EFFECTS OF NUTRITION AND HEREDITY UPON LITTER SIZE IN SWINE AND RATS

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INTRODUCTION

It is a common practice with the laymen working with multiparous animals to select breeding stock, both male and female, but more particularly female, from large litters in the belief that the factors governing size of litter are inherited by the progeny from their parents. It is of considerable economic importance to know whether or not litter size can be increased by the selection of breeding stock from the larger litters. If there are environmental factors which affect the size of litter, such, for example, as nutrition, then by improving these factors the breeder should be rewarded by an increase in the productiveness of his animals.

REVIEW OF LITERATURE

Rommel (17) found the average litter size of Poland China sows for the period 1882-1886 to be 7.04 pigs and for the period 1898-1902 to be 7.52 pigs, an increase of 0.48 pig per litter. Rommel and Phillips (18) observed that the average litter size of 5-year-old Poland-China sows was 8.40 pigs, while the average litter size of yearling sows was only 6.65 pigs. King (11) found that very young and very old female rats produced smaller litters as a rule than females of intermediate age. She concluded that both age and physical condition are important factors in the determination of litter size. Johansson (9) and Keith (10) in studies with swine, and Green (5) in studies with mice, among others, have also observed increase in litter size with increase in age of dam.

Wentworth and Aubel (28) found no difference in the average litter size of "big-type" and "small-type" Poland China swine. Their figures were 7.85 ± 0.05 and 7.89 ± 0.04, respectively. No data were given to show the actual difference in the size of the two types.

Hammond (7) concluded that the lower fertility of young sows is to a large extent due to the smaller number of ova shed, since he found the average number of corpora lutea in eight young sows to be 14.3 ± 0.39 and in nine old sows 19.77 ± 1.26. Loeb (12) found that when guinea pigs were underfed until they had lost up to 35 per cent of their body weight the Graafian follicles failed to develop or developed only partly, resulting in failure to ovulate. The underfeeding produced temporary sterility. He did not, however, report the

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2 National Research Council Fellow.
3 The authors wish to express their sincere appreciation to Dr. Leroy S. Palmer and Dr. Cornelia Kennedy for permission to use data obtained by them on litter size in rats, and to O. E. Mydland for help in keeping and tabulating the records of litter size in the small-animal breeding colony of the nutrition laboratory of the Division of Agricultural Biochemistry.
4 Reference is made by number (italic) to Literature cited, p. 520.
length of time before normal ovulation recurred after normal feeding was resumed, Workers at the Cornell Agricultural Experiment Station (14) report the results of 20 years of selection in poultry. As a result of mating high-producing birds with high-producing birds on the one hand, and low-producing birds with low-producing birds on the other, two lines were developed showing marked differences in egg production.

Rommel and Phillips (18), in a study of litter size in Poland China swine reported a correlation coefficient of $+0.06 \pm 0.008$ between the size of the litters in which the mothers were farrowed and the size of litters farrowed by daughters of these mothers. The correlation coefficient decreased from $+0.108 \pm 0.014$ for yearling to $+0.032 \pm 0.037$ for 5-year-old daughters. Rommell concluded that there was a small but definite tendency for fecundity to be inherited, although its influence tended to be lost with increasing age. Johansson (9) found no significant correlation between two different litters of the same sow, but when he correlated the average of the first four litters with the average of the fifth to eighth litters, he obtained a correlation coefficient of $+0.468 \pm 0.07$. He also found a correlation coefficient of $+0.129 \pm 0.079$ when he correlated the average size of the first four litters of the mother with the average size of the first four litters of their daughters. From an analysis of data covering 35 years obtained at one of the largest pig-breeding stations in Sweden, Johansson concluded that the fertility of the sow is affected by environmental influences during growth and maturity. This explanation was made by Johansson to account for the variability in litter size which he found in his data but for which he was unable to account to an appreciable extent on the basis of heredity.

Haines (6) obtained data on guinea pigs indicating that the environmental factors which influence size of litter are associated. Pearson and Weldon (22), correlating the size of litter of mother and daughter, concluded that in mice there is no evidence that litter size is inherited. Keith (10), working with 935 litters of seven breeds of swine, found no significant correlation in relation to its probable error between the size of one litter and the size of the succeeding litter when each breed was considered separately, but when all seven breeds were combined he obtained a correlation coefficient of $+0.34 \pm 0.03$ between the first and second litters and of $+0.367 \pm 0.04$ between the second and third litters. While these correlations appear to be statistically significant, they probably are of slight biological value because the large differences in litter size for the various breeds which were combined increase the length of the correlation surface and therefore increase the correlation coefficient. To be of biological value such comparisons should be confined to litters produced within a single breed unless it is first shown that there is no significant difference between the litter size of the breeds combined. It is possible that such a study as this, carried out under a carefully controlled environment, would give a different result.

