EFFECT OF SELECTION ON SEX RATIO IN GUINEA PIGS

by

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INTRODUCTION

Dr. Helen Dean King changed the sex ratio in inbred rats in two generations by selection to such an extent that the average ratio in her line "B" for 19 generations was 82 males to 100 females as contrasted to line "A" with an average ratio of 122 males to 100 females. The ratio 105 males to 100 females was taken as the normal for rats. Likewise the normal for guinea pigs may be regarded as 104 males to 100 females on the basis of nearly 52,000 guinea pigs recorded in data kept by Wright, Ibsen, and Papanicolaou as determined by Burhoe.

With the normal sex ratio for guinea pigs known it was possible to undertake an experiment to attempt to modify that ratio in a somewhat similar manner to that of Miss King with rats. In the present experiment with guinea pigs a further objective, in case selection is successful in changing the sex ratio, is to determine the heredity of factors which distort the normal sex ratio. As yet the success of selection in changing the sex ratio in this experiment has not been conclusively proved.

ACKNOWLEDGMENT

I wish to express my appreciation to Dr. H. L. Ibsen for the use of his extensive records on guinea pigs in connection with this experiment. Also I am indebted to him for helpful criticisms and suggestions at the inception of, and during the course of the experiment discussed in this thesis.

I am also indebted to Dr. Mary T. Harman for a helpful suggestion made near the beginning of my experiment which caused me to consider this phase of the problem.

METHODS AND MATERIAL

The first step was to determine the sex ratios produced by aged breeding females who had produced fifteen or more young. This was done by consulting each individual litter record for all the litters produced by each female. As a result of such a study two extreme groups of sex ratio production were discerned.

One such group of females produced a large excess of males. The combined number produced by eleven such females was 210 males and 96 females. A second group of eleven aged females who produced a large excess of females had a total number of 45 males and 125 females. From among the off-

spring of aged females who produced a large excess of males young were selected for the "Plus Female Line."

A third line, the "Intermediate Sex Ratio Line," was selected, these from among offspring of aged females who produced about equal numbers of both sexes. Eleven such females gave birth to 181 males and 172 females. The intermediate line is of value to use in detecting possible lethals that may affect the sex ratio in the two extreme lines. The sequence of sex ratio production for the above three groups of aged females is compared in Table I. The said aged females are designated as "P_1" in this thesis.

Table I.-- Comparison of sex ratios produced by three "P_1" groups of females

Successive litters	Totals of litters: Plus male ♂	Totals of litters: Plus female ♀	Totals of litters: Balanced ratio ♂ ♀	Number of litter: Plus male	Number of litter: Plus female	Number of litter: Balanced ratio	Average per litter: Plus male	Average per litter: Plus female	Average per litter: Balanced ratio	Grand totals: Offspring ♂ ♀	Grand totals: Number of litters	Grand totals: Average
1	21,7	5,13	10,10,2[1]	11	10[2]	10[2]	2.55	1.80	2.20	36,30,2	31	2.20
2	17,5	13,16	22,16	9[2]	11	10	2.44	2.64	3.80	52,37	30	2.97
3	18,12	5,19,1	9,15	11	10	10	2.73	2.50	2.40	32,46,1	31	2.55
4	17,8[1],2	5,17	18,18,1	11	10	11	2.46	2.20	3.37	40,43,3	32	2.69
5	19,11	4,20	20,16	11	11	11	2.73	2.18	3.60	43,47	33	2.73
6	24,7,1	4,23	18,11,2	10	10	11	3.10	2.70	3.55	46,41,3	31	2.87
7	19,4,1	5,10	13,14	9	6	10	2.56	2.50	2.70	37,28,1	25	2.60
8	16,9	2,3,1	17,8	9	3	9	2.78	2.00	2.78	35,20,1	21	2.67
9	15,8,1	2,2	10,12	8	2	10	2.88	2.00	2.20	27,22,1	20	2.45
10	13,7	0,2	9,12	8	1	8	2.50	2.00	2.63	22,21	17	2.41
11	11,5	-------	11,7	5	----	5	3.20	-----	3.60	22,12	10	3.40
12	9,3	-------	6,8	5	----	5	2.40	-----	2.80	15,11	10	2.60
13	5,7	-------	3,7	4	----	4	3.00	-----	2.50	8,14	8	2.75
14	5,2	-------	8,6	3	----	4	2.33	-----	3.25	13,8	7	3.00
15	1,1	-------	4,4	2	----	3	1.00	-----	2.67	5,5	5	2.00
16	-------	-------	1,5	----	----	3	-----	-----	2.00	1,5	3	2.00
17	-------	-------	0,2,1	----	----	1	-----	-----	3.00	0,2,1	1	3.00
18	-------	-------	2,1	----	----	1	-----	-----	3.00	2,1	1	3.00
Total	210,96 5	45,125 2	141,172 6	116	74	126	2.655	2.32	2.85	456,393	316	2.655

