# THE FEEDING AND BREEDING OF LABORATORY ANIMALS

## VI. THE BREEDING OF MICE

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(With 6 Figures in the Text)

## INTRODUCTION

There is much information about the biology of the mouse, most of which has been collected in *Biology of the Laboratory Mouse* (1941), and in a comprehensive review of the nutritive requirements of normal mice for growth, maintenance, reproduction and lactation (Morris, 1944). But the more elementary problem of colony management and its possible effect upon the quality and quantity of young produced has received scant attention; greater attention has been paid to housing and equipment than to studies of the actual productivity of a colony. Information about the number of litters which can profitably be reared by an individual, and the yield of young animals from a given allocation of space and labour, both questions of considerable importance to those who are concerned with the maintenance of breeding colonies, seems to be entirely lacking. The present paper gives a direct comparison of the results obtained from two common methods of breeding mice.

## TECHNIQUE

A comparison was made of the total production of young during a period of one year from each of two groups of twenty-four female mice mated on different systems.

### Monogamous pairs

In group 1, one male and one female were kept together throughout, and breeding was allowed to proceed at maximum intensity. The mouse has a post-partum oestrus, and gestation and lactation may thus occur simultaneously. Under these conditions gestation is usually prolonged beyond the usual 19 days (Lataste, 1887), so that there may be an interval of up to 4 weeks between the births of successive litters even when post-partum mating conception occurs. The mice of group 1 were examined once daily for the birth of litters, but handled, for weighing, only when the young were weaned. The young were counted at birth but were not weighed or sexed until they were weaned at 21 days old. They were not weighed individually but in litters.

### Polygnous mating

In group 2, one male was kept with four females in a mating box from which the females were removed to individual boxes towards the end of pregnancy and to which they were returned after a litter had been weaned or killed. Under this system mating could not occur at post-partum oestrus, and there was an interval of at least 6 weeks between successive births. Early in the experiment the females were examined daily for matings as shown by the presence of a vaginal plug, and for pregnancies as shown by the presence of a placental sign. In addition, they were weighed twice a week. Later, the daily examinations for vaginal plugs and placental signs were discontinued, but the twice-weekly weighings were continued throughout. As in group 1, the young were counted at birth, and sexed and weighed in litters at weaning when 21 days old. The females were weighed when they were returned to the mating box on the weaning (or death) of the litter.

Thus, the females of group 2 received much more handling and attention than those of group 1, but they were not subjected to the strain of continuous concurrent gestation and lactation.

### Duration of experiment

After 11 months the males were removed from all boxes and existing pregnancies were allowed to terminate. The experiment was started on 16 May 1945, and the last litter was weaned on 17 May 1946. The period of observation, therefore, covered a whole year.

### Mice

Albino mice, bred at the National Institute for Medical Research, Farm Laboratories, Mill Hill, were used. Indifferent breeders were not culled, but two females of group 1 became sick within a week of the start of the experiment and were replaced by healthy mice. Three females, one in group 1 and two in group 2, were in the early stages of pregnancy when they were received; the litters were discarded at birth, and the pregnancies have been ignored in the records.

### Housing and care

The animals were kept in a warmed room at a temperature of 18–20° C. The heating was not thermostatically controlled. They were all housed in the same type of cage, a box made of solid sheet zinc (11 × 8 × 4 in.) covered by a coarsely perforated zinc lid held in position by a rim. Sawdust and wood wool were supplied. The cages were cleaned twice a week.

### Diet

All animals received the same stock breeding diet of the following composition:

Diet 20

| Constituents | % | Theoretical composition (calculated from the *Bull. Minist. Agric., Lond.*, no. 124) Digestible nutrients (%) | |
|---|---|---|---|
| Wholemeal flour | 50 | Protein | 19·3 |
| Dried full-cream milk | 27 | Soluble carbo-hydrate | 45·3 |
| Dried yeast | 12 | Oil | 11·6 |
| Meat and bone meal | 6 | Fibre | 0·5 |
| Cod-liver oil | 3 | | |
| Sodium chloride | 1 | | |
| Calcium carbonate | 1 | | |

The diet was mixed in small quantities as required and was fed in the form of a dry powdered meal. Drinking water was supplied from a bottle. No supplements were given.

### Records

The recording was reduced to a minimum for both methods. Individual cards, 8 × 5 in., were kept for each animal on which all the information was entered. In addition, as a practical convenience, a label attached to each box bore the date of birth of litters and number of young born and weaned. It was thus possible to see at a glance which litters were due for weaning without having recourse to the cards. This method of labelling also indicated very early the unthrifty breeders.

## COMPARISON OF MONOGAMOUS AND POLYGYNOUS MATINGS

### Mortality of adults

In any colony of normal animals, even in the absence of a specific epidemic, sporadic deaths occur from time to time. The mortality, from all causes, which took place during the period of observations among the two groups is given in Fig. 1. It will be seen that there is a remarkable agreement between the two systems of management in this respect. After about 8 months, the remaining animals of both groups were losing condition, the mortality rate increased, and it would not be profitable to keep mice in a breeding colony much beyond this time.