Simpson (20) believed, from the results of a cross between a wild Schwarzwald boar and a Tamworth sow, that there was a definite tendency for litter size to be inherited as a dominant character. Wentworth and Lush (25) bred six Tamworth sows to a wild boar, and because the average litter size was 7.67 pigs as compared to 11 for the Tamworth breed, they concluded that the boar influenced the size of litter. Only 1 of the crossbred daughters reproduced, and she
produced but 1 litter, which consisted of 4 pigs. Since Wentworth and Lush found the result of their experiment in agreement with that of Simpson, they consider it suggestive of the dominance of the factors for wild litter size. Such results need to be verified by larger numbers, however, before the question is definitely answered.

Harris (8), in an analysis of data presented by Wentworth and Aubel (24), found a statistically significant correlation between the size of the litter in which a boar was farrowed and the size of the litters in which his daughters were farrowed. He also found a correlation of $+0.121 \pm 0.022$ between the size of the litters in which the grandsires and granddams were farrowed. Both these correlations are as large as the correlation which Wentworth and Aubel found between the size of the sow's litter and the size of the litter in which she was produced. There is no genetic reason for either of the two former correlations, hence one is led to question the source of the data from which the correlations were determined. Harris believed that such correlations might arise (1) through strains of animals of different breeders differing with respect to fertility, (2) through differences in the conditions under which breeders maintained their herds, provided such differences affected litter size, or (3) through actual dishonesty of certain breeders in reporting the size of litters for herdbook publication.

Buchanan Smith (21), from a review of the literature, reached the conclusion that litter size is definitely inherited as a comparatively simple Mendelian dominant, but says that perhaps hereditary factors are not as important in determining litter size as good husbandry and the mothering ability of the sow. His conclusions regarding the inheritance of litter size as a simple Mendelian dominant appears unwarranted in the light of the data at present available.

Evvard (2, 3) and Evvard, Dox, and Guernsey (4) found that nutrition was an important factor in determining the size of pigs farrowed, but they did not obtain significant differences in litter sizes.

**EXPERIMENTAL MATERIAL**

This study was made in an effort to discover (1) what relation, if any, exists between the size of the litter of which the dam formed a part and the size of litter that she produced, and (2) to determine whether size of litter is affected by the nutrition of the dam. Accurate records from a rat colony maintained by the nutrition laboratory of the Division of Agricultural Biochemistry were available to the writers. This colony is kept in a well-lighted room the temperature of which is maintained between 75° and 80° F. throughout the year. The animals are fed a diet of natural foodstuffs designed to produce normal growth and reproduction (15). In addition to the records from these above animals, the authors were given access to data collected by L. S. Palmer and Cornelia Kennedy, from which it was possible to study the effects of a diet low in nutritive value upon the fertility of the dam. Although the records were taken from an experiment planned for another purpose it is believed that they are entirely suitable for this study because of the accuracy with which they were conducted.

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5 This diet consisted of 310 parts cereal grains, 533 parts dextrin, 100 parts commercial casein, 50 parts timothy hay, and 0.3 per cent cod-liver oil. CaCO$_3$ and Ca$_3$(PO$_4$)$_2$ were included in the diet in such proportions so as to give certain degrees of acidity and alkalinity and certain percentages of calcium and phosphorus.
kept and because of the inbreeding that has been practiced. In this experiment the females were taken from the normal breeding colony. Most of them were virgin animals. They were placed on a special diet and mated to proven males so that the influence of the sire would not be a factor limiting size of litter.

A study of inheritance of litter size from an economic aspect was also made. Practically all the data for this study were taken from volumes 70 to 81, inclusive, of the herdbooks of the American Poland China Record Association, volume 81 being the last of the herdbooks obtainable at the Minnesota station. Most of the animals used in this study were born between 1918 and 1921. For a discussion of the accuracy of herdbook data the reader is referred to McPhee (13). He found that the herdbook data show fewer litters of 1 to 4 and 9, 11, and 12 pigs than did the experimental data, but the frequency of litters of 8, in the herdbook data, was almost double that in the experimental data. Assuming that all herdbook data are inaccurate and to the extent noted by McPhee, it may yet be said that the inaccuracies affect the litters in which the dams were produced to the same extent that they affect the litters produced by those dams, and probably would not, therefore, affect any correlation that might exist between the size of the dam’s litter and the size of the daughter’s litter.

