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THE INFLUENCE OF EXCESSIVE SEXUAL ACTIVITY OF MALE RABBITS

II. ON THE NATURE OF THEIR OFFSPRING

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TWENTY-TWO CHARTS

CONTENTS

INTRODUCTION

Too frequent copulation of males is often given as an important cause of weak and inferior offspring from the standpoint of growth and thriftiness. This idea seems to be rather universal, though evidence of such being the case is difficult to obtain.

Wright (p. 306) states that in his poultry-breeding operations he does not expect normal size or vigor in offspring from cocks used on too many hens, and further (p. 131), that cocks that are used on too many hens show the effect in that the eggs fertilized by them show signs of hatching but do not hatch because the embryos fail in many cases to reach full development. Pusch ('15, p. 182) expresses the almost universal belief in this matter, though he does not consider the idea well grounded when he writes: "Braucht man die Deckhengste, wie überhaupt jedes männliche Zuchttier, zu stark, so schädigt man nicht nur deren Begattungs- und Befruchtungsvermögen, sondern auch die Qualität ihrer Nachzucht; deshalb wird die Stutenzahl für wertvolle Vollbluthengste auch nur auf 30–40 Stück bemessen und die zu bedeckende Stute erst durch den Probierhengst auf ihre Rassigkeit hin geprüft." Day ('13, p. 219) expresses the belief that excessive use of the boar is likely to result in small, weak litters of pigs.

Just why sperm cells that are produced by a male in heavy sexual service should produce inferior offspring when they take part in fertilization is not clear. Can it be possible that the genetic makeup of the spermatozoa is changed by heavy service? Is it not possible that any sperm cell possessing life, however depleted and weak it may be, will carry into the egg a potentiality of full vigor? Or, on the other hand, can we conceive of different degrees of vital force in a sperm cell? Since all of the activities of the animal body are so beautifully coördinated, it would appear very rash to assume without conclusive evidence that males under natural breeding conditions would derange any vital function, such as reproduction, by continuing to copulate after the reproductive system was producing an abnormal product. As has been pointed out in our first paper (Lloyd-Jones and Hays, '17), there appears to be a relation between the number of services performed by the male and the fertilizing power of his semen, but as far as we have been able to measure, we are led to believe that only a slight change can be brought about by this treatment. Pusch ('15, p. 182) states that in Oldenburg, stallions are often allowed to make from four to six or even eight services daily. He also states that bulls have been used on 400 cows in a year, and that even poorly fed bulls will make from four to eight copulations daily, and this without bad effect.

Strictly speaking, 'vitality' of individuals cannot be measured, for the vitality of any individual really means the sum total of life force within every living cell of the organism; vitality, as used in speaking of animals, may, however, in part be measured by the rate of growth in weight, the skeletal development, and the ability of the individual to live to a good age. Such factors as body weight and the others mentioned above are measurable. The purpose of this investigation has been to study the effects of heavy service of males on the nature of their offspring, as far as we could measure the effect.

MATERIAL AND METHODS

1. Animals used

The character of the animals used in this investigation has been discussed to some extent in the first paper of this series. Stocks of the European domestic rabbit, Lepus cuniculus, secured from six different breeders, were used and no inbreeding was practiced at any time. The weight[1] and age of the females is an important factor in that it affects both the number in a litter and the individual weights of the offspring. Likewise the weight of the male probably is of much importance in affecting the weight of the young. The maturity of the male is a factor that should not be lost sight of, because all three of the males used were fully mature and were in their prime of life—about two years old. The average weights of the males are as follows: No. 1, 2850 grams; No. 3, 2575 grams; and No. 4, 2200 grams.

Shy breeders sometimes occur in rabbits, but most of these females proved to be regular breeders. No. 25, however, was barren and was discarded; No. 12 produced young three times, the last time August 5, 1916, after which time she appeared never to come in heat again and continually refused to copulate

[1] Prof. H. W. Vaughan has found that Large Type Poland-China Swine produce larger litters than the Small Type.

and was discarded; both No. 22 and No. 29 died after having given birth to but one litter upon which we secured data; and No. 18 died after she had given three litters to the experiment.

Age of the dam is an important factor as affecting the number in the litter and probably to some extent the weight of the individuals of the litter. For this reason the approximate ages of the breeding animals is here given in order that the reader may understand fully how much error may have been introduced through immaturity in the breeding females. One female gave birth to young when six months old; two, when seven; four, when nine; one, at ten, and one, at eleven months old. The remainder of the females was fully mature, that is, fifteen months old or over, at the time they gave birth to the first litter used in this experiment.

The fact should be noted that the three females that died during the experiment were all immature at the time they first reproduced and that only one of them (No. 18) had more than one litter upon which we secured data. Two of the three litters from No. 18 are 5th-service litters by male No. 3 and the other is a 1st-service litter by the same male. Female No. 22 gave a single litter from the 5th-service by male No. 1; and female No. 29, one litter from the 1st-service by male No. 4; female No. 12 has contributed but two litters to the records; namely a 1st- and a 10th-service litter by male No. 1.

It may appear to the reader that considerable error, resulting from the use of these immature females, was overlooked in making up our records of growth, but this has not been the case; therefore, a brief consideration of the system of matings used to overcome this error is not out of place here.

The system of matings was arranged so that each female was mated to at least two of the males and many to all three males, and where possible each female produced litters from all different services from each male, thus reducing parental variability to the males alone. By making the three breeding groups of females as nearly equal as possible in age and weight; by distributing the heavy service among the females in such a way as to secure all types of litters from both mature and immature females, and by making matings at such a time as to secure all types of litters at the same season of the year, as far as possible, we hoped to overcome many possible sources of error. However, as the experiment proceeded it was found impossible to apply these corrections absolutely and we are thus not fully justified in comparing litters in growth in body weight and in mean dimension and assuming that any consistent differences are due to the number of services performed by the males. We should not overlook the slightly better opportunities offered the 15th- and 20th-service litters, a considerable proportion of which were born during the latter part of the experiment and were produced when the females were all mature.

2. Records kept

The following records were kept: Date of breeding, pedigree, date of the next probable heat period—fifteen days after breeding; actual date of parturition; number in litter; number born dead; sex of offspring; individual weight of offspring on day of birth and for each five days thereafter up to ninety days; head length and breadth through extremes of ilium, taken at the same time as the weights; date of weaning; color, and mortality record.

3. Weighing and measuring

Breeding records were kept for each female so that it was possible to weigh each litter on the actual day of birth. At this time each litter was given a number which was the same as the number of the matings, and each individual was given an individual number and marked in such a way as to be easily distinguished from litter mates by color description or by clipping ears and tail. The individual weight records were kept each five days until the litter reached the age of ninety days.

The desirability of continuing all records to the full maturity of the progeny is very apparent. As the work was handled, forty or fifty animals were often weighed and measured on a single day and, with the other routine work of the experiment, entailed a very large amount of labor. Such extensive records were impossible for reasons that need not be discussed here. Weights were secured on a sensitive torsion balance and variations of 0.5 gram were recorded. Great errors may be introduced by a 'fill' if the records are not made at the proper times; therefore the records were secured at about the same hour each day before feeding, which was done once daily. However, there are certain errors in weight records which cannot be avoided by the experimenter. The general degree of health of the animals has much to do with fluctuations in weight as MacDowell ('14) found in growth studies of rabbits; nevertheless, as with other animals, weight seems to be the best available index of growth.

Two methods for studying the growth of the progeny produced were chosen, namely, growth in body weight and growth in body measurements. The first will be discussed here.

Body weight, according to Minot ('08, p. 87), represents the total mass of the living body, while body measurements are only partial indices of growth. That individuals show wide fluctuations in weight has been pointed out by MacDowell ('14, p. 191) in his studies on the rabbit. Although growing rabbits show marked variability in weight on different days, it was thought possible by the use of large numbers to secure growth curves that would fairly represent a race of rabbits kept under uniform conditions. There is a possibility that these growth curves would diverge more as the animals grow older, because MacDowell has shown that though most rabbits apparently make a a normal growth to maturity, others fall much below the normal and do not reach the average weight in what is considered the normal period. But complete records were out of the question as indicated above. Even though this is the case, it is very important to ascertain if this reputed inferiority of progeny which is supposed to result from the weaker sperm cells of the overworked male is going to be apparent when his progeny are in the most active stage of growth, i.e., during the first ninety days of postnatal life. If progeny from the advanced services of males are more poorly equipped with the necessary something to enable them to make normal growth, would this not be apparent when the young rabbits are thrown upon their own resources, as was done during the sixty days following weaning time that the records were kept?

Concerning the second method of studying growth, namely, by body measurements, it is important to discover whether body development follows apace with body weight and to check one against the other. For this reason, all litters born up to August 9, 1916 (45 in number), were measured as well as weighed, at five-day intervals up to the age of ninety days.

A measure of head length was considered valuable, as measurements of the skull have been found to be less variable than measurements of long bones. MacDowell ('14, p. 38) found this to be true in rabbits. Hatai ('08) observed the same thing in the albino rat, and Quetelet ('71) likewise found the same in man.

The head length as here reported was measured by the use of calipers and represents the distance obtained by placing the stationary arm at the crest of the occipital bone allowing the beam of the calipers to extend sagitally downward parallel with the face. The movable arm was then brought up until it rested snugly against the end of the nose and down over the mouth. The lower arm of the instrument was then just beneath the inferior extremity of the premaxillae and the upper arm was just above the superior region of the occipital bone. There is very little flesh or soft tissue covering the bones in this region, about the only structures obscuring the bones are the skin and the hair coat. It is apparent, that a head measurement in this particular region approximates rather closely the actual skull size.

Since there is the possibility that some other body measurement would make an entirely different growth curve from that of the above-described head measurement, it was considered desirable to secure one other measurement that could be taken with considerable accuracy on the live animals. Moreover, we wished to obtain a 'mean dimension' from the average of two measurements, therefore some easy body measurement was searched for. There is no little difficulty in securing external measurements of the body with accuracy, as the writer has learned from much experience with cattle and swine. A measure of the breadth between the extremes of the ilia was thought to be as easily determined as any of the possible body measurements and would represent a dimension of breadth in contrast to head length, which might be considered a dimension of depth. The iliac expanse was therefore used as the second measurement.

Both measurements were taken just after weighing on the five-day periods beginning at birth and continuing to the age of ninety days. Steel calipers were used with vernier graduated to hundredths of a centimeter. Three independent readings of each dimension were taken by removing the calipers and shifting the arm after each reading. Readings were put down just as read, and care was taken to avoid any tendency on the part of the observer to modify readings to make them check with others. As a rule, it was possible to obtain readings that varied less than 0.1 centimeter from each other. An average of the three readings was taken as the correct reading for each measurement.