1. Sex could not be determined.
2. Double litters omitted.

Matings in the "F_1", for the most part, were brother and sister. Other matings, however, were all made between animals whose "F_1" mothers produced the appropriate sex ratio. The selected offspring of the "F_1" mothers are termed the F_1 in this thesis. Generations subsequent to the F_1, mentioned hereafter, are really female generations because in many cases daughters were mated to their sires and sons to their dams. This type of mating differs from Miss King's method in that she employed brother-sister matings exclusively, and both from within the same litter produced by their mother. Since Miss King used the sex ratio of the litter as a basis of selection, this present experiment differs from hers on this point too because the total production to date of the dam is taken as the basis for selection.

SEX RATIO FOR STOCK ANIMALS

The average sex ratio for Dr. Ibsen's guinea pigs may be regarded as 105.5 males to 100 females on the basis of the records of 18,888 animals as determined by Surhoe. In order to know if the sex ratio for the stock guinea pigs was remaining average at the same time that the experiment to modify the sex ratio was in progress two stock litters were taken for every litter of sex ratio experiment animals born. The number of recent stock animals thus studied totaled 612 males to 571 females, or a ratio of 107.2 males to 100

females, not significantly different from the 105.8 to 100 ratio given above.

The combined number for the three sex ratio lines in the present experiment is 297 males to 300 females, a ratio of 99 to 100. When this is combined with the sample of stock litters the total numbers are in a ratio of 104 males to 100 females, or the same as the normal based on records of 51,778 guinea pigs as earlier stated in this thesis.

AVERAGE LITTER SIZE

As sex-linked lethals may greatly modify sex ratios as was the case with Moenkhaus's Drosophila, a study was made of the average litter size, first for the litters produced by the P_1 females, as shown in Table I, then for the combined F_1, F_2, F_3, and F_4 generations for each of the three sex ratio lines, and at the same time the average litter size for the sample stock litters. The various average litter sizes are given in Figure 1.

	Plus Male	Plus Female	Intermediate	Total
P_1	2.655	2.32	2.85	2.655
F_1 - F_4	2.494	2.30	2.53	2.45
Stock	-----	----	----	2.417
Number of litters F_1 - F_4	93	79	77	501

Fig. 1. Average litter size and number of litters.

The figures for the F_1 females indicate that no lethal factors played a part in greatly modifying the normal sex ratio that occurred.

ENVIRONMENTAL FACTORS

The effect of environment on the sex ratio has been given by Burhoe on the basis of records for 18,883 guinea pigs. The following he proved as having no significant effect on the sex ratio produced: 1. Age of dam at the time her litter is born; this may also be noted in Table I of this thesis. 2. Size of litter has no appreciable effect on the sex ratio. 3. The varying length of the period of time elapsing between successive litters of a dam has no effect on the sex ratio. 4. The sex ratio of stillborn, and of guinea pigs that died soon after birth did not seem different from that of the sex ratio for normal pigs. 5. The month of birth has no marked effect in sex ratio.

The only exception found by Burhoe was that 15 month old females produced a significantly larger excess of males than did females of other ages. However, new data in which females of the same age produced an excess of females sufficient to counteract the old data to such an extent that the new total shows that 15 month old mothers do not produce a significant excess of males, according to tabulations

recently made by Ibsen.

Consequently, we can regard environmental factors as not affecting sex ratio produced by guinea pigs.