### Total production of young weaned

Since the number of females in the two groups remained alike throughout the experiment, it is permissible to make a direct comparison of the total number of young weaned in successive periods. This has been done for the first 6 months and the full period. The results are shown in Table 1. It will be seen that, for both periods, about twice the number of young were weaned from the females of the monogamous pairs, and that the average litter size and the average weight of the young at weaning are alike for the two groups. As would be expected, the average weight of young at weaning is inversely proportional to the average size of the litter. This relative productivity under the two methods is shown equally well by individual performances. The most fertile monogamous pair produced 134 young, of which 121 (90 %) were weaned; in the polygynous series the most fertile female gave birth to sixty-nine young of which sixty-five (94 %) were weaned. The interval between the births of first and last litters in the two cases were 321 and 314 days respectively. One monogamous female gave birth to sixteen litters in succession, fifteen from post-partum oestrus matings, but failed to rear the sixteenth litter. This female, however, always had small litters, and her total production was only mediocre (sixty-two young born, of which fifty-one were weaned). Only one female from the polygynous series had even as many as eight pregnancies during the period. In all, 197 pregnancies were recorded from the monogamous pairs, as compared with 110 pregnancies in the polygynous series. The average production per female by the two methods is given in Table 2.

These figures for total production could be considerably improved by frequent culling of unproductive animals; four females from the monogamous pairs and three females from the polygynous series failed to rear any young in the year. This would be a high proportion in an economically run breeding colony.

### Young weaned in successive months

Since the observations were made on the same females throughout and the two groups were small, especially for the last few months, slight seasonal variation in reproductive performance would be largely masked by the concurrent effects of order of parity and age of female. However, there was no seasonal failure of reproduction nor a serious diminution in performance other than that due to the two factors already mentioned, which would not operate in an efficient breeding colony. Parkes (1924) reported the complete failure of reproduction during

November to February among mice kept in a room without adequate heat, which was not observed after the removal of the colony to a heated room, but later he failed (1928) to stop reproduction by transferring breeding females to a cold store. Moreover, Laurie (1946) has reported that high fertility is to be found in wild mice inhabiting food cold stores at $-15°$ C.

it would not as a rule be profitable to keep females in a breeding colony after they had reared eight or nine litters. For the A strain of mice reported by Bittner, a maximum litter size of 6·46 was found for third litters, and there was a regular decline in average litter size for later pregnancies.

*Mortality of young before weaning.* Four litters in the polygynous series were killed and eaten at
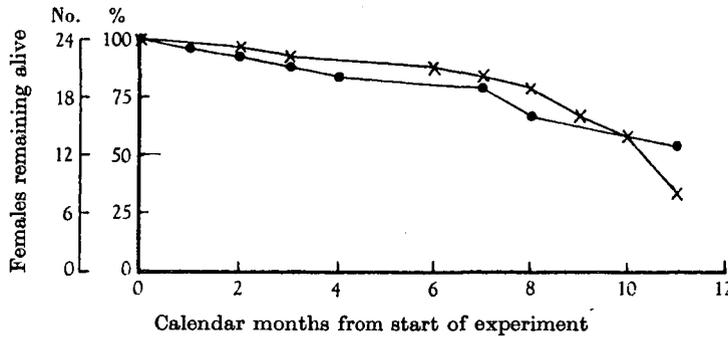


Fig. 1. Number of females remaining alive.    ●——● Monogamous pairs, thirteen survived the full period.
×——× Polygynous groups, eight survived the full period.

Table 1. *Total young weaned, litter size and weight of young*

| | After 6 months | | | After 12 months | | |
|---|---|---|---|---|---|---|
| Method | No. of young | Average litter size at weaning* | Average weight of young (g.) | No. of young | Average litter size at weaning* | Average weight of young (g.) |
| Monogamous pairs | 677 | 7·1 | 9·9 | 1149 | 6·8 | 10·1 |
| Polygynous groups | 306 | 6·4 | 10·3 | 559 | 6·4 | 10·6 |

* Litters from which no young were weaned have been omitted from this average.

Table 2. *Average production per female over a period of one year*

| Method | No. of females at start | No. of pregnancies | No. of young Born | No. of young Weaned | % weaned |
|---|---|---|---|---|---|
| Monogamous pairs | 24 | 8·2 | 56·5 | 47·9 | 85 |
| Polygynous groups | 24 | 4·6 | 28·1 | 23·3 | 83 |

### Litter size

*Parity.* In mice and rats the average litter size varies with the order of parity. Second or third litters tend to be the largest, and thereafter the number of young per litter falls with increasing order of parity (King, 1916–17; Parkes, 1924; Donaldson, 1924; Bittner, 1936). In an unselected vigorous strain of mice the effect of parity on the observed litter size at weaning, as shown in Table 3, is considerably less than that reported by Bittner (1936) for a closely inbred strain of mice, and litter size is maintained, with some fluctuations, until after the ninth litter. It falls off beyond this, and

birth so that only remains of young were found, and it was impossible to know how many had been born. These litters have not been included in calculating average litter size. In addition, there were recorded, from among the separated pregnant females, seven cases of severe vaginal bleeding which were probably abortions. Such events may have occurred with the monogamous pairs, but, if so, they were not observed.