Little difficulty was experienced in securing what was considered a correct reading on head length. This was not always true for the other dimension. Three factors probably enter to modify this reading: 1, the amount of 'fill;' 2, the degree of fatness; 3, the position of the hind limbs. Food and water in the alimentary tract seem to bulge the walls of the abdomen to such an extent as to often obscure the points of the ilium and make their exact location difficult. The variability of the feeding habits of the rabbit is thus a factor of no little importance in connection with the measurement of iliac extremes. Some individuals carry much more fat over the ilium bones than others. In fat individuals the points of the bones are often greatly obscured, especially in the younger rabbits. This condition is much more common among the smaller and better nourished individuals and may prevail to some extent throughout the period of observation. There is considerable flexibility in the pelvic girdle before the symphisis pelvis becomes bony and firm as the animals approach maturity. The ilium, ischium, and pubis are also distinct and more or less flexible in early life. This great flexibility causes the position of the hind limbs to be an important factor in modifying the position and the breadth of the extremes of the ilium as determined by the calipers. In so far as possible an effort was made to have the animals sit with the limbs in the natural position while being measured. The hair was also clipped from this region of the body in order that it might not obscure the point of the bones.

4. Methods of interpreting weights and measurements

In order to make the data for different-sized litters more nearly comparable, all weight and measurement records are reduced to an 'individual mean' for each litter for each of the nineteen periods of observation. The individual mean for each litter was calculated by dividing the total weight or total measurements of each litter by the number of individuals for each of the nineteen periods. From these individual litter means the series of cumulative growth graphs are constructed.

In attempting to compare the growth graphs of rabbits in the different service groups, a very perplexing problem arose as to how to best compare results in litters that vary so much in number of individuals. The number of individuals born in a litter is an intensely important factor in influencing the weight of the young. Our observations have shown this as did also observations of Minot ('91, p. 111) on guinea-pigs. His results, based upon 351 observations, show that the average birth weight is 85.5 grams in litters of one, the weight gradually decreased with the increase in number of individuals to as low as 52.2 grams in litters of eight.

Another item that makes comparisons of litters in different service groups difficult is the fact that litters in the 1st and 5th service groups are likely to contain more individuals than those from the 15th and 20th services. For this reason the individual mean of these advanced service litters is greater and they grew faster because of a more generous supply of milk from the mother. In this connection we find that King ('16, p. 51) discovered that in rats "body weight at birth indicates the probable capacity of the individual for subsequent growth." This being the case, small litters from the advanced service should grow more rapidly than the larger litters from the 1st and 5th services.

In order to make the litters in the different service groups comparable with each other, whatever their number, it was thought first that litters of different numbers of individuals could be standardized to a mean litter number. Jackson ('13, p. 17) in comparing the standard deviation of individual rate with the standard deviation of the entire race, reduced all individuals to a common basis by multiplying the body weight of each rat by a factor obtained by dividing the mean of the total population at a given age by the mean of the given litter. Since the object we have in view is not the study of individuals, this formula cannot be used. Further attempts were made to obtain a factor for reducing large and small litters to a comparable basis, but so far with no success. Again, it was thought possible that the coefficient of correlation between number of individuals in the litter and average weight per individual might be made use of to reduce the litters to a comparable basis, but without any satisfactory results. Again, a comparison of different-sized litters in the several service groups by constructing graphs upon a base line representing the different litter numbers and the vertical line representing the variable weights at birth, a second chart to show the time required to make eight times the birth weight, and a third chart to show the time required to make twenty-four times the birth weight were attempted. By this means the data could be much condensed, but such a system proved to be impracticable and was discarded. Finally, it was deemed best to compare litters of the same number of individuals. Accordingly, the growth rate in the different service groups must be shown by a whole series of charts, the graphs on each chart representing a certain litter number. In each case the chart shows the number of litters which are lumped in each graph. Thus each chart gives a direct comparison of the growth rate of the five service groups, namely, 1st, 5th, 10th, 15th, and 20th, the comparison being always between litters of the same number.

As a further measure of divergence in rate of growth between the service groups, the coefficient of variability of weight for all litters in each of the five service groups is valuable, presented at birth, at weaning time or thirty days, and at ninety days. The object here sought is to find out if there is a greater variability in any one of the service groups, which might be expected if any of the service groups contain weak offspring. This study will also reveal if heavy service tends to produce a wide range of variability in birth weight or a wide range in the weights of individuals at the time that they are thrown upon their own resources at weaning time, and it will show further if the individuals tend to deviate more from the mean as they grow older. Deviations, if they are going to occur, might be expected to occur, more strikingly at these three periods than at any other time during the observations. This coefficient of variability was determined by the following formula:

$$\begin{array}{l}\text{For each}\\ \text{litter in}\\ \text{service}\\ \text{group.}\end{array} \left\{ \frac{\dfrac{\dfrac{(\text{Sum of deviations of litters from mean})^2 \times (\text{frequency of class})}{\text{Number of individuals.}}}{\text{Mean of respective litters.}} \times 100}{\text{Number of litters in service group.}} \right\}$$

The above formula is used for the birth weights, the thirty-day weights, and the ninety-day weights.

The measurement data secured were combined into one general expression, the 'mean dimension.' The advantage of using one expression to stand for body measurements lies in the fact that we have a mathematical expression for the cross section of the animal. Graphs expressing cumulatively the percentage increase in head length and iliac extremes are found to cross between the thirty-fifth and fortieth day of postnatal development; but previous to this date and later, up to the time of the conclusion of the observations at ninety days, the graphs bear a close relation to each other, therefore it was deemed correct to combine the two measurements to obtain the mean dimension.

The mean dimension was obtained by the following formula:

$$\frac{\text{Mean head length} + \text{mean iliac extremes.}}{2}$$

Mean head length is the sum of the averages of the three read ings for each individual in a litter divided by the number of individuals in the litter. Mean iliac extremes represents the sum of the average of the three measurements divided by the number in litter. By using the above formula for mean dimension, the calculation was made for each litter for each of the nineteen periods of observation. Graphs presented on the measurement data are made up in exactly the same way as has been described for making the graphs for weight, comparing only litters of the same number of individuals. A grand average graph is likewise made up regardless of litter size. The graphs based upon identical litter size are considered reliable for purposes of comparing the offspring in the different service groups, but the grand average graph is subject to considerable error.

DATA AND RESULTS

1. Growth in weight of young as related to frequency of copulation of sire

For studying the offspring with a view of determining if there is any relation between the number of services made by the males and the rate of growth, there appears to be no better measure than body weight. Body weight measures the animals as a whole and should thus reveal any inherent weakness that retards their growth.

Below are presented charts 1 to 12 taken from the composite weight records of the young of all three males. Each chart represents a single litter number at birth, all litters of one size, in each of the five service groups being grouped together and the same grouping being followed for all litter numbers as described on page 580. Each service group is represented by a different line, as is disclosed by the legend on the charts. The number of litters represented by each curve is given in each case. Chart 13 shows the weighed grand average for all five service groups. It was obtained by adding together the individual mean of each litter and dividing by the total number of litters at each observation period. We have already shown that such a chart comparing directly the growth ratio of the different service groups

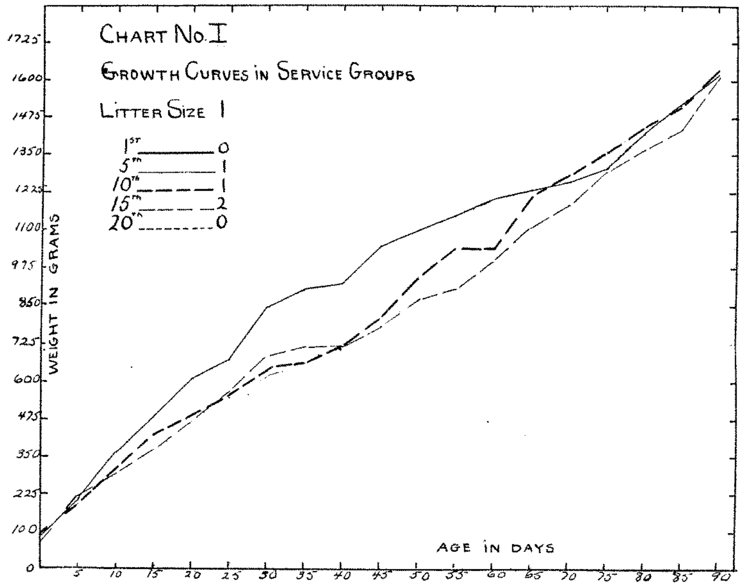
Chart No. I
Growth Curves in Service Groups
Litter Size 1
1st 0
5th 1
10th 1
15th 2
20th 0
Weight in Grams
Age in Days
1725
1600
1475
1350
1225
1100
975
850
725
600
475
350
225
100
0
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

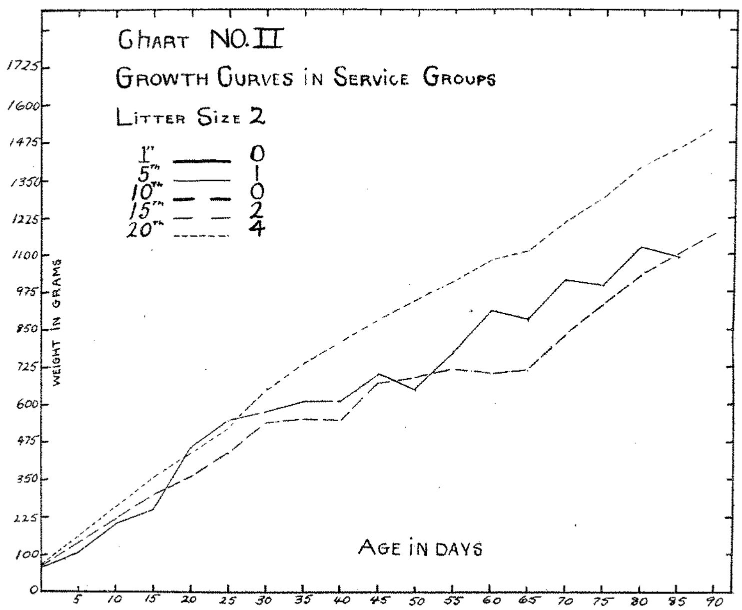
Chart No. II
Growth Curves in Service Groups
Litter Size 2
1st 0
5th 1
10th 0
15th 2
20th 4
Weight in Grams
Age in Days
1725
1600
1475
1350
1225
1100
975
850
725
600
475
350
225
100
0
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