EFFECT OF EACH PARENT IN DISTURBING THE NORMAL SEX RATIO

With the environmental factors that may possibly affect the sex ratio disposed of one can inquire into the question of which parent affects the sex ratio in guinea pigs. Accordingly a study was made of the "Plus Male" and "Plus Female" P_1 aged females in regard to the different males each female was mated to. As may be seen in Table II ♀D 42.1 and ♀D 70.1 of the "Plus Male Line" were mated to seven and four different males respectively. Yet these two females consistently produced an excess of males to their different mates.

Table II.-- Direct influence of each parent on the sex ratio produced

Sex ratio by mates	"Plus Male" Females									
	D 42.1	E351.1	G134.1	E353.3	F435.1	G331.2	D944.2	E943.1	F 39.3	D 70.1
Minor mate	3,0;2,1	9,4	----	----	----	7,4	10,4	2,1	3,2	4,3
	2,1	----	----	----	----	----	----	----	----	5,0
Other mates	----	----	----	----	----	1,1	----	1,0	2,2	4,0
Major mate	4,3;5,1	10,3	9,3	20,15	14,10	10,4	16,9	10,3	8,1	9,5
	4,2;6,0	----	----	----	----	----	----	----	----	----
Major mate's other get	----	2,6	9,4[1]	3,1		7,10	10,9	2,2	10,11	----
Major mate's total get	----	12,9	18,7	37,26		17,14	26,18	12,5	18,12	----

	"Plus Female" Females								
	E105.4	D905.1	E739.2	E645.2	E652.1	F182.1	E792.2	F317.2	D600.2	E154.3
Minor mate	----	3,3	----	----	3,3	3,4	----	----	2,5	2,0
Major mate	4,14	1,6	2,11	2,10	1,8	4,10	3,7	4,9	2,11	6,15
Major mate's other get	21,19	12,8	32,24	22,23	11,20	3,5	9,7	7,2	21,23	18,15
Major mate's total get	25,33	13,14	34,35	24,33	12,28	7,15	12,14	11,11	24,34	24,30

1. ♀E351.1's; dam to ♀G134.1 and ♀E353.4; the latter is dam to ♀F435.1

In regard to the mates of the P_1 aged "Plus Females" it is well shown that the "major mate" in several instances was mated to females whose sex ratios diverged in both directions from a balanced sex ratio. On the surface this suggests that perhaps the male does not directly affect the sex ratio of the young that he sires. This same idea was often suggested when the sex ratio for each aged female was determined, and instances were found where a male was mated to two females of divergent and opposite sex ratios though less extreme than the "P_1" from whom young were selected for the sex ratio experiment.

Miss King also states that the female seems the most important in modifying the normal sex ratio and arrived at her conclusion in somewhat the same manner. More light is offered on this question under the next heading.

EFFECT OF MALE PARENT AND OF SELECTION

It has been told how the "P_1" females were found and how the F_1 males and females were selected. It remains to be told how the F_1 produced and how the next generation has produced thus far. It has been told in the last foregoing paragraphs how the female was perhaps more important than the male in modifying the sex ratio. This is again shown in Table III where the effects of selection thus far in the

"Plus Male Line" is shown. In the "F_1 Females" group of columns is first the column of F_1 females, followed by a column showing their respective sex ratio, then a third column giving their mates who are sires to the F_2 females in the next column. Males H 545.1 and G 708.2 were mated to F_1 females who produced excess females much in contrast to their dams who produced a great excess of males. However, these males' daughters by these F_1 females usually produced a surplus of males as if the sires transmitted genetic factors that caused their daughters to more often modify the normal sex ratio in a plus male direction than in a plus female direction. The same indication is shown in one instance in the "Plus Female Line" where a brother-sister litter mates mating produced 4 males and 2 females, but their daughters bred mostly to their sire have produced 17 males and 9 females thus far.

The "Plus Male Line" now shows promise of yielding to selection; the "Plus Female Line" shows but little promise; the "Intermediate Line" fluctuates around the normal sex ratio. This is shown briefly in the next section in Figure 2.