Litter size at weaning is of considerable importance in many types of work, and the loss of young before weaning may be a serious matter. Under both systems of management this loss
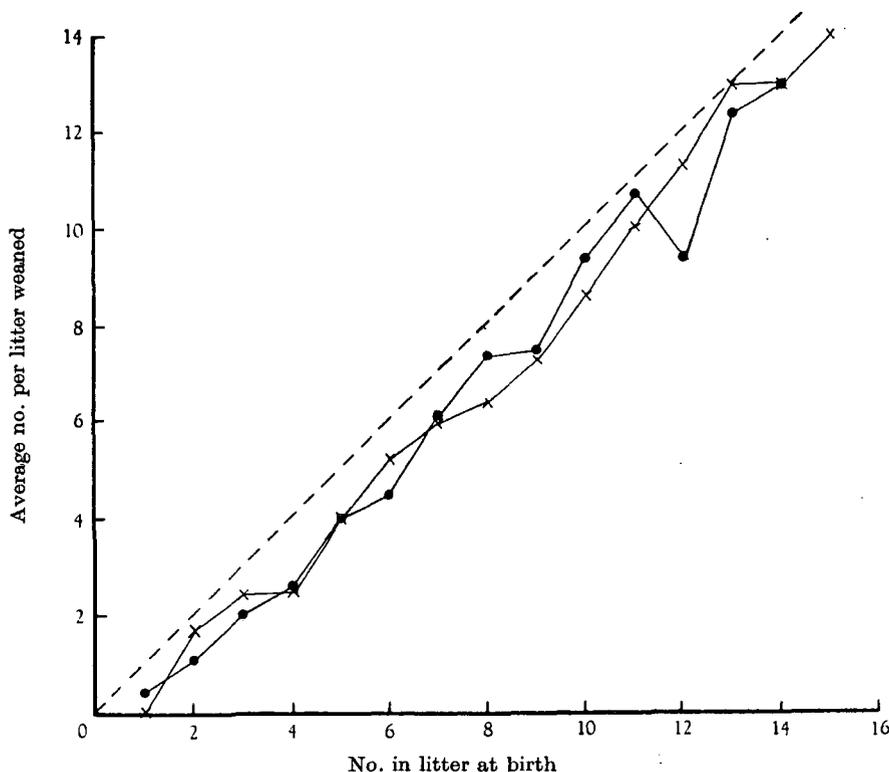
Fig. 2. Effect of litter size at birth upon the number of young weaned. ------- Ideal, no loss before weaning. ●——● Monogamous pairs, 197 litters born.  ×——× Polygynous groups, 110 litters born.

Table 3. *The effect of parity on litter size at weaning*

(Calculated only for litters of which some young were weaned.)

| Parity | Monogamous pairs | | Polygynous groups | |
|---|---|---|---|---|
| | No. of litters at weaning | Average no. of young at weaning | No. of litters at weaning | Average no. of young at weaning |
| 1 | 19 | 5·9 | 19 | 6·9 |
| 2 | 19 | 7·3 | 17 | 6·5 |
| 3 | 16 | 7·3 | 15 | 5·3 |
| 4 | 17 | 8·3 | 14 | 6·3 |
| 5 | 16 | 6·3 | 11 | 6·8 |
| 6 | 15 | 7·3 | 7 | 6·6 |
| 7 | 14 | 6·4 | 4 | 6·0 |
| 8 | 13 | 8·3 | 1 | 3·0 |
| 9 | 12 | 7·1 | — | — |
| 10 | 11 | 5·1 | — | — |
| 11 | 7 | 4·4 | — | — |
| 12 | 6 | 6·3 | — | — |
| 13 | 3 | 6·0 | — | — |
| 14 | 1 | 3·0 | — | — |
| 15 | 1 | 3·0 | — | — |
| 16 | — | — | — | — |
| Totals | 170 | 6·8 | 88 | 6·4 |

amounted to about 16 % (Table 4), of which half took place at birth and the other half during lactation. No attempt was made to determine the still-birth rate or to separate stillborn young from those killed or neglected by the mother. No tendency was observed for larger litters to include more stillbirths or to suffer a greater loss during lactation than smaller litters. On the contrary, the absolute loss was about the same for all litter sizes (Fig. 2), and the proportionate loss was therefore greater for small litters.

The effect of parity is more marked than that of litter size, and the loss of young before weaning rises with increasing orders of parity (Fig. 3). The observation of both effects may be complicated by the fact that better mothers will be differentially represented in the higher litter sizes and higher orders of parity.

Probably the most important single factor in the mortality of the young before weaning is the age of the mother. In both groups, irrespective of parity, there was a decline in the percentage of young weaned towards the end of the test period. The average for all litters showed a steady decline for litters born after about 6 months of test when

the breeding females were from 8 to 9 months of age. A similar effect of age of female is reported for rats by King (1916–17).