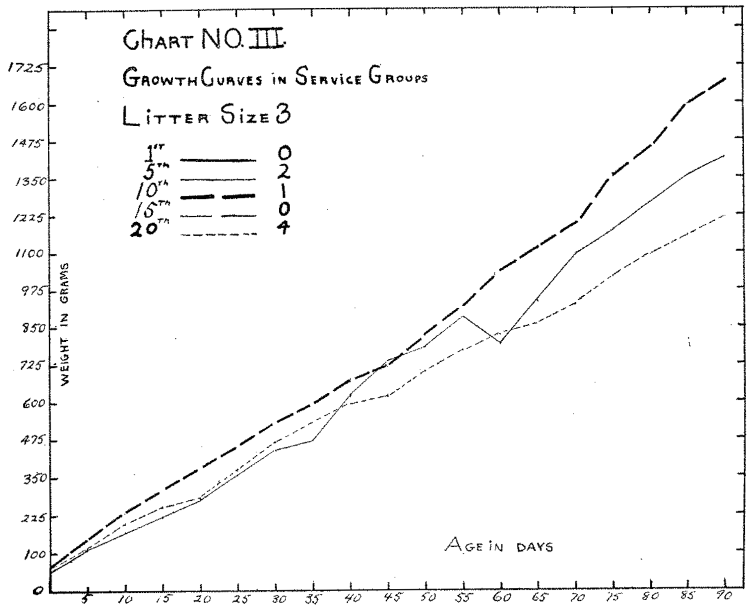
Chart NO. III
Growth Curves in Service Groups
Litter Size 3
1st 0
5th 2
10th 1
15th 0
20th 4
Weight in grams
Age in days
0
100
225
350
475
600
725
850
975
1100
1225
1350
1475
1600
1725
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90

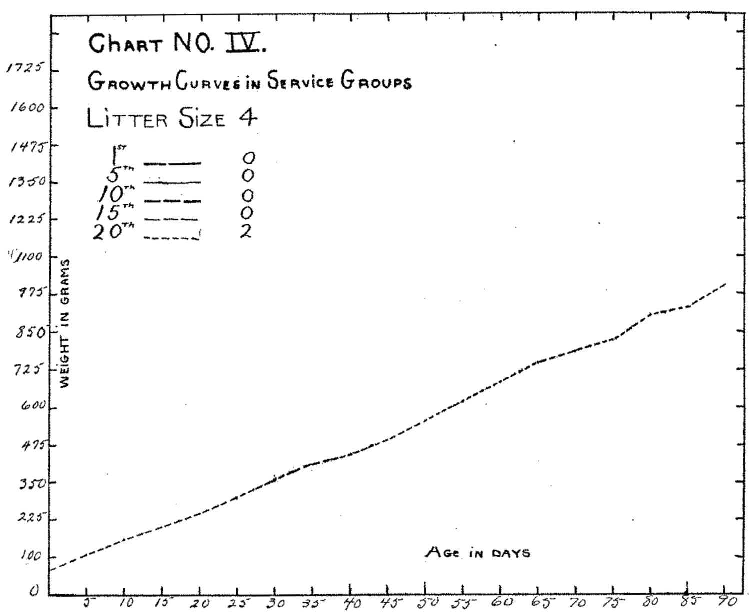
Chart NO. IV.
Growth Curves in Service Groups
Litter Size 4
1st 0
5th 0
10th 0
15th 0
20th 2
Weight in grams
Age in days
0
100
225
350
475
600
725
850
975
1100
1225
1350
1475
1600
1725
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90

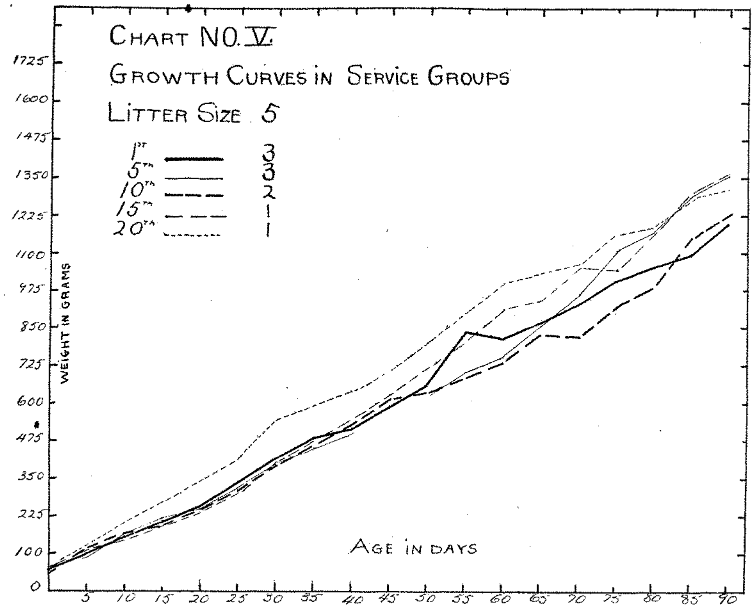
Chart No. V
Growth Curves in Service Groups
Litter Size 5
1st 3
5th 3
10th 2
15th 1
20th 1
Weight in grams
1725
1600
1475
1350
1225
1100
975
850
725
600
475
350
225
100
0
Age in days
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

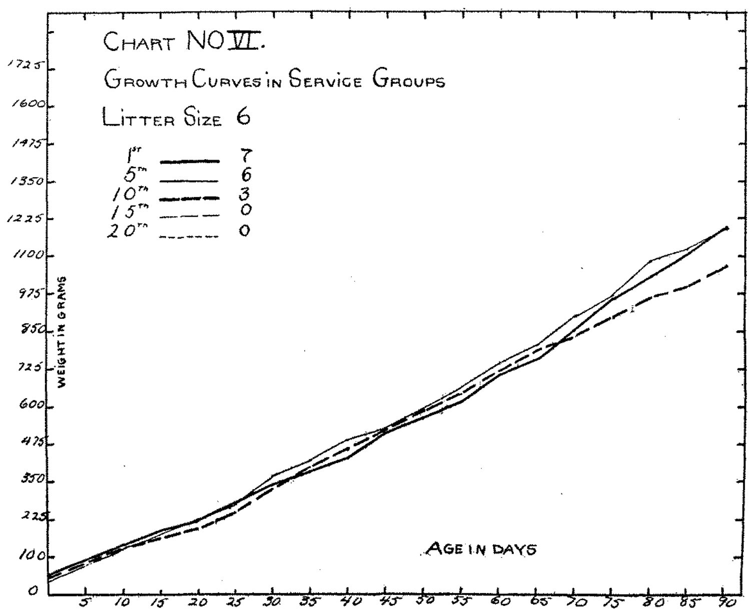
Chart No. VI.
Growth Curves in Service Groups
Litter Size 6
1st 7
5th 6
10th 3
15th 0
20th 0
Weight in grams
1725
1600
1475
1350
1225
1100
975
850
725
600
475
350
225
100
0
Age in days
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

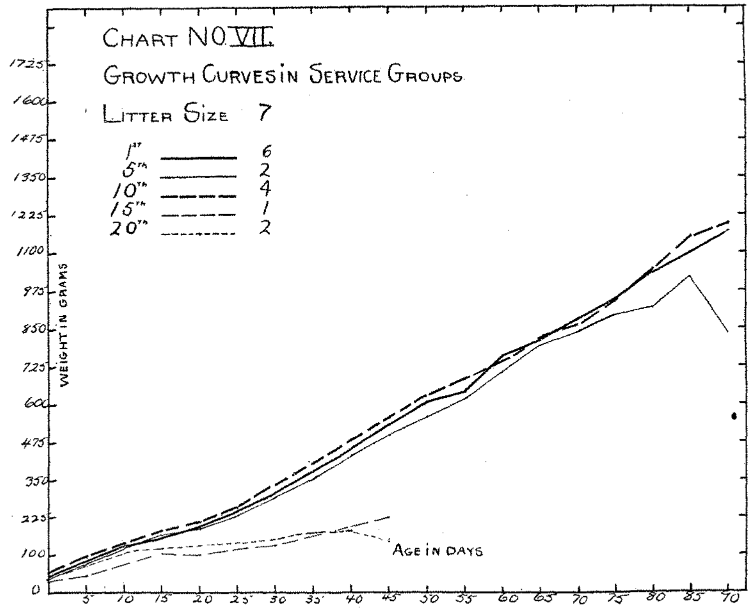
Chart No. VII
Growth Curves in Service Groups
Litter Size 7
1st 6
5th 2
10th 4
15th 1
20th 2
Weight in grams
Age in days
1725
1600
1475
1350
1225
1100
975
850
725
600
475
350
225
100
0
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

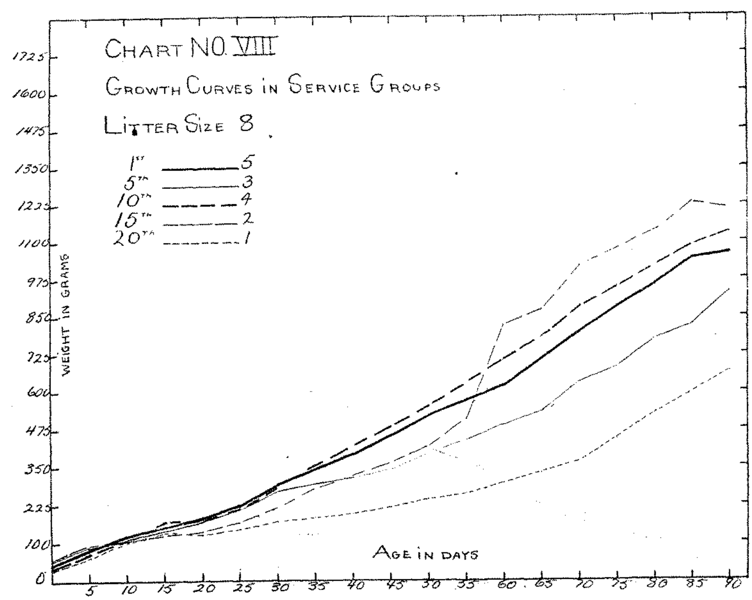
Chart No. VIII
Growth Curves in Service Groups
Litter Size 8
1st 5
5th 3
10th 4
15th 2
20th 1
Weight in grams
Age in days
1725
1600
1475
1350
1225
1100
975
850
725
600
475
350
225
100
0
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

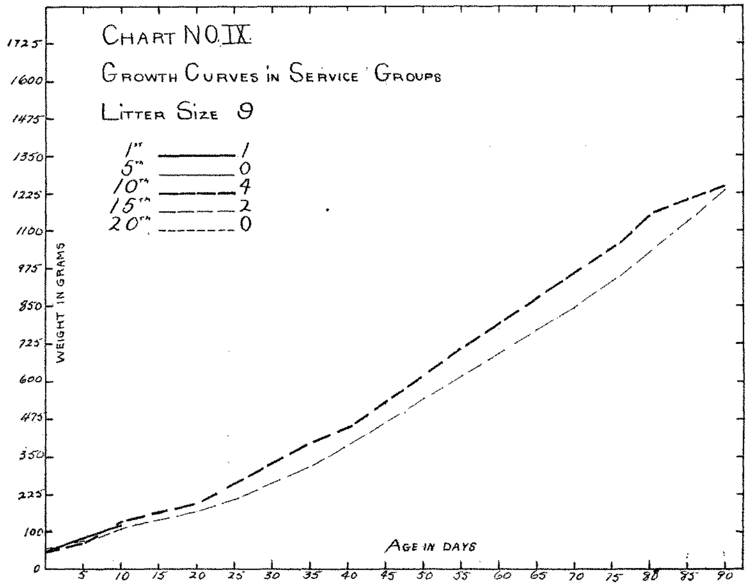
Chart No. IX
Growth Curves in Service Groups
Litter Size 9
1st 1
5th 0
10th 4
15th 2
20th 0
Weight in grams
Age in days
0
100
225
350
475
600
725
850
975
1100
1225
1350
1475
1600
1725
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20
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70
75
80
85
90

