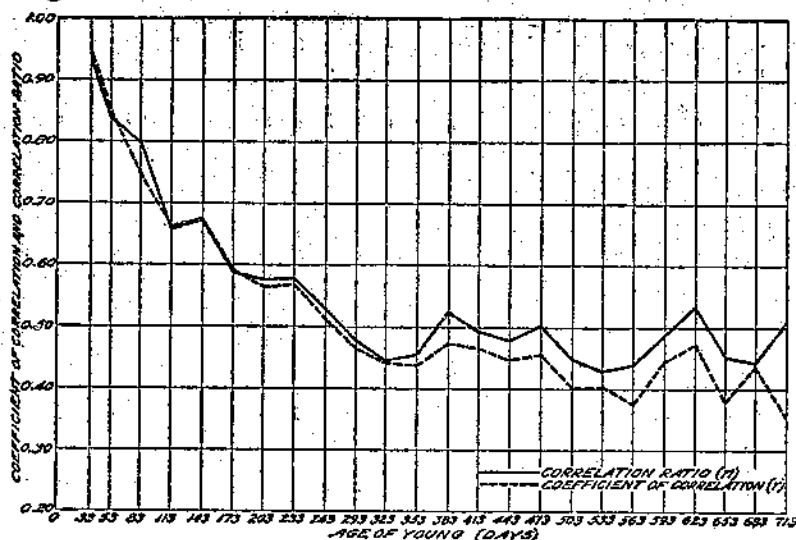


FIGURE 14.—Comparison of coefficient of correlation (r) and correlation ratio (η) between gain from birth to 33 days and weights at later ages in inbred family 2

A comparison of the values of η and r was made between gain correlations similar to the ones between gain and weight mentioned previously. The same gains, i. e., gain between birth and 33 days,

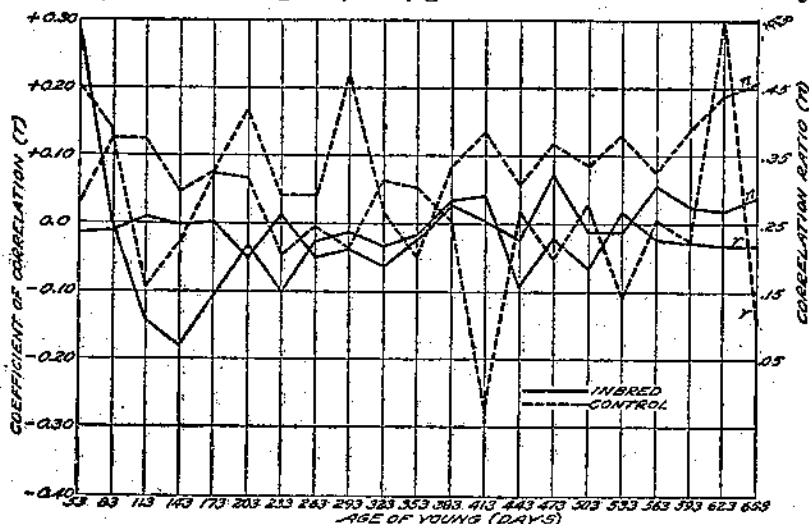


FIGURE 15.—Comparison of coefficient of correlation (r) and correlation ratio (η) between gain from birth to 33 days and later gains in the average of five inbred lines and the control stock of guinea pigs

33 and 53, and 53 and 83 days, were correlated with all gains following these periods. Here the values of η and r were considerably different, but the parallelism between them seems to indicate lack

of correlation. The comparative correlation values of r and r for inbreds and controls are shown in Figure 15.

A consideration of the correlations in the different families shows few differences. In the correlation between gain to 3 days and weights taken later, family 13 has the highest correlations at 13, 53, and 83 days, it being higher even than the correlations for stock B for the same periods. For the gain from 3 to 13 days family 13 has the highest correlation of any of the inbred or control stock at 23, 33, 53, and 83 days, and for the gain between 13 and 23 days the same family has the highest correlations at 23, 33, and 53 days. This is probably the result of the similar rate of growth of family 13 and the other lines including B during these periods as shown by McPhee and Eaton (14). Family 13 grows very rapidly, and although perhaps not so heavy as the B stock through these early periods, catches up to and surpasses B stock in weight from about 2 to 5½ months.