In the mice used for these observations the influence of individual mice was particularly striking, individuals giving birth regularly to large or small
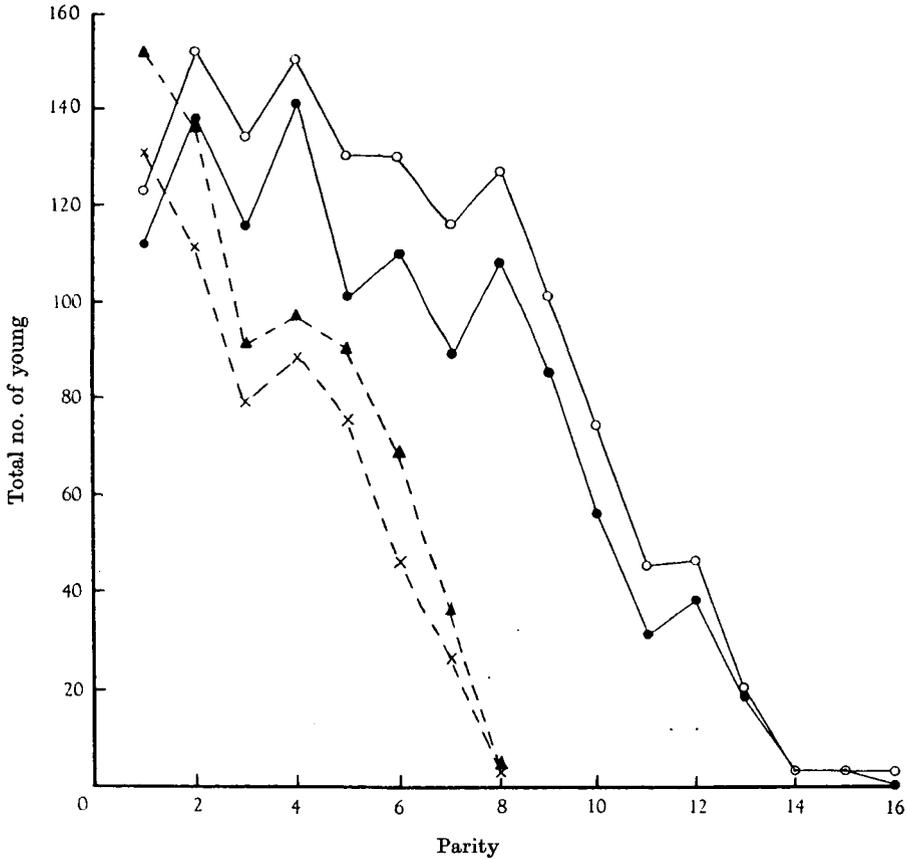


Fig. 3. Effect of parity on loss of young before weaning.   O——O Monogamous pairs, total number of young born.   ●——● Monogamous pairs, total number of young weaned.   ▲-----▲ Polygynous groups, total number of young born.   ×----× Polygynous groups, total number of young weaned.

Table 4. *Mortality of young before weaning*

|  | Young counted at birth | | Young killed within 24 hr. of birth or stillborn | | Young died during lactation | | Young weaned | |
|---|---|---|---|---|---|---|---|---|
|  | No. | % | No. | % | No. | % | No. | % |
| Monogamous pairs | 1356 | 100 | 101 | 7 | 106 | 8 | 1149 | 85 |
| Polygynous groups | 675 | 100 | 66 | 10 | 50 | 7 | 559 | 83 |
| Totals | 2031 | 100 | 167 | 8 | 156 | 8 | 1708 | 84 |

*Genetic factors.* Litter size is also dependent upon genetic factors, different strains of mice having different average litter size (see *Biology of the Laboratory Mouse*, 1941). As a rule hybrid strains produce larger litters than closely inbred stocks.

litters. The highest average litter size attained by any one female was 10·1 young per litter at weaning from nine pregnancies. Ten monogamous females, in a total of seventy-eight pregnancies, failed to give birth to a single litter of ten or more, while

nearly half (fifty out of a total of 119) of the litters from the remaining eleven females were of ten or more young at birth.

### Weight of young at weaning

Lactation in the mouse reaches a maximum in about 10 days and then gradually declines until weaning. Total milk production is increased with increasing litter size for litters of from four to thirteen young, but not in direct proportion to the number of young, with the result that as litter size increases the amount of milk available for each individual is reduced (Enzmann, 1933). Detailed studies of the relation of litter size to weight at

### Sex-ratio

The sex-ratio at weaning, tabulated according to the system of mating, and the reproductive condition of the mother at mating, is given in Table 5. In no case does the observed sex-ratio differ from 1 : 1.

### The interaction of concurrent lactation and gestation

In small rodents, when a mating takes place at post-partum oestrus and the female becomes pregnant during a concurrent lactation period, the gestation period of the second litter is prolonged if
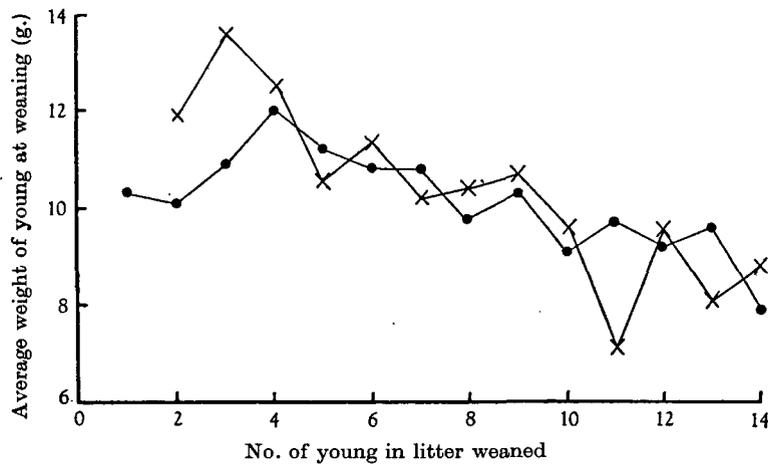