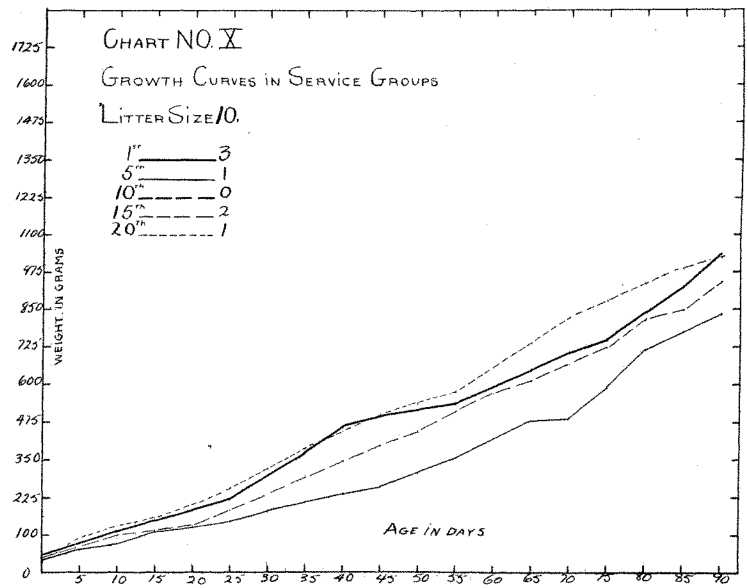
Chart No. X
Growth Curves in Service Groups
Litter Size 10.
1st 3
5th 1
10th 0
15th 2
20th 1
Weight in grams
Age in days
0
100
225
350
475
600
725
850
975
1100
1225
1350
1475
1600
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70
75
80
85
90

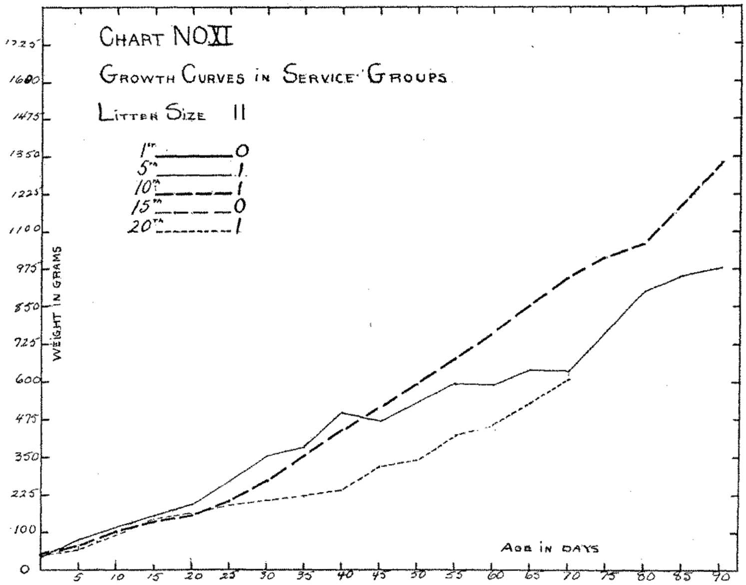


CHART NO. XI
GROWTH CURVES IN SERVICE GROUPS
LITTER SIZE 11
1st 0
5th 1
10th 1
15th 0
20th 1
WEIGHT IN GRAMS
AGE IN DAYS
1725
1600
1475
1350
1225
1100
975
850
725
600
475
350
225
100
0
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

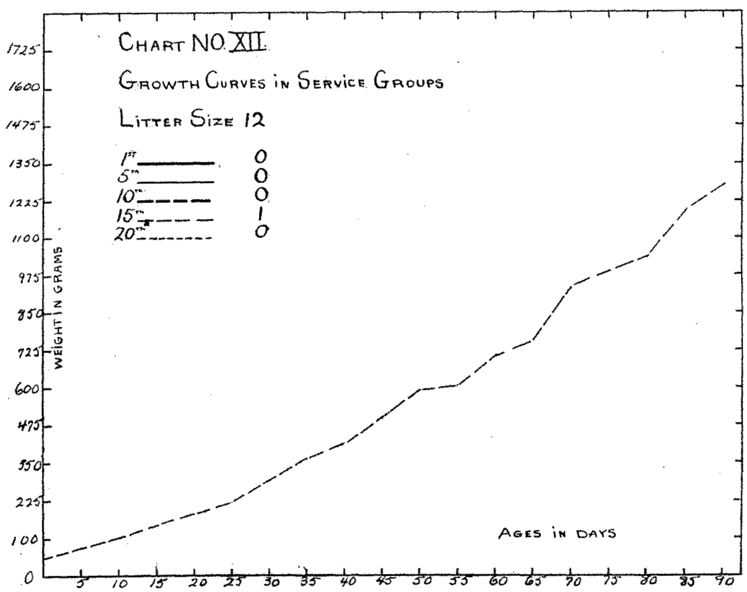
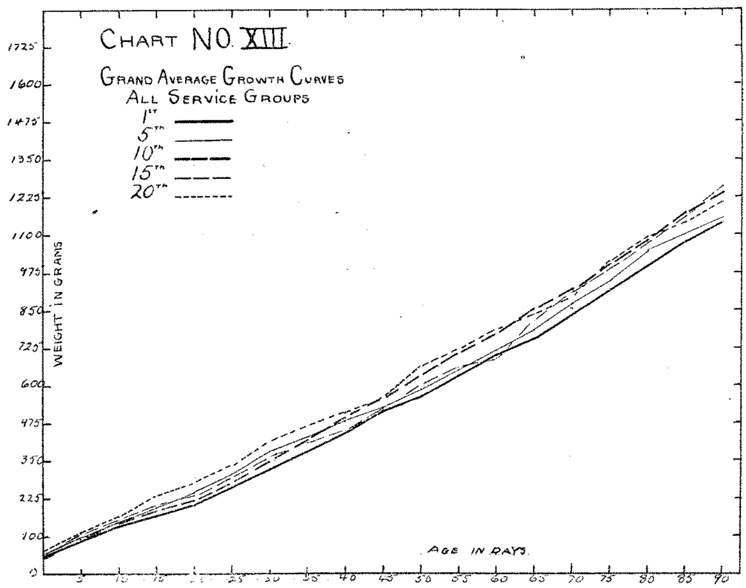


CHART NO. XII
GROWTH CURVES IN SERVICE GROUPS
LITTER SIZE 12
1st 0
5th 0
10th 0
15th 1
20th 0
WEIGHT IN GRAMS
AGES IN DAYS
1725
1600
1475
1350
1225
1100
975
850
725
600
475
350
225
100
0
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90



may not be made with absolute justice because, as will be shown later, the litters in the advanced service groups tend to be smaller. A rough comparison of all progeny may be made in this way, however.

Charts 1 to 12, inclusive, present the results in a form that may be easily grasped by the reader, but there are a few points revealed by a study of these graphs that require some discussion. With but few exceptions, the 20th-service graph lies above all other graphs. This is a striking and surprising result and the question at once arises as to the cause of the almost uniform heavier birth weight and more rapid growth of the 15th- and 20th-service litters compared with litters of the same size from less advanced services. The results are in direct contrast to what, according to the traditions of breeders, would be expected. On their face they actually show that the heavier the service of the male, the more thrifty the offspring. It seems best to here consider the possible factors that may play a part in causing the superiority of these advanced service litters over litters from the 1st, 5th, and 10th service.

During the production of the majority of the 1st- and 5th-service litters the breeding animals were housed in somewhat cramped quarters. Conditions there were not conducive to the most rapid growth of the young and were not as favorable for the breeding females because of small space and rather poor ventilation and poor light. Furthermore, the progeny were crowded into rather limited exercising pens, and probably for this reason they did not develop at so rapid a rate as would have been the case under the more favorable quarters used later. The majority of the 10th-service litters, on the other hand, and about half of the 15th-service litters were produced while the stock was housed in more ample quarters where the space was large, the ventilation good, and everything was conducive to health and thriftiness. In fact, the quarters used at that time were practically as good as the present permanent and excellent quarters where the 20th-service litters were produced. The superior environment of the advanced service litters is no doubt partly responsible for the greater growth of the advanced service litters compared with the moderate service litters; but environment cannot be entirely the cause of the superiority of the 20th-service litters over the 15th, and the 15th-service litters over the 10th-service litters. Let us therefore seek a further explanation.

Parentage may be an important factor affecting the weight. As has been previously noted, the variability of the female breeding stock is considerable, the range of weight was from 2500 to 3250 grams, averaging 3050 grams, but the females have been so distributed among the three breeding males as to make three groups of practically uniform weight and variability in size. Nevertheless, lack of uniform weights in the progeny may still be partly due to variability of the female breeding stock.

The size of the sire may also be a factor in controlling individual mean weight. The three sires used were quite different in weight; their weights are as follows: No. 1, 2850 grams; No. 3, 2575 grams, and No. 4, 2225 grams in ordinary breeding condition. Male No. 1 sired eleven of the seventeen litters included in the 20th-service group. He, being the largest of the three males, would be expected to sire the heaviest offspring at birth, and such offspring

TABLE 1

Average birth weight of litters sired by the three different males used, by service groups

MALE MEMBER	1ST		5TH		10TH		15TH		20TH	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight	Number	Weight
1	6	46.7	6	45.2	7	45.2	7	52.5	11	59.7
3	12	50.9	8	45.0	2	45.0	2	42.7	00	00
4	8	42.4	6	58.8	4	58.8	4	49.6	6	53.3
Weight at ninety days										
1	5	1209.5	3	1236.6	7	1238.1	7	1262.0	6	1299.3
3	11	1170.0	6	1217.8	7	1095.3	2	1270.7	00	
4	7	1054.9	6	1096.1	5	1424.3	2	1199.7	3	1009.0

could be expected to keep ahead of the other classes of offspring at least for ninety days. This way of explaining the position of the 20th-service graph above the others is called in questions by chart 3 and also by table 1. The graph of the 20th-service litter lies below the others. This graph represents the growth of a single 20th-service litter (after the first weight) also by Male No. 1 and out of the heaviest female in the breeding stock (No. 15). Therefore, the fact that this litter lies below 5th- and 10th-service litters on this chart cannot be explained as the result of small ancestry.