DISCUSSION

FACTORS AFFECTING LITTER SIZE

The condition of the dam as expressed by age and weight was found to be an important factor in determining size of litter in guinea pigs. In general, the size of litter in the inbred lines increases until the dam reaches 12 to 16 months of age, and then decreases. In the control stock B the maximum size of litter is reached when the dams are about 18 months old. This is probably due to the longer growth period of the B stock. The correlation of age of dam to litter size is 0.19 in the inbred stock and 0.31 in the control stock, probably indicating that litter size is more uniform in the inbred lines and less influenced by the dam's age than in the control stock.

The correlation of dam's weight to litter size is higher than the correlation of age to litter size in both the inbred and control stock. The correlation of dam's weight to litter size is 0.26 in the inbred lines and 0.34 in the control stock. The true relation is probably not in weight by itself but in general physical condition of the dam, which is reflected to a large extent through her weight.

Since age of dam has a high correlation to litter rank, the correlation of litter rank to litter size should be practically the same as the correlation between dam's age and litter size. This was found to be the case, being 0.18 for the inbreds and 0.32 for the control stock.

The effect of season of year on litter size takes place at time of conception. There is a slight seasonal variation in litter size, the largest litters being born late in the summer or in the fall when the feed and temperature conditions about two months before the birth of the litter were favorable.

Heredity influences to a certain extent the size of litter, as shown by the variation in the different inbred lines and the control stock, but not so much as might generally be expected. Among several characteristics studied in guinea pigs, it was found that litter size was less variable than weight. Therefore, heredity is a smaller factor in determining litter size than weight, and the inbred lines still show 77 per cent as much variability in litter size as the control stock.

FACTORS AFFECTING BIRTH WEIGHT

It has been shown previously that heredity determines to a large extent the birth weight of a guinea pig and that seasonal conditions and feed play a lesser part, feed, however, probably having more influence than season of the year in which a guinea pig is born.

In both the inbred and control stock the condition of the dam, as expressed by her weight and age, was found to exert an influence on the birth weight of the young, but the weight of the dam had more effect than her age. If the dam's weight is kept constant, the partial correlation between birth weight of young and age of dam is only -0.06 , whereas when age is constant, the partial correlation of birth weight of young with dam's weight is 0.31 . In determining weight of the young, therefore, it is more important to select females of the average weight for their breed or family than to select for age. Likewise, on litter size, the dam's weight exerts a greater influence than does her age, the partial correlation with constant age being 0.18 , whereas with constant weight, the partial correlation is 0.03 . This also shows that weight of dam with constant age has less effect on litter size than it does on birth weight of young under the same conditions, whereas age of dam with constant weight has a greater effect in determining litter size than it does birth weight.

In the relation of the factors, birth weight, weight of dam, and litter size, litter size plays a larger part than does dam's weight in determining birth weight of young, the partial correlation being -0.79 when the dam's weight is constant and 0.67 when litter size is constant. Birth weight of young was found to be also highly correlated with length of gestation period, and this in turn with litter size. When length of gestation period is constant, the partial correlation of birth weight with litter size is -0.55 , and when litter size is constant the partial correlation with gestation period is 0.23 . By multiple correlation and path coefficients it was found that the two factors, litter size and gestation periods taken together, determine about 64 per cent of the birth weight; age of dam, and litter rank together determine about 4 per cent; and age and weight of dam determine about 12 per cent.

Since the effect of age of dam on birth weight is so slight, the three factors, weight of dam, length of gestation period, and litter size are considered as the principal factors affecting birth weight aside from the prenatal growth rate. Even these three factors determine only 68 per cent of the birth weight in the inbred stock. In the control stock they determine 84 per cent of the birth weight. This is more than would naturally be expected, and an explanation of it is necessary. It was noted that correlations in the B stock were higher in most cases than in the inbred stock. One would expect correlations to be higher in the inbred stock since inbreeding reduces variability of weights and litter size, birth weight being only 73 per cent as variable as in the B stock and litter size 88 per cent as variable. In the data taken, however, it was observed that the age of dam, weight of dam, and length of gestation period were more variable in the inbred stock than in the control. This is due to the fact that only the more vigorous animals were mated

in the B stock, whereas in the inbreds, brothers and sisters were mated, regardless of their vigor unless it was obvious they would die within a short time. Therefore, the variability in their weights was greater than in the weights of the B stock animals that were mated.

In the inbred stock it is the custom to mate litter mates as far as possible, but in several cases, especially in families 35 and 39, old females have been mated to young males and vice versa, in order to advance certain generations. In the control stock the males and females were as near the same age as possible, but no animals more closely related than second cousins were mated. Thus there should be less variability in the ages among the inbred females. The apparent less variability in the ages of the females of the control stock is probably due to the greater regularity of breeding, the litters of which come at more consecutive ages of the dam than among the inbred stock where two or more oestrus periods between successive litters are often skipped.