Fig. 4. Average weight of young at weaning (21 days old) and number of young in litter weaned. ●——● Monogamous pairs, 128 litters with concurrent gestation. ×——× Polygynous groups, 88 litters.

birth and growth of young have been made by Parkes (1926), Enzmann & Crozier (1934–5), Crozier & Enzmann (1935–6), and Crozier (1939–40). Contrary to the experience of these authors, in the present experiments the maximum weight at weaning was not attained by litters of one but by litters of four (monogamous matings) and of three (polygynous matings). For larger litters there is, in both groups, a steady decline in average weight at weaning (Fig. 4). Only one litter of eleven young, an unusually poor one, was weaned from the polygynous matings, which explains the sudden drop in the curve at this point. For 128 (75 %) of the 170 litters weaned from the monogamous pairs, lactation was accompanied by the concurrent gestation of the next litter. The average for these litters has been plotted separately. Concurrent gestation has been without effect upon the growth rate of the young during the lactation period.

more than three young are being suckled. The prolongation is due to delayed implantation of the fertilized ovum. In a review of the literature, Brambell (1937) has collected published figures for mice and rats and has calculated regression lines showing the relation between the number of young suckled and the prolongation in days of the gestation period for the two species. He was unable to find evidence that the number of young in utero exerted any influence on the duration of gestation.

During the course of the work here described, detailed records have been collected for 141 matings at a post-partum oestrus, and further evidence can be given of the interaction between the number of young being suckled, the number of young in the uterus and the length of the gestation period in mice.

The full analysis of the available information is shown in Table 6. The relatively high proportion

of killed litters, four out of thirteen (31 %), resulting from post-partum oestrus matings in the non-lactating female, is obviously connected with the fact that the animals in this group were poor mothers, since failure to rear a litter was charac-teristic of them all. No diminution was observed in the proportion of fertile matings at post-partum oestrus with high orders of parity. Crew & Mirskaia (1930) state that in mice 'fruitful mating is exceedingly rare in the suckling mother', and it must be assumed that different strains of mice behave differently in this respect. In these mice, fertile matings were recorded for 141 out of a possible 181 (78 %) post-partum oestrus periods. In all, records are available for 128 litters in which gestation and lactation were concurrent.

### Table 5. *Sex-ratio of the young at weaning*

| | | Male | Female | Sex-ratio males per 100 females | Notes |
|---|---|---|---|---|---|
| Monogamous pairs | First litters | 56 | 56 | 100 | — |
| | Subsequent litters from matings other than at a post-partum oestrus | 95 | 97 | 97·9 | 8 young from this group were not sexed |
| | Litters from post-partum oestrus mating with concurrent lactation of the previous litter | 382 | 397 | 96·2 | 14 young from this group were not sexed |
| | Litters from post-partum oestrus mating where previous litter was not suckled | 19 | 25 | 76·0 | — |
| Polygynous groups | First litters | 64 | 67 | 95·5 | — |
| | Subsequent litters | 207 | 221 | 93·7 | — |
| Totals | All litters in both groups | 823 | 863 | 95·4 | — |

### Table 6. *Monogamous pairs. Post-partum oestrus matings*

| Parity no. | Total no. of possible post-partum oestrus periods | Total no. of recorded post-partum oestrus fertile matings | % | Non-lactating females: previous litter killed. Resulting litters | | Lactating females: previous litter weaned. Resulting litters | |
|---|---|---|---|---|---|---|---|
| | | | | No. killed | No. weaned | No. killed | No. weaned |
| 1 | 21 | 13 | 62 | . | 1 | 1 | 11 |
| 2 | 19* | 16 | 80 | . | . | 3 | 13 |
| 3 | 18* | 14 | 74 | . | 2 | 1 | 11 |
| 4 | 18 | 15 | 83 | . | 1 | 1 | 13 |
| 5 | 18 | 17 | 94 | ·1 | 1 | 2 | 13 |
| 6 | 18 | 11 | 61 | . | 1 | 2 | 8 |
| 7 | 16** | 13 | 72 | 1 | 1 | 1 | 10 |
| 8 | 15 | 10 | 67 | 1 | . | 1 | 8 |
| 9 | 14* | 11 | 73 | . | 1 | 1 | 9 |
| 10 | 10 | 8 | 80 | . | 1 | 2 | 5 |
| 11 | 7 | 7 | 100 | 1 | . | . | 6 |
| 12 | 4 | 3 | 75 | . | . | . | 3 |
| 13 | 1 | 1 | . | . | . | . | 1 |
| 14· | 1 | 1 | . | . | . | . | 1 |
| 15 | 1 | 1 | . | . | . | 1 | 0 |
| 16 | 0 | . | . | . | . | . | . |
| Totals | 181 | 141 | 78 | 4 | 9 | 16 | 112 |

* Females died during lactation; there was no record of whether or not they had mated at the post-partum oestrus. These five births have therefore been omitted from the total number of possible post-partum oestrus periods.