Table 1 shows that the size of the male ancestor is not a very important factor in relation to the size of the young at birth. At the age of ninety days, however, the effect of the heavier sire becomes more important, but nevertheless is probably not as important as some other factors concerned as will be pointed out later.

When we consider the 15th-service group, we find that seven litters were sired by Male No. 1, two by No. 3, and four by No. 4. Again we should expect a more uniformly heavy progeny than if all males had contributed an equal number of litters to the data. Chart 8 shows the superiority of the 10th-service group over the 15th-service group up to the fifty-fifth day, after which time the graph rises above all others.

Thus far we have attempted to account for the heavier weights and the greater rate of growth of the advanced service litters as due entirely to factors other than the nature of the spermatozoa and not to any inherited superiority. The effect of such factors does not seem adequate to explain the apparent superiority of the advanced service litters, therefore there is good evidence that a real superiority exists among the advanced service litters as compared with the light service litters. The female ancestors in both service groups were practically equal in weight. One of the 15th-service litters represented in chart 9 was sired by Male No. 1, the other by No. 3. Two of the four litters combined in the 10th-service graph were sired by No. 1 and two by No. 3. The smaller weights of the 15th-service litters during the early part of the observations cannot for the above reasons be explained by male ancestry of different weights.

One other hypothesis may be proposed to account for the probable superiority of the advanced service progeny over those from very moderate service. Pearl ('17, p. 296) treated both cocks and hens with ethyl alcohol, methyl alcohol, and ether at different times during the breeding season in order to study the effects on their progeny. He found the offspring from treated parents in every way superior to those from untreated parents. Pearl assumes that alcohol and other poisons act as selective agents upon the germ cells of treated animals. It is possible that selective action might be brought about by heavy sexual service of the male. We have previously shown that heavy sexual service induces the liberation of sperm which often show no progressive motion and are short-lived. Some few of the sperm from these advanced services do exhibit the physical properties that indicate high vital force. The possibility exists then that what few spermatozoa do take part in fertilization are superior to the average in the light service groups because the bulk of the spermatozoa in the advanced service groups are not equipped to take part in fertilization, while this is probably not true in the light service groups. Such a hypothesis as the above will thus account for the superiority of the advanced service progeny.

TABLE 2

Number of litters included in graphs of charts 1 to 12, inclusive, and the male ancestry

MALE MEMBER	SERVICE GROUP				
	1st	5th	10th	15th	20th
1	6	6	7	7	11
3	12	8	7	2	0
4	8	6	6	4	6

Concerning the graphs for the 10th-, 5th-, and 1st-service litters, we note that as a rule the 1st-service litters are inferior in weight to either the 5th- or 10th-service litters and that the 10th-service litters are for the most part superior to the 5th-service litters. As previously noted, less favorable environment and greater immaturity of some of the female animals are thought to be the chief factors entering here. The male ancestry is almost uniformly distributed among the three males. Below we note from the table just how the ancestry is distributed.

Table 2 shows us that the three males are about equally distributed in the progeny groups from the 5th and 10th services. In the 1st-service group, however, No. 3 has sired twice as many litters as No. 1 and 50 per cent more than No. 4. Since Male No. 3 is a smaller animal than No. 1, we have here a partial explanation for the apparent inferiority of the 1st-service litters over all others. In the 15th- and 20th-service groups the progeny of Male No. 1 predominate, and Male No. 3 sired no litters in the 20th-service group.

A word of explanation in regard to a few remarkable features of some of the charts may be of value at this point. On chart 3 the depression in the 5th-service graph at sixty days is due to a failure to obtain data on the heavier of the two litters making this graph. This particular litter was unintentionally overlooked for four weighings. On chart 5, the drop in the 10th-service graph at sixty-five days is due to the incomplete record on one litter at the time the graphs were constructed and this litter was made up of very heavy individuals.

Chart 13 represents the grand average growth of all litters in the five service groups as explained on page 582. Each graph thus represents the individual mean for the combined litters in each service group. These composite service group graphs bear out the general deductions that we have madefrom a study of the graphs taken one by one comparing litters of a given number with each other in the five service groups. There is one outstanding objection to the use of such graphs as are shown on chart 13. There is a perceptible negative correlation between number of services of the sire and the number of offspring in litters resulting (Lloyd-Jones and Hays, p. 492). In other words, heavy service does reduce the size of litters, especially in the two most advanced service groups used here. Consequently the greater supply of nutrients furnished by the mother in utero as well as the greater supply of milk available after birth will enable the advanced service litters to outstrip the other litters during the periods of observation in this experiment. This condition would hold if all litters were equally fit genetically; and we have no evidence that any class of offspring is rendered less fit by heavy service of their sire.

To recapitulate, certain errors have been introduced into the growth studies in body weight, chief among which are environmental factors, the age and weight of the dam and the weight of the sire. These errors have been partially corrected, and the conclusion seems justified that there is no evidence in this data to show that the amount of sexual service that the male has been required to perform in any way affects the rate of growth of his offspring in body weight for the first ninety days of postnatal life.

2. Litter coefficient of variability

The coefficients of variability in table 3 presented below were obtained in the following manner: The coefficient of variability for each litter in each of the five service groups was determined at birth, at thirty days, and at ninety days by the formula:

$$\frac{\text{Standard deviation of each litter.}}{\text{Mean of the litter.}}$$

TABLE 3

2. Coefficient of variability of individuals within the litters at three different periods

AGE	SERVICE									
	1st		5th		10th		15th		20th	
	Number of litters	Per cent	Number of litters	Per cent	Number of litters	Per cent	Number of litters	Per cent	Number of litters	Per cent
days										
Birth	26	10.81±1.01	20	10.73±1.14	19	12.52±1.37	11	11.43±1.64	16	8.80±1.05
30	23	10.72±1.07	17	8.27±0.96	19	10.05±1.10	11	9.56±1.29	11	7.89±1.11
90	23	10.10±1.02	14	6.77±0.86	17	7.55±0.87	8	10.70±1.80	9	8.94±1.42
Average.		10.55		8.82		10.13		10.55		8.56

The coefficients of variability for all 1st-service litters at birth were then added together and this sum was divided by the number of litters concerned to secure the coefficient as given in table 3. Likewise the coefficients of variability for all 1st-service litters at thirty days were added together and this sum divided by the number of litters concerned to obtain the coefficient as given in table 3. This method was used on the weights at ninety days to get the coefficient, and a similar procedure used on the weights in the other four service groups to obtain their respective coefficients. For the information of the reader the number of litters concerned in each case is presented in the table. MacDowell ('14, p. 44) shows in studies on weight of adult rabbits that there is less variability within the litters than between individuals of different litters. For this reason and because we wish to compare progeny of different ancestry, the method of expressing the coefficient of variation of the populations as the average of the individual litter coefficients of that population is considered accurate.

Table 3 shows that the coefficient of variation in rabbits is greater at birth than at any other time during our observations. This fact holds good in all service groups. While the coefficient on the average is small, it serves to indicate that prenatal nutrition must be subject to wide variations, otherwise greater uniformity in weight at birth should be expected. The thirty-day period is the weaning time for all of the litters studied in this experiment. We note from the table that the coefficient of variation falls below what it was at birth in all service groups. Here again there is no evidence of an increased percentage of 'weak' offspring in advanced service groups, for if such were the case we should expect the coefficient to increase when the animals were thrown into competition for nutrition during the first thirty days of postnatal life, and even one inferior individual would alter the coefficient for the litter. At the ninety-day period there is again a decrease in the coefficient of variation in all service groups, except the 15th- and 20th-service groups. The large size of the probable error here indicates that the 15th-and 20th-service groups cannot safely be assumed to be exceptions.

Taking up a comparison of the coefficients for the different service groups, there appears to be slightly less variability in the offspring as the number of services increases, but this decrease is not universal. Since the probable error is rather large, this difference is no way significant. As has been previously stated, there is also a slight reduction in the number in the litters in the same direction. Our data show us further that there is less variability in the smaller than in the larger litters. This fact affords us an explanation for the slight reduction in the coefficient of variation as the number of services increases.

In table 3 a further fact seems apparent that occasional genetically weak offspring do not occur in any one of the service group more frequently than in any other service group. The table also shows us that for the first ninety days of postnatal growth there is a tendency for individuals of the same litter to approach nearer to a mean weight than was the case either at birth or at thirty days of age. Fetal nutrition is thus more variable than either the nutrition furnished by the mother during the first thirty days after birth or the ordinary food supply furnished from thirty days to ninety days.

TABLE 4

Service-group coefficients of variability at three different periods

AGE	SERVICE									
	1st		5th		10th		15th		20th	
	Number of litters	Per cent	Number of litters	Per cent	Number of litters	Per cent	Number of litters	Per cent	Number of litters	Per cent
days										
Birth	26	17.62±1.65	20	28.10±3.10	20	23.03±2.46	13	15.59±3.39	16	21.94±2.62
30	23	19.70±1.96	18	42.65±4.80	21	35.53±3.69	13	52.13±6.91	11	46.37±6.66
90	23	24.25±2.41	17	23.89±2.76	21	19.63±2.04	11	24.97±3.53	9	30.91±4.92
Weighted average..		24.40		31.56		26.11		34.73		31.65

3. Service group coefficients of variability

In table 4 are presented the service-group coefficients of variability for all of the progeny studied in the experiment. These coefficients are obtained in the following manner: The sum of the mean individual weights of each litter in the 1st-service group was divided by the number of litters, to get an average at birth, at thirty days, and at ninety days. The standard deviation of this average was then calculated and the coefficient of variability (e) obtained by the formula:

$$\frac{\text{Standard deviation of the average}}{\text{Average}} = \text{C}$$

The same method was used for all five service groups.

The service-group coefficient of variability differs from the litter coefficient of variability given in table 3 in that the former measures the range in weight between the individual litter means of the different service groups, while the latter is a measure of the range in weight between individuals of the same litter.

The service-group coefficient of variability is valuable in studying the effects of heavy service of males upon the growth in body weight of their offspring because it will bring to light occasional litters in which every individual is inferior. For example, table 3 shows that there is not an occasional inferior individual in the advanced service progeny. This fact does not remove the possibility of some entire litters being inferior because it is possible to conceive that at one time a male rabbit might sire an exceptionally good litter on the 15th or the 20th service because of extra high reserve, but the majority of his progeny might be inferior in growth as entire litters. By table 4 we shall attempt to discover if litters as a whole are inclined to be more variable in any particular service group.

Table 4 shows that at birth there is less variability in the 1st-service progeny than in any other progeny. This implies that the individual mean weight of the 1st-service litters more nearly represents the mean of every litter in the service group than is the case in any of the other four service groups. There appears to be little tendency for variability to increase as the amount of service increases as shown in the other four service groups at birth.