Table III.-- Maternal generations, "Plus Male" experiment

P_1 Females		F_1 Females			F_2 Females			F_3 Females	
Females	Sex ratios	F_1 Females	Sex ratios	Their mates	F_2 Females	Sex ratios	Their mates	F_3 Females	Ratios
D 42.1	26,9	H 393.2	1,8	G 530.1	H 700.1	4,6	----	----	----
----	----	----	----	----	H 700.2	3,2	H 545.1	I 330.2	2,1
----	----	----	----	----	H 700.3	7,2	----	----	----
----	----	----	----	H 545.1	I 2.1	5,3	----	----	----
----	----	----	----	----	I 2.2	7,1	H 545.1	I 697.3	2,0
----	----	----	----	----	I 279.1	0,1	----	----	----
----	----	----	----	----	I 279.2	1,0	----	----	----
E 943.1	13,4	G 708.1	4,5	G 708.2	H 865.3	4,3	----	----	----
----	----	G 973.4	4,15	G 708.2	H 588.3	3,1	G 708.2	I 400.1	3,0
----	----	----	----	----	H 588.4	2,0	----	----	----
----	----	----	----	----	H 878.1	4,3	----	----	----
----	----	----	----	----	I 118.1	2,3	----	----	----
----	----	----	----	----	I 118.2	1,1	----	----	----
----	----	----	----	----	I 118.3	1,4	----	----	----
Total	39,13	----	9,28	----	----	44,30	----	----	7,1
E 351.1	19,7	G 134.2	4,2	G 444.4	H 465.2	5,8	H 112.2	I 698.3	1,1
G 134.1	9,3	G 605.1	6,7	G 444.4	H 401.1	4,2	----	----	----
----	----	----	----	----	H 701.1	5,7	H 461.2	I 637.3	2,0
----	----	----	----	----	H 701.3	1,1	H 112.2	I 53.2	5,3
----	----	----	----	----	H 701.2	2,2	----	----	----
----	----	----	----	----	H 947.1	3,1	H 616.1	I 509.1	2,2
Total	28,10	----	10,9	----	----	20,21	----	----	10,6
Grand Total	67,23 101,46	----	19,37	----	----	64,51	----	----	17,7
Total for other females	143,73	----	10,13	----	----	6,9	----	----	0,0

STATISTICAL TREATMENT OF RATIOS OBTAINED

As just stated the sex ratios produced by the F_1 and the F_1 females in the "Plus Male Line" were sharply contrasted. Statistically the ratio produced by the F_1 "Plus Male" females is highly significant as the deviation from the normal is over nine times its probable error on the basis of a table of probable errors for a 1:1 ratio compiled by P. A. Emerson.

	P_1	F_1	F_2	F_3	F_4	Total F_1-F_4
Plus male	210,96	29,50	70,60	17,7	0,0	110,117
Plus female	45,125	43,68	32,21	2,1	0,0	82,90
Intermediate	181,172	56,49	21,25	17,15	3,4	94,91

Fig. 2. Sex ratio by maternal generations.

Likewise when the sex ratio produced by the F_1 "Plus Female Line" is statistically treated its deviation is found to be virtually nine times its probable error.

Since $\frac{D}{PE} = 9$ occurs but once in about 730,000,000 trials when the deviation from expectation is due to chance alone, we may regard the distorted ratios produced by the two extreme groups of females as due to causes other than chance alone (according to a table by Pearl and Miner).

The 29:60 ratio in the F_1 "Plus Male Line" has a

deviation from normal that is considerably less than five times its probable error and therefore may be considered not significant. When the 29:50 ratio is compared with the 70:60 ratio produced by the F_2 "Plus Male" females the difference is still likewise insignificant. Hence selection in the "Plus Male Line" so far has produced results that are not significant statistically.

THE CAUSE OF DISTORTED SEX RATIOS

As already shown the normal sex ratio is not affected appreciably by environmental factors. Neither do sex-linked lethal factors appear to play a part in swerving the normal sex ratio for guinea pigs. Whatever the exact cause indications are that it is inherited through both parents, and that the daughter modifies the sex ratio of her young irrespective of the male that she is mated to. As earlier stated in this thesis the female seems to directly modify the sex ratio of her young from the normal without any direct effect of the male that she was mated to. Miss King suggests that possibly the ovum in some way determines the type of sperm that is more apt to fertilize it than is the other type of sperm.

SUMMARY

1. The distorted sex ratios produced by the two extreme groups of P_1 females are statistically significant.

2. Their distorted sex ratios were probably not caused by sex-linked lethal factors.

3. The effects of selection in modifying the sex ratios in generations following the P_1 have as yet had no significant result.

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