The normal gestation period for this stock of mice is 19 days. Of thirty-eight pregnancies dated from the observation of a vaginal plug, twenty-seven (71 %) had a gestation period of 19 days, six of 18 days, three of 20 days, and one at each of 17 and 22 days. In the polygynous matings, only forty-eight

out of eighty-seven cases (55%) were fertile within a week of returning the female to the male after the weaning of a litter.

In considering the possible relation between number of young being carried and length of gestation it has been necessary to regard the number of young born as the best available index for the

would be very small. The comparisons have therefore been made, using all possible litters, between the number of observed young in the second litter at birth, and the number of young weaned in the first litter. The length of gestation has been taken as the interval in days between the births of successive litters.

Table 7. *Length in days of individual gestation periods related to the number of young weaned from the first litter (lactation) and the number of young born in the second litter (gestation)*

| Gestation. No. of young counted at birth ($X_1$) | Lactation. No. of young weaned ($X_2$) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 0 |
| 1 | 22 | . | 22 | 23 | . | . | . | . | . | . | . | . | . | . | 22 |
|   | 21 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 2 | 21 | 21 | 21 | 20 | 23 | . | . | . | . | . | . | . | . | . | 20 |
|   | . | . | 21 | 21 | . | . | . | . | . | . | . | . | . | . | 22 |
|   | . | . | 23 | . | . | . | . | . | . | . | . | . | . | . | 19 |
| 3 | . | 22 | 21 | 22 | 23 | 23 | . | . | 23 | . | . | . | . | . | 23 |
|   | . | . | . | . | 24 | . | . | . | . | . | . | . | . | . | . |
| 4 | 23 | . | 21 | 22 | 22, 21 | 22 | 23 | 23 | . | . | . | . | . | . | 22 |
|   | . | . | 21 | . | 23, 23 | 22 | 22 | . | . | . | . | . | . | . | 21 |
|   | . | . | . | . | 24 | . | 25 | . | . | . | . | . | . | . | . |
| 5 | 20 | 21 | 21 | . | 26 | 22 | 25 | . | 23 | . | 28 | . | . | . | 21 |
|   | . | . | 21 | . | . | 23 | . | . | . | . | 26 | . | . | . | 21 |
| 6 | . | 21 | 21 | 21 | 21 | . | 22 | . | . | . | . | . | . | . | 20 |
|   | . | . | . | 22 | . | . | . | . | . | . | . | . | . | . | 21 |
|   | . | . | . | 20 | . | . | . | . | . | . | . | . | . | . | . |
| 7 | . | . | 23 | . | . | 29 | 29 | 24, 25 | 24 | . | 26 | . | . | . | 27 |
|   | . | . | . | . | . | 21 | 31 | 22 | . | . | . | . | . | . | . |
|   | . | . | . | . | . | 25 | . | 24 | . | . | . | . | . | . | . |
| 8 | . | 21 | . | . | 22 | 21 | 24 | 22 | . | . | . | . | . | . | . |
|   | . | 21 | . | . | 24 | . | 22 | 25 | . | . | . | . | . | . | . |
| 9 | 20 | . | 19 | 21 | 21 | 21 | 25 | . | 25 | 23 | 30 | 25 | 26 | . | . |
|   | . | . | . | 23 | 21 | . | . | . | 23 | 23 | 27 | . | . | . | . |
|   | . | . | . | . | . | . | . | . | . | . | 26 | . | . | . | . |
| 10 | . | . | . | . | . | . | 22 | . | 24 | 26 | . | . | 23 | . | . |
|   | . | . | . | . | . | . | . | . | 25 | 20 | . | . | . | . | . |
|   | . | . | . | . | . | . | . | . | 23 | 22 | . | . | . | . | . |
| 11 | . | . | . | . | . | . | 26 | 23 | 27, 26 | 22 | 25 | . | 23 | 27 | 20 |
|   | . | . | . | . | . | . | . | 26 | 23 | 23 | 24 | . | . | . | . |
|   | . | . | . | . | . | . | . | . | 25 | . | 22 | . | . | . | . |
| 12 | . | . | . | . | . | . | 26 | . | 23 | 27 | 29 | 24 | . | . | . |
|   | . | . | . | . | . | . | . | . | 21 | 26 | . | . | . | . | . |
| 13 | . | . | 20 | . | . | . | . | . | . | 25 | 24 | 24 | . | . | . |
|   | . | . | . | . | . | . | . | . | . | . | 26 | . | . | . | . |
| 14 | . | . | . | . | . | . | . | . | . | . | 24 | 25 | . | . | . |
|   | . | . | . | . | . | . | . | . | . | . | . | 23 | . | . | . |
| 15 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 16 | . | . | . | . | 21 | . | . | . | . | . | . | . | . | . | Nos. in cells = Y |

number of young carried. Similarly for suckling litters the number of young raised to weaning age has been taken as the index of the number of young suckled. Selection of only those litters reared intact, in this case 65% of litters weaned (see Crozier & Enzmann, 1935-6), was not considered satisfactory. It has been assumed that the additional stimulation supplied by young which died during lactation