**LITTER SIZE IN RATS**

The average size of litters for the various groups of rats was as follows:

<table>
<thead>
<tr>
<th>Group</th>
<th>Average number of rats born per litter</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8.75 ± 0.09</td>
</tr>
<tr>
<td>2</td>
<td>7.51 ± 0.10</td>
</tr>
<tr>
<td>3</td>
<td>7.51 ± 0.10</td>
</tr>
<tr>
<td>4</td>
<td>5.67 ± 0.15</td>
</tr>
<tr>
<td>5</td>
<td>11.06 ± 0.45</td>
</tr>
</tbody>
</table>

The difference between litter size, in the various groups, where $E_{diff} = \sqrt{E_1^2 + E_2^2}$ is as follows:

Group 1 minus Group 2 = 1.24 ± 0.14; Group 1 minus Group 4 = 3.08 ± 0.17; Group 2 minus Group 4 = 1.84 ± 0.18; Group 5 minus Group 1 = 2.31 ± 0.46.

It will be observed that the average size of the dam’s litter (8.75 ± 0.09) was significantly greater than the average size of litter produced by these dams (7.51 ± 0.10). This difference is due largely to the fact that a higher percentage of the progeny litters were first litters, as may be seen by comparing the average size of these litters (Group 2) with the average size of first litters (Group 3). The litter size is the same in both groups. If, however, the average litter size in Group 1 is compared with the average litter size in Group 4 (the group on a diet of low nutritive value) a difference of 3.08 ± 0.17 is found—a difference which is highly significant. Thus it is apparent that environment may prevent the genotype from expressing itself, for the females in these two groups were born from the same stock and
should have produced litters of the same size. There is also a significant difference between the average litter size of Groups 2 and 4. In Group 5, which consisted of litters obtained from F1 females produced by crossing two unrelated strains of inbred rats, there is a significant increase in litter size, which must have come about through the influence of hybrid vigor.

Although Group 5 contained too few litters to make the difference observed between Groups 1 and 5 conclusive, the results do indicate the possibility of increasing litter size by crossing two inbred strains and following it by selection.

Figure 1 shows the correlation surface for the litter size of the dams (Group 1) when compared with the size of the litters which they produced (Group 2). The correlation coefficient for this figure is of the same order as its probable error, and is essentially zero. Figure 1 shows the high variability of litter size of the progeny from any class of mothers. It may be concluded from the data here shown that selection of dams from large litters has little influence upon size of litter in rats.

Various workers have found that there is an increase in litter size with the increase in age of the dam. Figure 2 shows a frequency surface for the size of first litter for female rats at various ages. These data give a correlation coefficient of $+0.10 \pm 0.04$, an insignificant
value for the numbers studied. This finding is in agreement with that of Johansson (9) in regard to the relation between age of dam and size of first litter in swine. To determine whether the size of the second litter of rats is related to the size of the previous litter, all the second litters, 74 in number, were correlated with the first litters. The resulting correlation coefficient was $+0.24 \pm 0.07$. While the correlation is not large and is not based on a large number of litters, it does indicate the possibility of increasing litter size by selection.

**LITTER SIZE IN THE POLAND CHINA BREED OF SWINE**

From the American Poland China Record 1,035 litters were selected at random. Most of these litters, it will be recalled, were born between 1918 and 1921. The average size of the dam's litter was $8.69 \pm 0.047$, whereas the average size of 1,035 litters produced by them was $8.57 \pm 0.048$. A comparison of these values with those of Rommel (17) shows an increase of slightly more than 1 pig per litter during the time that elapsed between Rommel's investigations (1898-1902) and those herein reported (1918-1921). The difference in litter size of $1.05 \pm 0.05$ between these two groups is very significant. This difference is found to exist rather uniformly for all ages of the dam up to 60 months, as shown in Figure 3. It will be remembered that Rommel
found for the earlier period an average size of litter in this breed of 7.52 pigs. This was an increase of 0.48 pig per litter for the period 1898–1902 as compared to the period 1882–1886. The fact that there has been more than twice the increase in fertility in the Poland China breed from 1900 to 1920 than from 1880 to 1900 would indicate that the factors affecting litter size had had a greater influence during the former period than during the latter. This suggests the possibility that the change in type which occurred from 1900 to 1920 may have been a factor contributing to this increase in size of litter. It will be remembered, however, that Wentworth and Aubel did not find any

![Figure 3](image-url)

**Figure 3.**—Average number of pigs produced per litter by Poland China sows ranging in age from 12 to 60 months. The broken line represents results reported by Rommel and Phillips for the year 1902, the solid line those secured from herdbook records for litters born between 1918 and 1921. A correlation coefficient showing the relation between the size of the dam’s litter and the size of the litter which she would produce was found to be $+0.11 \pm 0.02$. There is no significant difference between this correlation and the correlation which Rommel and Phillips found in 1906 in the Poland China breed. From a study of the frequency surface for this correlation as shown in Figure 4, it may be concluded that the selection of dams from large litters would have but a slight effect upon the litter size of their progeny. Since Rommel and Phillips found a greater correlation coefficient for young dams and their progeny than for older dams and their progeny, it was decided that this correlation coefficient should be corrected for the influence of age of dam upon litter size. When this was done by the
partial correlation coefficient method, it was found that \( r_{md} = +0.092 \pm 0.02 \). Only a slight decrease in the correlation coefficient was thus obtained when the age of the dam was made constant.