Concerning the variability between litters at thirty days of age, practically the same relationship exists between the progeny of the different service groups as has been already noted in considering the progeny at birth. The table shows us one additional fact at the thirty-day age; namely, that the greatest variability in weight during the ninety days of the observation exists at weaning time or thirty days. This fact is additional evidence that the nutrition furnished by the mother while suckling the young may vary in absolute amount or may be distributed in limited quantities because of the large number of individuals that she may suckle.

At the age of ninety days there is a striking uniformity in the coefficients for all five service groups. Only in the case of the 20th-service group is there any noticeable digression, and this is probably due to the small number of litters concerned.

Table 4 as a whole does not in any way indicate that inferior litters exist more frequently in any one service group than in any other, and the fact has already been pointed out in connection with the study of the weight graphs than in average body weight the advanced service litters are equal and in some cases superior to that of the litters in the light service groups. The fact that variability within litters is small compared with the variability in service groups is well illustrated by a comparison of the coefficients in tables 3 and 4.

4. Growth by measurements as related to frequency of copulation

Charts 14 to 21 are presented to show the growth in the mean dimension as obtained on forty-five litters. The method of making measurement and the determination of the mean dimension have been already explained, pp. 581–582. Each graph represents averages of the mean dimension for all litters of the same size in the respective service groups. The mean dimension for a litter is obtained by adding all head measurements to all measurements of ilial extremes and dividing the sum by the total number of readings included in the sum. The expression thus obtained is the average individual mean dimension for the respective litters and may be compared with the average individual weights used in the previous charts.

These charts of body development show that there is a maximum increase in the mean dimension up to about the twentieth day, after which there is a very noticeable flattening of the graphs. From about the twentieth day on to the end of the observations at ninety days the progressive increase in the mean dimension is about constant. The increase in the mean dimension is thus in marked contrast to the increase in body weight previously illustrated by charts 1 to 13. Body weight has been shown to make a rather constant increase up to the end of ninety days, and this is well illustrated by the fact that the weight graphs show little if any tendency to flatten out.

Though the number of litters making up a mean dimension graph is in most cases small, they serve to illustrate the same principle as the weight graphs, namely, that the advanced service progeny are fully equal to the 1st- or 5th-service progeny at all times during the ninety days of the observation. On

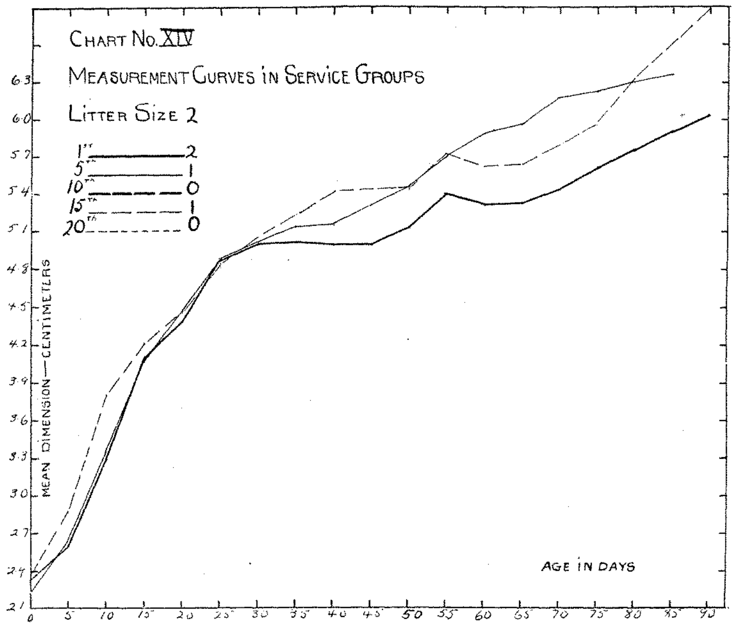


CHART No. XIV
MEASUREMENT CURVES IN SERVICE GROUPS
LITTER SIZE 2
1st 2
5th 1
10th 0
15th 1
20th 0
MEAN DIMENSION—CENTIMETERS
AGE IN DAYS
6.3
6.0
5.7
5.4
5.1
4.8
4.5
4.2
3.9
3.6
3.3
3.0
2.7
2.4
2.1
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

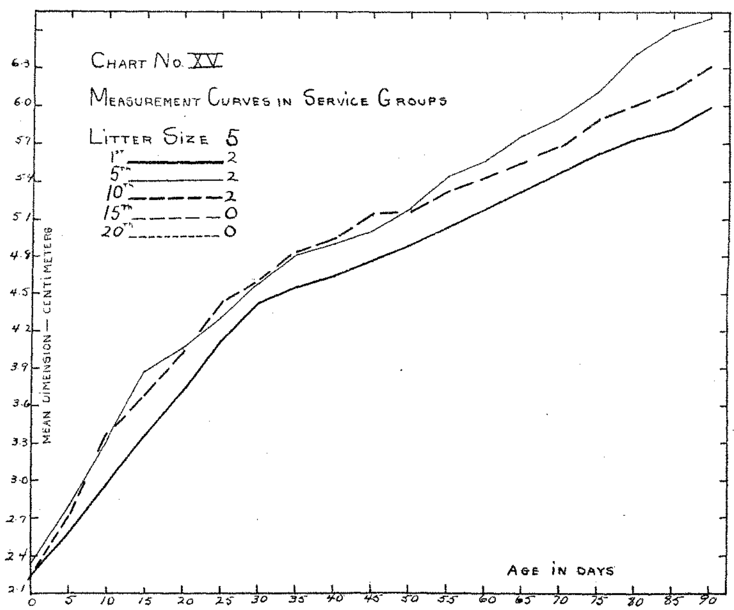


CHART No. XV
MEASUREMENT CURVES IN SERVICE GROUPS
LITTER SIZE 5
1st 2
5th 2
10th 2
15th 0
20th 0
MEAN DIMENSION—CENTIMETERS
AGE IN DAYS
6.3
6.0
5.7
5.4
5.1
4.8
4.5
4.2
3.9
3.6
3.3
3.0
2.7
2.4
2.1
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

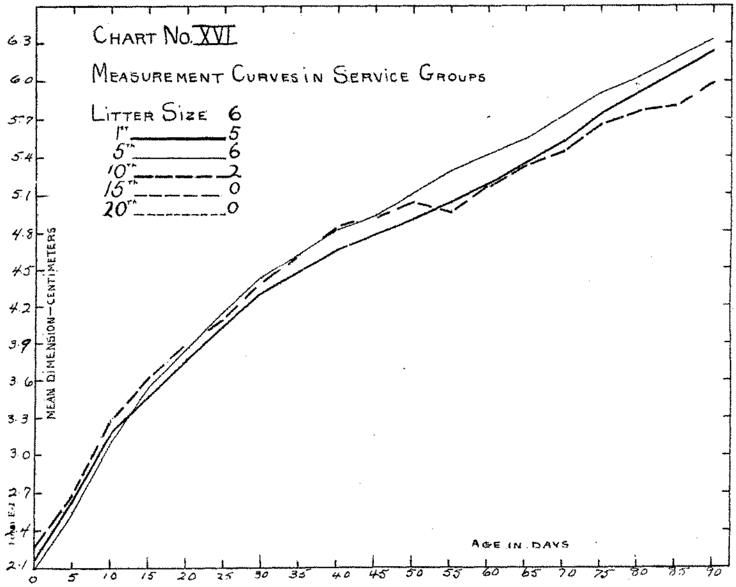


Chart No. XVI
Measurement Curves in Service Groups
Litter Size 6
1st 5
5th 6
10th 2
15th 0
20th 0
Mean Dimension—Centimeters
Age in Days
6.3
6.0
5.7
5.4
5.1
4.8
4.5
4.2
3.9
3.6
3.3
3.0
2.7
2.4
2.1
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

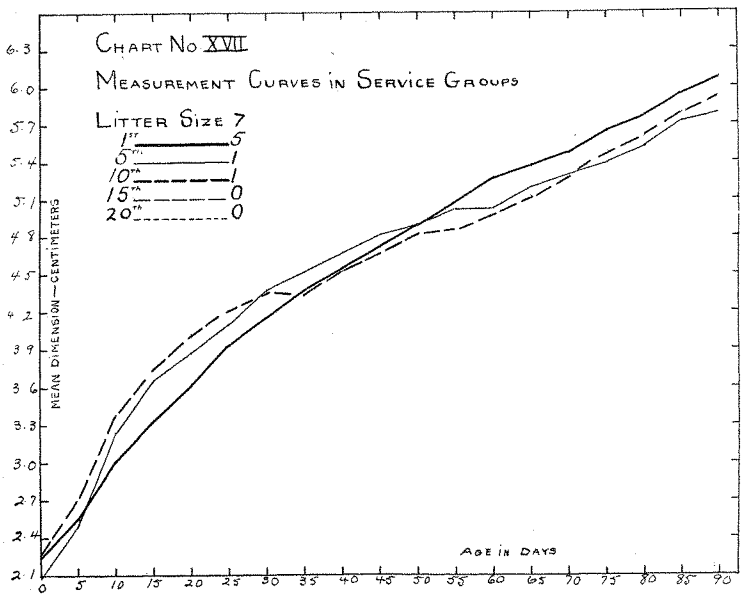


Chart No. XVII
Measurement Curves in Service Groups
Litter Size 7
1st 5
5th 1
10th 1
15th 0
20th 0
Mean Dimension—Centimeters
Age in Days
6.3
6.0
5.7
5.4
5.1
4.8
4.5
4.2
3.9
3.6
3.3
3.0
2.7
2.4
2.1
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

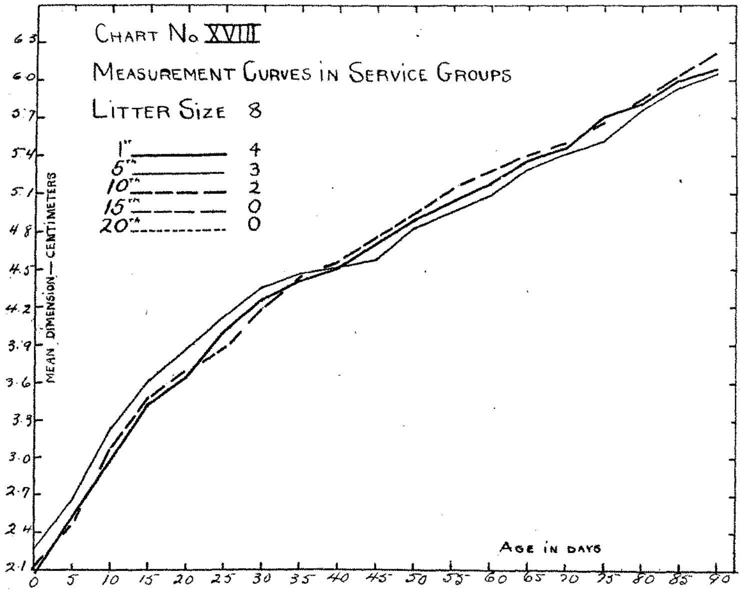


Chart No XVIII
Measurement Curves in Service Groups
Litter Size 8
1st 4
5th 3
10th 2
15th 0
20th 0
Mean Dimension—Centimeters
Age in days
6.3
6.0
5.7
5.4
5.1
4.8
4.5
4.2
3.9
3.6
3.3
3.0
2.7
2.4
2.1
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