Full data for 128 litters where gestation and lactation were concurrent are given in Table 7, in which has been entered the length of gestation of the second litter for all combinations of litter size observed, and for thirteen litters where there was no suckling of the first litter. These results are presented graphically in Figs. 5 and 6, in which average values for each successive pair of litter

sizes have been plotted. In Fig. 5 it can be seen that for any one average litter size at birth there is an increase in the average length of gestation with an increase in the number of young suckled. By contrast (Fig. 6), for any one average litter size suckled there is no corresponding increase with the number of young born, and the prolongation of

where $b_1$ and $b_2$ are partial regression coefficients. These coefficients measure respectively the dependence of $Y$ on $X_1$ for constant values of $X_2$, and of $Y$ on $X_2$ for constant values of $X_1$. The equation found is

$$Y = 20{\cdot}98 - 0{\cdot}0519X_1 + 0{\cdot}3984X_2,$$
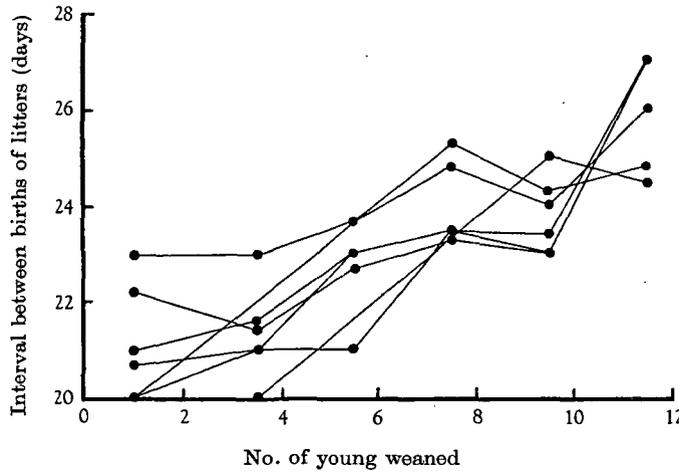


Fig. 5. Regression within groups. Interval between births of successive litters and the number of young weaned in the first of the two litters.
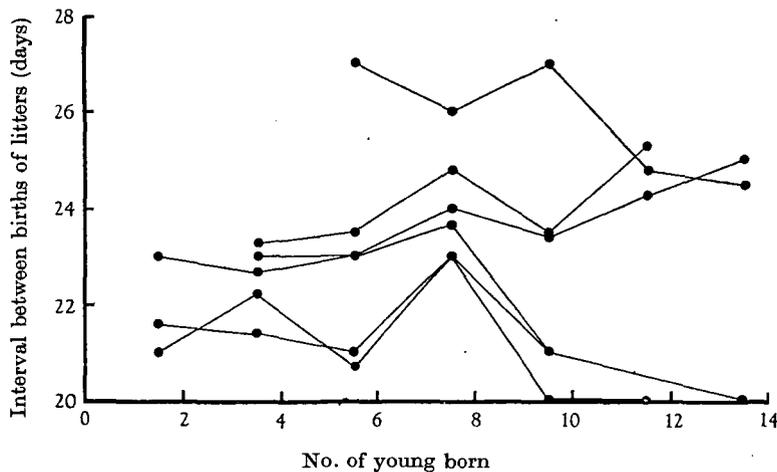


Fig. 6. Regression within groups. Interval between births of successive litters and the number of young born in the second of the two litters.

gestation under these conditions can be regarded as wholly determined by lactation.

From the data in Table 7, the regression of $Y$, the length of gestation, on $X_1$, the number of young born, and $X_2$, the number being weaned, was calculated. The form of the equation is

$$Y = a + b_1 X_1 + b_2 X_2,$$

and the standard errors of $b_1$ and $b_2$ are $0{\cdot}0592$ and $0{\cdot}0567$ respectively. Hence, $b_1$ is not significant, while $b_2$ is highly significant; there was no significant dependence of the length of gestation $Y$ on the number of young born $X_1$ in this series.

It remained possible that a linear relationship between $Y$ and $X_2$ does not adequately describe their interdependence. Therefore, a further regression

introducing the square of $X_2$ was computed to see if simple curvature exists, giving the equation

$$Y = 20 \cdot 84 + 0 \cdot 3652 X_2 + 0 \cdot 0018 X_2^2,$$

whence it may be concluded that the introduction of $X_2^2$ has not added any useful information (the standard error of the term $0 \cdot 0018$ is $0 \cdot 0116$) and that the simple regression

$$Y = 20 \cdot 85 + 0 \cdot 3664 X_2$$

adequately describes the relationship.

It remains possible that the individual group means deviate significantly from this regression. To test this possibility, an analysis of variance was made.

| Source of variation | D.F. | Sum of squares | Mean square | F | P |
|---|---|---|---|---|---|
| Linear regression | 1 | 259·06 | 259·06 | 77·4 | < 0·001 |
| Deviations from regression | 13 | 80·53 | 6·19 | 1·85 | Just under 0·05 |
| Error | 125 | 418·20 | 3·35 | — | — |

From this it may be concluded that, although by far the greater part of the variation shown by group means is accounted for by the linear regression of $Y$ on $X_2$, the deviations from regression are bordering on significance, and that it is advisable to examine the data further.