Apparently inbreeding has made length of gestation period more variable than it is in the control stock. Just why this results is not apparent unless inbreeding influences some physiological factors which cause the dam to expel the fetuses more irregularly. The fact that there is a larger percentage of premature births in the inbreds than in the control stock seems to bear this out.

In correlating the different variables it is assumed that the variability of B stock is normal in all factors. In the inbreds, however, birth weight of young, for example, has been reduced in variability whereas weight of dam has become more variable under the conditions of the experiment. This makes the correlation lower in the inbreds than in the control stock. However, the differences in the correlations are not statistically significant. When the correlation is made between two variables both of which are reduced, as litter size and birth weight, the correlation will not be altered if there is proportionate change in the two factors concerned. This appears to be the case, for the correlation values of litter size and weights, birth weight and later weights, and gains and later weights are closer between the inbred and control stocks than are the correlation values of age or weight of dam and any of the weight factors. The differences between the correlation values are not statistically significant.

FACTORS AFFECTING GAINS AND WEIGHTS BEFORE WEANING

Since gain from birth to weaning is dependent mostly on the ability of the young themselves to get food, only weight and age of dam are considered as contributory influences. They have nearly the same influence in both the control and inbred stocks. Weight of dam determines 9 per cent of the total gain to weaning in both stocks of guinea pigs, and age of dam determines 7 per cent for the inbreds and 8 per cent for the controls.

Gain between birth and 3 days of age is correlated with gains during the following three 10-day periods up to weaning at 33 days. The first 3-day gain determines the gain during the next 10 days by 10 per cent in the inbreds and 11 per cent in the B stock. The first 3-day gain determines the gain during the second 10-day period

by only 3 per cent in the inbreds and 7 per cent in the B stock. The relation remains practically unchanged in the inbred stock for the gain during the third 10-day period, but in the B stock there is practically no dependence whatever on the first 3-day gain.

Gain between 3 and 13 days has more effect on the later gains to weaning than does the first 3-day gain, as in the inbred stock it determines about 18 per cent of the gain for the period from 13 to 23 days and 4 per cent for the period from 23 to 33 days. The determination for the two corresponding periods in the B stock is 7 and 4 per cent, respectively.

The weights during any period between birth and weaning are, of course, dependent on the gains during any of these periods. Gain during the first 3 days determines 13 per cent of the weight at 33 days in the inbreds and 22 per cent in the control stock. The 10-day period from 3 to 13 days apparently determines, more than any other gain, the weight at 33 days, as it determines 61 per cent of the weight of the inbred and 66 per cent of that of the control stock. The gain during the 10 days immediately preceding weaning determines weaning weight by only 34 per cent in the inbreds and 24 per cent in the B stock. From these facts it is evident that the gains to weaning have very little dependence on the dam, either on her age or weight. Gains during different 10-day periods between birth and weaning do have considerable dependence on one another. The period of greatest importance between birth and weaning seems to be that between 3 and 13 days. It is during this period that the guinea pig apparently recovers from readjustment from prenatal to postnatal life, that readjustment taking place during the first three days after birth. It was found that gains during this period were very low or even negative in many cases. In the 3 to 13 day period the guinea pig is able to obtain its own food supply and thus get well started in growth.

FACTORS AFFECTING GAINS AND WEIGHTS AFTER WEANING

In the group of animals whose early weights and gains were recorded, the correlation between birth weight and weaning weight was 0.71 and 0.72 in the inbreds and B stock, respectively, thus making weaning weight 50 per cent dependent on birth weight. At 83 days, or practically 3 months of age, the weight is only about 25 per cent dependent on the birth weight. In the inbreds birth weight determines about 12 per cent of the weight at 1 year of age and in stock B about 22 per cent. Weight at 3 days of age has practically the same determination of any future weight as has birth weight because of the small change between birth and 3 days, as has been mentioned previously. Weight at 13, 23, and 33 days each determines to an increasing extent later weights. At 173 days, 13-day weight has a determination of 30 per cent in both inbreds and B stock, and the percentage is only slightly less at 353 days. At 173 days, 23-day weight determines about 36 per cent of the weight in both stocks. At 353 days it determines 18 per cent of the weight of the inbreds and 31 per cent of the weight of the controls. In the group in which weights between birth and 33 days were not recorded, weaning weight determines about 38 per cent of the weight at 173 days for

both stocks, practically the same percentage at 353 days for B stock and 21 per cent for the inbreds. The percentage for B stock changes only slightly at 533 days and 713 days, whereas for the inbreds the percentages were 16 and 9 per cent, respectively, for these periods.