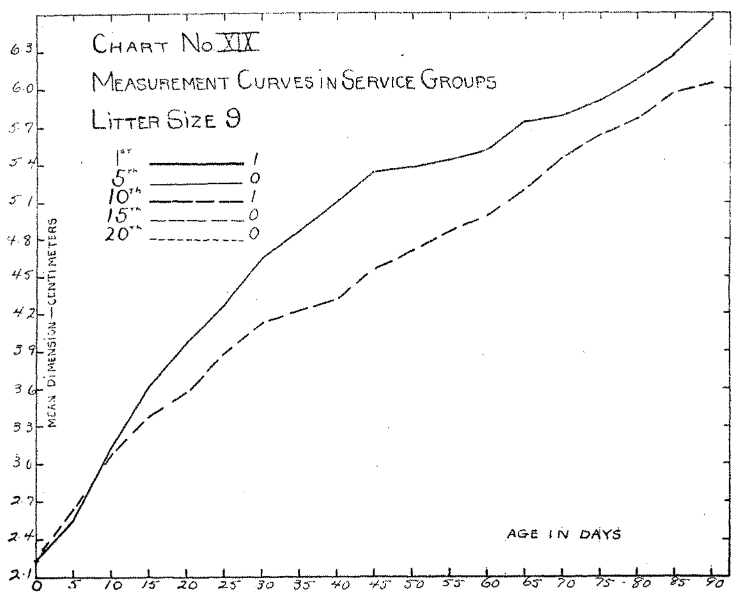


Chart No XIX
Measurement Curves in Service Groups
Litter Size 9
1st 1
5th 0
10th 1
15th 0
20th 0
Mean Dimension—Centimeters
Age in days
6.3
6.0
5.7
5.4
5.1
4.8
4.5
4.2
3.9
3.6
3.3
3.0
2.7
2.4
2.1
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

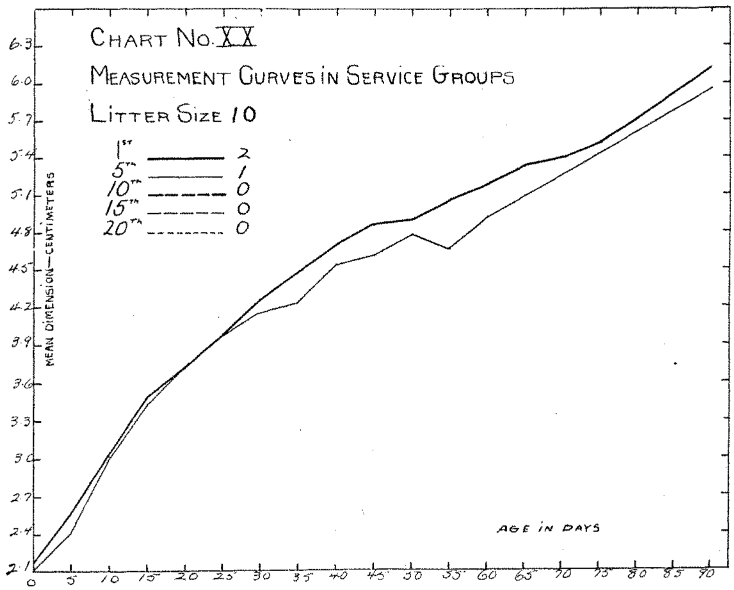


CHART No. XX
MEASUREMENT CURVES IN SERVICE GROUPS
LITTER SIZE 10
1st 2
5th 1
10th 0
15th 0
20th 0
MEAN DIMENSION—CENTIMETERS
AGE IN DAYS
6.3
6.0
5.7
5.4
5.1
4.8
4.5
4.2
3.9
3.6
3.3
3.0
2.7
2.4
2.1
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90

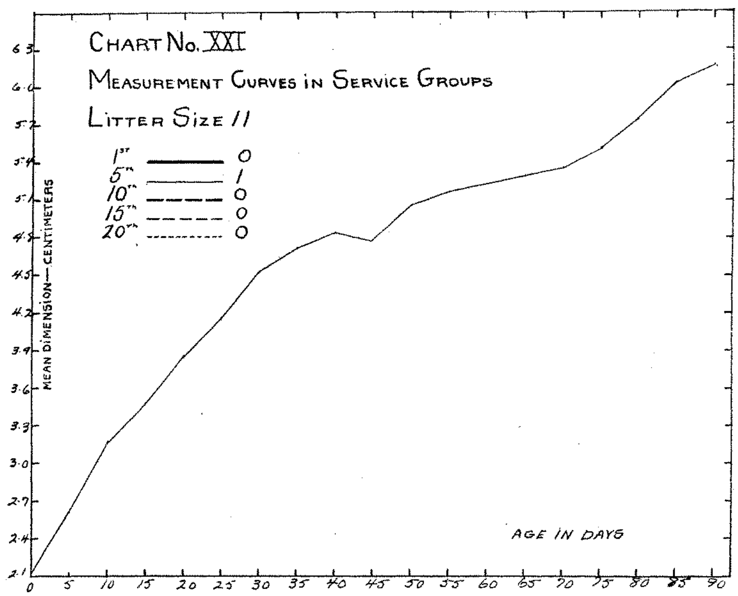
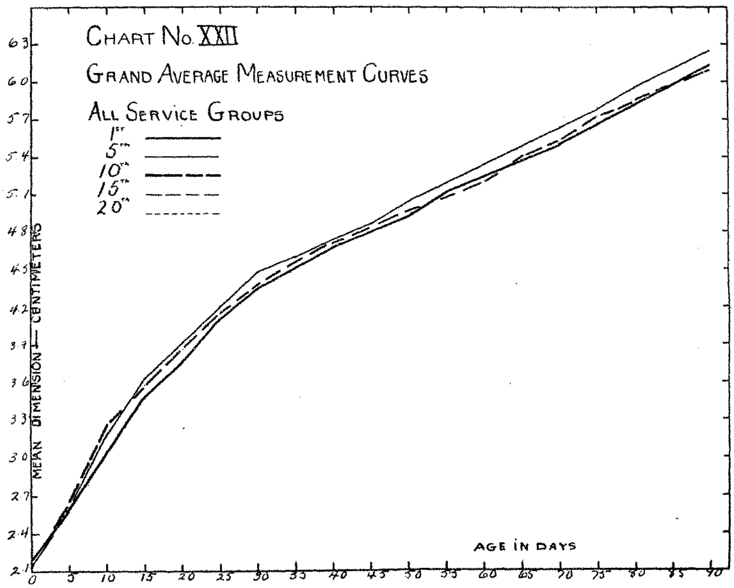


CHART No. XXI
MEASUREMENT CURVES IN SERVICE GROUPS
LITTER SIZE 11
1st 0
5th 1
10th 0
15th 0
20th 0
MEAN DIMENSION—CENTIMETERS
AGE IN DAYS
6.3
6.0
5.7
5.4
5.1
4.8
4.5
4.2
3.9
3.6
3.3
3.0
2.7
2.4
2.1
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90



charts where but a single litter makes up a graph a rather sudden break may sometimes be noted in the graph. This, in our opinion, is the result of error in measurement, and for this reason the graphs made up of several litters will be less influenced by minor errors and hence should be more representative of actual dimensions.

In chart 22 are presented grand average graphs made up as the average of twenty-one 1st-service litters, fifteen 5th-service litters, eight 10th-service litters, and one 15th-service litter. Here the coincidence of the 1st-, 5th-, and 10th-service graphs is very striking. This fact bears out our previous conclusions from body weight studies that heavy sexual service of the male has no effect upon the growth of his offspring. Our evidence in studying the increase in the mean dimension does not show any effect on the progeny, from the heavy service of the male. The 15th-service graph is made up of but one litter of two individuals sired by Male No. 1 and out of an average sized female. The fact that this litter is few in numbers and has as a sire the largest of the males will probably account for their larger mean dimension.

TABLE 5

Percentage mortality in offspring during the first five days of life and between the fifth and the ninetieth day of life

	SERVICE				
	1st	5th	10th	15th	20th
Number of animals born	180	119	139	84	77
Number dying first five days	16	15	16	11	7
Per cent dying first five days	8.89	12.61	11.51	13.09	9.09
Number dying between 5 and 90 days	21	36	17	9	19
Per cent dying between 5 and 90 days	11.67	30.25	12.23	10.71	24.68

Summarizing the results of the measurement studies, we note that there is very close proximity of the graphs for the different service groups. This points very strikingly to the probable fact that heavy service of males has no effect upon the growth of their offspring in the length of head and in the breadth of ilial expanse.

In table 5 the progeny are grouped by services and the number and the percentage mortality is given for each service group. Under the row marked "Number dying first five days" are included all animals dead at birth as well as those that died during the first five days of life. The other row of the table includes only animals actually dying between the fifth and the ninetieth day of postnatal life.

The percentage of mortality during the first five days shows a slight increase as the number of services increases up to the 15th-service group. Comparing the 1st-service group with the 20th-service group, we note that the percentage mortality in the first five days is practically the same in both groups. Since the environment has been more favorable for the 20th-service litters than for the 1st-service litters, as previously pointed out, there is no indication that twenty copulations by a male do in any way tend to reduce the percentage of his progeny that will survive the first five days of postnatal life. The table shows practically the same percentage of mortality during the first five days in both the 5th- and the 15th-service groups. The explanation for the rather high percentage of mortality in the 5th-service group is that two litters were destroyed outright by the mother and a number of the other 5th-service litters were born during extremely hot weather when the mortality was very high even among the older animals. The 10th-service group shows a higher death rate than the 1st-service group. In all these cases the percentage of mortality during the first five days does not seem to depend upon the number of services that the male is required to make.

Table 5 shows that there is very little consistency between the mortality percentages as revealed in the first part of the table and between the percentages of deaths that occurred between five and ninety days. The first five days is a very critical time in the life of the young rabbit and very slight exposure may bring disaster. When this period is over the deaths usually result from bowel disorders or from septicaemia. Bowel disorders are most common during the very hot weather of summer in the stock, and it is very unfortunate that a large number of the animals in the 5th-service groups should have been so attacked. The 10th-service progeny also show a higher death rate than the 1st-service progeny, even though these 10th-service litters were housed under more favorable conditions than were the majority of the 1st-service litters. The mortality percentage of the 15th-service offspring is the highest of any of the service groups during the first five days of life, but it falls below that of all other service groups between the age of five and ninety days. Practically one-fourth of the 20th-service rabbits died between the fifth and the ninetieth day of postnatal life. An outbreak of septicaemia happened to occur among a number of these litters. This being the case, we are inclined to believe that this sudden outbreak of disease rather than any inherent weakness of the progeny resulting from heavy sexual service of the sire is here operating to cause the high percentage of mortalities.