The obvious step is to omit the first four groups ($X_2 = 0$ to 3) and to recalculate the analysis of variance without them, since these groups seem, by eye (Fig. 5), to be a little off the line. The results are:

$$Y = 20 \cdot 81 + 0 \cdot 3719 X_2.$$

| Source of variation | D.F. | Sum of squares | Mean square | F | P |
|---|---|---|---|---|---|
| Linear regression | 1 | 98·18 | 98·18 | 25·8 | < 0·001 |
| Deviations from regression | 9 | 66·61 | 7·40 | 1·95 | Just over 0·05 |
| Error | 92 | 349·62 | 3·80 | — | — |

The improvement in fit is so slight that the exclusion of the four groups is hardly justified. It is concluded that, throughout the range of the series, the length of gestation is affected by the number of young concomitantly suckled, and that this effect is best described by a simple linear regression of the one on the other. The significance of the regression is very high indeed.

## DISCUSSION

With the exception of the total number of young weaned no difference has been observed in the reproductive performance of monogamous and polygynous mice. The usefulness of a female in the

colony was approximately doubled when she was allowed to re-mate at the post-partum oestrus and thus to have a continuous series of pregnancies. With adequate diet and a vigorous stock of mice, the continuous concurrent gestation and lactation did not visibly affect the maternal organism. A few females continued to give a satisfactory reproductive performance for as long as 10 months. The quality of the young at weaning, as regards growth rate and litter size, were in no way inferior to those reared by females in which lactation was uncomplicated by the presence of another litter. To what extent the performance may have been assisted by the use of a particularly good diet it is not possible to say. Under such conditions the nutritional requirements of the female must be exceptionally high, since two litters have to be supplied simultaneously with nourishment from the food eaten by the mother. Unfortunately, with a dry diet in meal form as was used, it is not possible to obtain a reliable measurement of food consumption.

A further not inconsiderable practical advantage of monogamous pairing is the elimination of the fluctuations in demands on labour and equipment arising under any system of management in which the pregnant females are separated into individual boxes before the birth of the litter. In another experiment involving polygynous mating of groups of seventy females divided among fifteen mating boxes, the numbers of pregnant females separated during the course of first pregnancies on each of two diets rose to a maximum of sixty-two and fifty-nine respectively both on the same day, and later fell again to four and five respectively when the females were again returned to the mating boxes. Thus the time and labour necessary for cleaning, feeding, etc., was about four to five times as great at one period as at the other. In a small animal house administrative difficulties of meeting a fluctuating demand of this order needs no comment. The overall requirement for labour taken over a long period is probably much the same for the two systems.

Theiss (1944) describes a system for breeding mice in which advantage is taken of the intensive production possible when the male is kept continuously with the female but in which several females are housed with one male. He claims that better results can be obtained by this method as the females help one another in nest building and in suckling the young. The females themselves are marked for each successive pregnancy, and poor breeders are thus quickly identified. He states that under this system males and females can be used for from 6 to 8 months, and that in this time an average of six litters per female should be obtained with an average litter size at birth of 6·0 young. Theiss does not, however, give any figures for overall

production at weaning. Further, under such a system the identity of individual litters is largely lost. Even when the intervals between the births of litters from different females in the same box are sufficiently long for the young of different litters to be identified, there is the risk that they have received varying amounts of milk from more than one female and cannot therefore be regarded as such a homogeneous unit as litters suckled by their own mothers. There would be considerable economy of space in such a method but added difficulties in keeping the animals clean.

From the results here presented it is possible to calculate the overall production of a mouse colony kept under the system of monogamous pairs. In 11 months from the birth of the first litter until the weaning of the last litter, from twenty-four pairs of mice, 1116 young were weaned, or about 100 young per month. The twenty-four cages in which the mice were housed occupied one small rack in a room 12 ft. square, holding six or even seven such racks. Thus, from 144 sq.ft. of floor space the total production of young weaned could have been $100 \times 6 = 600$ young per month or 50 young per sq.ft. per year. In an efficient breeding colony production would be improved by the selection and replacement of breeding stock. Young mice do not reach maturity until they are about 2 months old; if they are to remain in a breeding colony for a further 8 months about one-fifth of the animals would be growing stock. The space required for growing replacement stock would have been adequately supplied by the seventh rack, as the young animals can be housed in groups. Thus, 50 young per sq.ft. per year may be regarded as a conservative estimate of the expected production of the colony.

## SUMMARY

1. The total reproductive performance of two groups each of twenty-four mice over a period of one year under two different systems of mating has been recorded.

2. In the first system (monogamous pairs) the male was kept continuously with the female; in 78% of cases the females became pregnant again at post-partum oestrus and were thus subjected for the most part to unbroken intensive breeding.

3. In the second system (polygynous groups) several females were kept with one male and were removed to individual cages for the birth and rearing of the litters and were returned to the male again only after the litter had been weaned.

4. Under the first system 1149 young were successfully reared to weaning in one year by the twenty-four females; under the second system 559 young were weaned during the same period.

5. Mortality of breeding females, litter size, weight of young at weaning, the effect of parity, loss of litters and of young between birth and weaning and the sex-ratio of the young weaned were alike for both methods of mating.

6. The interaction of concurrent gestation and lactation upon the length of the gestation period is discussed, and regression lines showing the relation between the number of young suckled, the number of young in the uterus and the length of the gestation period are given.

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