Since in Figure 3 there was a gradual increase in litter size with increase in age of dam up to 60 months, it was thought that there should be a fairly high correlation between age of dam and size of the litter that she would produce. This correlation was found to be \( +0.31 \pm 0.02 \), which is significant. These data, therefore, further verify the fact previously shown that there is a gradual increase in fertility of sows up to the age of 60 months.

Johansson (9) found a somewhat larger average litter size for sows farrowing their first litter at 14 to 16 months than at any other age up to 22 months, but considering the numbers with which he worked the differences he obtained were not statistically significant. The correlation between age of dam and size of first litter for 262 dams ranging in age from 10 to 15 months, inclusive, was also found in this study to be statistically insignificant. This is in agreement with Keith's (10) findings and also in agreement with the data for rats presented in Figure 2.

\[ r_{md} = \frac{r_{md} - r_{am} \cdot r_{ad}}{\sqrt{1 - r_{am}^2} \cdot 1 - r_{ad}^2} \]

\( a = \) age of dam, \( m = \) size of dam's litter, \( d = \) size of daughter's litter
DISCUSSION

The number of animals born to a multiparous mother is influenced to a large extent by the physiological condition of the female before and at the time of oestrus. Haines (6) in studies of guinea pigs found that the major factors controlling litter size operate at conception. He found also that litter size is generally small from January to April, while from June to November it is unusually large. It seems probable that this difference is due largely to the nutrition of the mothers, for it is much easier to procure suitable green feed in summer than in late winter or early spring.

The size of litter depends primarily upon the number of ova which are released and which become fertilized. Parkes and Drummond (16) believe that any male capable of producing viable sperm is capable of fertilizing all of the ova produced. Warwick (23) in an examination of 3,967 fetuses, found 3.68 per cent in various stages of degeneration. It is not known, of course, to what extent heredity and environment, respectively, may account for this. There are many physiological conditions which affect the general health of the animal, and which would result in a smaller litter size. The data presented in this paper show that in the case of rats poor nutrition of the dam is one of the major factors affecting the number of young born per litter. It seems very probable, therefore, that improved feeding methods have influenced the measurable increase in litter size of the Poland China breed during the years 1885 to 1900 and 1900 to 1920.

Differences in litter size of breeds of swine have been definitely established by Bitting (1), Rommel (17), and Severson (19). Severson reported a litter size of 8.2 for Poland Chinas, Keith (10) found 7.91 during the period 1903–1925, Rommel reported 7.52 in 1906, and the present study shows 8.69. Such results as these suggest that there may be differences in litter size within a breed, an idea that is in keeping with the theory advanced by Harris (8) that strains of animals from different breeders may differ with respect to fertility. This difference, if it actually does exist, may not indicate any real difference in the fertility of the strain in question but may be explained upon a nutritional basis, that is, sows maintained at different locations and by different breeders may also be maintained on different planes of nutrition. This idea is supported by the studies of Johansson (9), who found that there had been no change in litter size at Bondeson's pig breeding station in Sweden for 35 years, where undoubtedly the best feeding practices were employed at all times.

If the size of litter is a valuable criterion in the selection of breeding stock, then the number in the litter of which the dam was a part should give an indication as to the size of litter that she will produce, and the size of the first litter should give an indication of the size of subsequent litters. The present study with rats and Johansson's study with swine show that the average size of litter produced by all individuals born in litters of any given size, as 10 for example (figs. 1 and 4), will be the average size of litter for the breed or species studied. The same is true of the size of second litters produced by dams all of which had produced the same size of first litters. This can be accounted for by environmental factors which affect litter size.
It does not, however, disprove the idea that litter size is or may be inherited, for it is well known that breeds differ with respect to litter size.

**SUMMARY**

A study of 1,035 litters of Poland China pigs, as derived from herd-book records, shows that there was an increase in average litter size amounting to one pig per litter in this breed between 1900 and 1920.

The swine data show an increase in average litter size with increase in age of dam up to 60 months.

The correlation coefficient between the size of litter in which the dam was born and the size of litter produced by her was very low in swine and essentially zero in 364 litters of rats.

The nutrition of the mother rat has a pronounced influence on the size of litter that she produces. Small litters result when the female is maintained on a poor diet.

The correlation coefficient obtained between age of dam and size of first litter in both rats and swine was found to be statistically insignificant.

The data used in this study show that, because of the influence of environmental factors on litter size, the size of the first litter is not an accurate indication as to what will be the size of subsequent litters. Consequently, while the data indicate the possibility of increasing litter size by selection, the size of the first litter should not be taken as the standard by which to select stock for breeding purposes.

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