6. Relation of number of services made to sex of offspring

A study of the relation of sex of the offspring to the amount of sexual service the male is required to perform is important because such data will show if either male or female producing

TABLE 6

Sex ratios in service groups. Males to 100 females

	SERVICE				
	1st	5th	10th	15th	20th
Number of individuals concerned	78	76	117	84	77
Ratio	129	77	80	53	28

sperm (Bachhuber, '16) is weakened by excessive functioning of the male reproductive organs. Table 6 presented below shows the sex ratio of the offspring in the different service groups.

Table 6 shows that in the 1st-service group there are 129 males to every 100 females. After the 1st-service group there is a regular decline in the number of males produced, with the exception of the 10th-service group. There is apparently some underlying cause to bring about the high percentage of females to males in all the advanced service groups, and there is a direct relation between the amount of service previously performed by the male and the proportion of female offspring that he will sire.

The properties of the spermatozoa are perceptibly modified by heavy sexual service of males (Lloyd-Jones and Hays, '17), there being a larger percentage of weak sperm in the advanced service sperm.

Two possibilities exist: either female-producing spermatozoa are formed more largely than male-producing spermatozoa as the amount of service of the male increases or the male-producing sperm are in themselves weaker than the female-producing sperm and consequently fewer of them survive to take part in fertilization. On the first point there is no evidence available. Concerning the second point, Stockard ('13) offers the hypothesis that in the case of guinea-pigs the larger female-producing sperm are more affected by alcoholization of the male than the smaller male-sperm producing. In the case of excessive sexual service, however, the large female sperm may be more vigorous because of their size or their greater chromatin content and thus outdistance the male-producing sperm in the struggle of fertilization, thus giving a higher percentage of female progeny in the heavy service groups as compared with the light service groups.

TABLE 7

Sex as related to mortality. Percentage mortality of the sexes

PERIOD	SEX	SERVICE			
		5th	10th	15th	20th
First five days	♂	8.69	7.14	0	9.09
	♀	6.85	11.90	17.74	9.09
Between five and ninety days	♂	6.52	8.93	9.09	27.27
	♀	12.33	15.47	11.29	24.24

In table 6 we considered the relation of sexual service to the sex of the offspring and found that a predominance of females to males is the rule in the heavy service groups. In table 7 we shall consider sex of the offspring dying before the close of the observation period at ninety days.

Table 7 shows that up to the 15th-service group there is a higher death rate among the female offspring than among the male offspring. In the 20th-service group, however, the fact will be noted that females are just as likely to survive as males for the first five days of postnatal life. Between the fifth and the ninetieth day there is a slightly lower death rate of females than males in the 20th-service group. These facts seem to indicate that in comparison with males of the same class, female offspring from the 20th-service are in respect of their ability to survive superior to ordinary offspring from the less advanced service groups. The fact still seems evident that these female offspring in the 20th-service group are slightly more likely to die than ordinary offspring.

SUMMARY OF FACTS

1. Body weight of the rabbit is a measure of growth that is subject to considerable variations largely brought about by slight changes in the environment.

2. The rate of increase in body weight continues at a uniformly rapid rate for the first ninety days of the rabbit's life.

3. The factors that appear to govern the weight of the young at birth are age of mother, state of health of mother, weight of

mother, weight of sire, character of food of mother, and number of individuals born in the litter.

4. The factors that govern the rate of postnatal growth of the young for the first ninety days are weight at birth, number in litter, milk supply furnished by the mother, and, after weaning, the character of the food supplied to the young and general character of the quarters.

5. No inferiority in the offspring from the heavy service groups is revealed by comparing the body weights with those of the light service groups.

6. The average litter coefficient of variability in body weight at birth at thirty days and at ninety days is no greater in the progeny in the heavy service groups than in the light service groups. Greater variability might be expected if a part of the offspring are made genetically inferior by inferiority of the male element in the advanced service groups.

7. The service group coefficients of variability indicate greater variability in the weight of the general population than within the litters, but do not indicate that heavy service produces 'weak' litters.

8. Body development seems to progress at the maximum rate during the first twenty days of postnatal life, after which time there is a rather marked decline in the rate of increase in head length and breadth of ilial expanse.

9. No inferiority in the offspring from the advanced services is revealed from a study of body growth by measurement.

10. Offspring in the more advanced service groups do not show a significantly higher percentage of mortality during the first five days of life than do the offspring in the light service groups.

11. A higher mortality does not seem to exist in offspring from the advanced service groups as compared with the light service groups between the ages of five and ninety days.

12. Heavy sexual service of males gives a decrease in the proportion of male to female offspring that is very perceptible.

13. Female offspring are to some degree more likely to succumb than male offspring in all service groups except the twentieth.

14. The high percentage of deaths of female progeny is largely due to the predominance of females to males in the litters.

15. By no means thus far used has any inferiority of progeny from heavy sexual service been discovered. They are fully equal if not superior to progeny from very light service of male.

DISCUSSION

The amount of sexual service that the male performs has a marked effect upon the physical properties of his spermatozoa (Lloyd-Jones and Hays, '17); the whole basis of this work is to discover if these effects are in any way made manifest in the offspring.

Growth in body weight must be assumed to be due to a complex of stimuli acting upon every living cell of the organism. If it were possible to modify the contribution of growth stimuli from the male germ cell by extreme sexual use of the male, an effect should be produced upon every cell of the body in his offspring and a reduction of these stimuli would thus result in a decreased body growth. The sum total of the body increase in the offspring from the heavy service series is fully equal and even superior to the increase in the offspring in the light service groups. This apparent superiority has been attributed to various factors, largely environmental and possibly to superior male reproductive cell. After these factors are corrected for, which we have found impossible to do, we believe that the rate of growth in body weight would be identical in all five service groups. A study of body weight as reported here will only reveal the character of the total population and will not reveal the occurrence of an occasional inferior individual.

The coefficient of variability of litters, on the other hand, is valuable in that it will reveal the occasional inferior individual in the litter. If only a part of the offspring in the heavy service groups are inferior as far as rate of growth is concerned, there should be a greater coefficient of variability in the litters from heavy service than among the light service litters. No such evidence appears in our data, and this fact we feel warrants the assumption that not even a part of the offspring in the heavy service group are more inferior as far as ability to increase in body weight is concerned than the offspring in the light service groups.

The service group coefficient of variability does not reveal that any inferiority of entire litters is brought about by heavy sexual service of males. This coefficient does show that the largest coefficient of the first ninety days of postnatal life is found just at the close of the suckling period at thirty days. The coefficient further shows that the variability in weight of the general population is much greater than within the litters.

Body measurements furnish us with further material for the study of the offspring in the different service groups. These data do not reveal any new facts to indicate any greater inferiority of offspring in any one of the five service groups. Here again the same modifying factors have been in operation that have affected the body-weight data, and a correction, if possible, for these we think would show that the offspring in all five of the service groups are identical in body dimensions.

Concerning the question of rate of mortality in progeny from light and heavy service, we have no evidence that there is a higher death rate in the advanced service groups over that observed in the light service groups.

A direct relation apparently exists between the amount of sexual service of males and the percentage of females that they will sire. The ratio of males to females is highest in the 1st-service group and progressively decreases up to the 20th-service group. There is a possibility that heavy service exerts a selective action upon the sperm cells and may eliminate from fertilization the majority of the male-producing spermatozoa. The large female-producing sperm cells may show a greater rate of motility, greater endurance, or for some other cause out-distance the male-producing spermatozoa, thus resulting in a preponderance of female offspring in advanced service groups.

A possible explanation for the high percentage of deaths among females lies in evidence showing that the percentage of female offspring is increased by heavy service of the male as shown on page 607. The weight (Minot, Jackson, King) of female offspring in multiparous animals at birth is slightly less than that of the males. If this is true for the rabbit, it may render the females less able to compete with the male offspring for nourishment during their early life when food supply is of such vital importance in determining the survival of the young. The fact that the great majority of the offspring dying in early life have been females seems to warrant the assumption that females are actually less able to compete with the males during the early part of life. The data do not justify the conclusion that there is any higher rate of mortality in the advanced service groups than in the lighter service groups after the first five days of postnatal life. If inferiority of offspring exists in the advanced service groups because of the predominance of females, which we may assume under all ordinary conditions are less able to survive than males, it is apparent that no real inferiority exists, but that the mortality is greater because the percentage of females is greater in the heavy service groups.

In conclusion, it may be noted 1) that the methods used for measuring the character of offspring from different degrees of sexual service of sires fail to show that any inferiority of the offspring can be induced by using a male excessively; 2) that the male in heavy sexual service furnishes germ cells that are fully the equal in their contribution to his offspring of those elaborated by a male in very moderate sexual service.

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BIBLIOGRAPHY

Bachhuber, L. J. 1916 The behavior of the accessory chromosomes and of the chromatoid body in the spermatogenesis of the rabbit. Biol. Bul., April.

Day, C. E. 1913 Productive swine husbandry. Philadelphia.

Hatai, S. 1908 Studies on the variation and correlation of skull measurements in both sexes of mature albino rats. Amer. Jour. Anat., vol. 7.

Jackson, C. M. 1913 Postnatal growth in the albino rat. Amer. Jour. Anat., vol. 15, No. 1.

King, H. D. 1916 On the postnatal growth of the body and of the central nervous system of albino rats that are undersized at birth. Anat. Rec., vol. 11.

Lloyd-Jones, Orren, and Hays, F. A. 1918 The effects of frequency of copulation on the properties of the seminal discharge. Journ. Exp. Zoöl., vol. 25.

MacDowell, E. C. 1914 Size inheritance in rabbits. Carnegie Inst., Pub. No. 196.

MacDowell, E. C. 1914 Multiple factors in mendelian inheritance. Jour. Exp. Zoöl., vol. 16.

Minot, C. S. 1891 Senescence and rejuvenation. Jour. Phys., vol. 12.

Minot, C. S. 1908 Age, growth, and death. New York.

Pearl, Raymond. 1917 The experimental modification of germ cells. Jour. Exp. Zoöl., vol. 22, No. 2.

Pusch, G. 1915 Algemeine Tierzucht. Dritte Auflage, Stuttgart.

Quetelet, A. 1871 Anthropometrie, On Measure des differentes Facultes de l'homme.

Stockard, C. R., and Papanicolaou, G. 1916 A further analysis of the hereditary transmission of degeneracy and deformities by the descendants of alcoholized mammals. Amer. Nat., vol. 50.

Vaughan, H. W. 1916 Pedigree studies. (Unpublished.)

Wright, L. The illustrated poultry book.