It was found that the gain during the first three days had little effect on later weights up to weaning. The same is true of weights after weaning. Gain between birth and 3 days of age determines only 11 per cent of the weight at 83 days in the inbreds and 8 per cent in the control stock. At 173 days the determinations are 4 and 8 per cent, respectively, and at 353 days 3 and 15 per cent. The 10-day gain from 3 to 13 days seems to be the most important in the determination of weights to 1 year of age, and the effect in the inbred and control stocks is closer at this period apparently than in others, perhaps because of a greater uniformity in the rate of gains during this period. At 83 days the gain between 3 and 13 days in both stocks determines 35 per cent of the weight, at 173 days 25 per cent, and at 353 days 13 and 15 per cent in the inbreds and B stock, respectively. The gain between 13 and 23 days is about as uniform in its influence and only slightly less in percentage effect on future weights as gain from 3 to 13 days. The effect is about 2 per cent less on the weight at 83 days of age, 6 per cent less at 173 days of age, and nearly the same at 353 days of age. The gain from 23 to 33 days is more variable and less in magnitude in its effect on weights at different periods, than those preceding it. At 83 days the determination is 24 per cent in both stocks, at 173 days 15 and 13 per cent in the inbreds and controls, respectively, and at 353 days 5 and 12 per cent, respectively.

Total gain from birth to weaning has a greater effect up to 113 days of age in determining the weights of the inbreds than of the B stock; the same effect, at 143 days, in determining the weights of both stocks; and a slightly greater effect, after 143 days, in determining the weight of the B stock. At 83 days the weight is 54 per cent dependent on the gain between birth and weaning in the inbreds and 49 per cent in the B stock. At 173 days the weight is dependent on this gain, 32 and 36 per cent in the inbreds and controls, respectively, and at 353 days, 18 and 36 per cent. The influence continues high in the B stock, being more than 25 per cent at 533 days and at 713 days, whereas in the inbreds the influence is only 13 and 11 per cent at these ages.

When the different inbred lines are considered separately as to extent of correlation between weights and between gains and weights, there is considerable variation. However, in ranking the families as to highest and lowest correlation values, family 35 has the highest correlation between any weight and its later weights, whereas family 39 has the lowest correlation. When gain is correlated during any of the early periods before weaning with later weights, family 13 has the highest correlation and family 39 the lowest. Total gain from birth to weaning correlated with later weights to 713 days is highest in family 35 and lowest in family 39. In both groups of gain correlations family 2 holds second place. It will be noted that family 39 held lowest place in all three groupings, a fact which probably indicates greater variability in weights and gains than in the other families, or less relationship between these factors.

SUMMARY AND CONCLUSIONS

The birth weight of guinea pigs is influenced more by the feed the dam is receiving than by season of the year. Size of the litter is more influenced by season of the year than it is by feed.

Condition of the dam, as measured by her age and weight, influences only slightly any of the factors affecting the young included in this study. Dam's age has a greater influence in determining litter size than in determining weight of young. On the other hand, dam's weight has a greater influence on the weight of the young than it has on litter size. Age and weight of dam together determine about 12 per cent of the birth weight.

The factors on which birth weight is most dependent are litter size and length of gestation period, which, taken together, determine more than 60 per cent of the birth weight.

Mortality varies with litter rank, the percentages born alive increasing to about the fourth or fifth litter, then gradually decreasing. Of the young raised of those born alive, the percentage gradually increases to about the eighth litter and then rapidly decreases.

There is very little correlation between size of first litter and size of later litters and likewise between weight of young in first litter and weight of young in later litters. Thus first litters seem to be a poor indication of what a female will produce later.

Weights at birth are correlated with all later weights, but the correlation decreases as maturity is approached.

Gains are likewise correlated with all later weights, but the farther removed the weight from the gain concerned, the lower the correlation. The period of gain having the highest correlation with all later weights was that between 3 and 13 days of age, indicating that rapid early growth is important in determining mature weights. The following 10-day growth period is only slightly less so.

There is very slight or no correlation between gain at different periods.

Inbreeding does not necessarily increase the correlation among various factors. Variability may be reduced in both variables correlated, but proportionately in each direction, thus leaving the correlation unchanged. In other cases one variable may be reduced more than another, and the correlation may be lower in the inbred than in the control stock.

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