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Progeny:sperm ratios and non-functional sperm in *Drosophila melanogaster**

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1. INTRODUCTION

From a study of the frequencies of segregation products from Bar-Stone translocation males of *Drosophila melanogaster* it was suggested by Novitski & I. Sandler (1957) that not all products of spermatogenesis are functional. Peacock & Erickson (1965) compared the number of sperm stored in, with the number of progeny derived from, *yellow* females inseminated by Oregon-R males and found that over a wide range of sperm counts, a progeny:sperm ratio of approximately 0·5 obtained. They concluded that one-half of the stored sperm effected fertilization and proposed that 50 % of the sperm produced by the male are non-functional. The present paper reports evidence that under conditions yielding a progeny:sperm ratio of 0·5 from matings of Oregon-R males with *yellow* females, significant departures toward a ratio of 1·0 are observed from matings of Oregon-R males (brothers of the above) with Oregon-R females.

2. MATERIALS AND METHODS

In all experiments, Oregon-R males were collected within 1 h after eclosion, aged individually for 24 h and single-pair mated with a 5-day old *yellow* or Oregon-R female. Both males and females were raised and aged at 26 °C. Following observed mating, the male was removed from the vial and a period of some 3 h allowed to elapse to permit complete storage of the sperm in the female. Mated females were designated alternately for progeny counts or sperm counts. For progeny counts, individual females were placed in half-pint bottles, transferred daily for 8 days, then every other day for an additional 6 days and finally every third day for 6 days. For sperm counts, females were etherized, placed on a glass microscope slide and the storage organs excised in a drop of Beadle–Ephrussi saline solution. The excess saline was removed and two drops of acetic orcein (2 % orcein in 60 % acetic acid) were added to the preparation for staining. After the addition of the coverslip the preparation was analyzed microscopically under oil with phase optics. The linear nature of the ventral receptacle permits accurate scoring of sperm heads. Upon completion of the sperm count in the ventral receptacle, pressure was applied to the preparation breaking the chitinous walls of the spermathecae. In this way, greater numbers of sperm are revealed to be present in these organs than can be deduced from an examination of the intact structures. Experiments II, III and IV consisted of concurrent matings of Oregon-R males with Oregon-R females and Oregon-R males with *yellow* females. Fol-

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lowing the dissection of the females, the slides were coded so that the source of the storage organs (Oregon-R or *yellow*) was unknown to the investigator at the time of the sperm count.

3. RESULTS AND DISCUSSION

The results of the experiments are shown in Table 1. It may be seen that a progeny: sperm ratio of 0·79 was obtained in Expt I from matings of Oregon-R males with Oregon-R female. From the three experiments, each consisting of concurrent matings of Oregon-R males with Oregon-R females and Oregon-R males with *yellow* females, the respective progeny: sperm ratios turned out to be as follows: 0·75 and 0·38 (Expts. II*a* and *b*); 0·77 and 0·48 (Expts III*a* and *b*); and 0·62 and 0·42 (Expts IV*a* and *b*).

Table 1. *Progeny and sperm counts resulting from matings of Oregon-R* (+) *males with Oregon-R* (+) *females, and Oregon-R* (+) *males with* yellow (y) *females*

(See text for further details.)

Expt	♂	♀	Mean no. sperm	No. observations	Mean no. progeny	No. observations	Progeny: sperm ratio
I	+	+	413·3	54	329·0	54	0·79
II*a*	+	+	399·2	18	302·7	20	0·75
b	+	*y*	435·1	15	166·9	16	0·38
III*a*	+	+	484·9	14	372·6	17	0·77
b	+	*y*	542·7	17	261·5	16	0·48
IV*a*	+	+	566·7	25	350·2	23	0·62
b	+	*y*	572·8	13	242·7	13	0·42

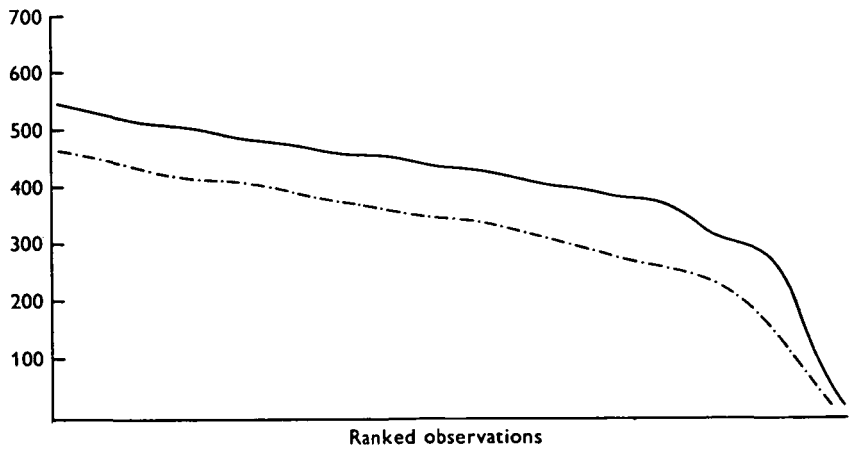

Fig. 1. Distribution of sperm counts (top curve) and progeny counts (bottom curve) from matings of 24-h-old Oregon-R males with 5-day-old Oregon-R females.

The results from Expt I are shown graphically in Fig. 1 and combined results from the corresponding matings in the last three experiments involving Oregon-R females and those involving *yellow* females are illustrated in Figs. 2 and 3 respectively. The graphs represent the distribution of individual observations ranked in order of magnitude (top curve = sperm counts; bottom curve = progeny counts); the slopes illustrate the varia-

tion among counts from the individual matings. It may be seen that the progeny:sperm ratio in Fig. 1 holds at about 0·75 or so, ranging between 0·65 and 0·85. Turning to a comparison of the combined results of the corresponding matings in the concurrent runs (Expts II–IV), we find the following: (1) the highest sperm count in Oregon-R females was 681, in *yellow* females 685; the lowest in Oregon-R females was 240, and in *yellow* females 242; (2) the distributions of the remaining counts were alike as may be judged by comparing the slopes of the appropriate (top) curves in Figs. 2 and 3; and (3) the mean

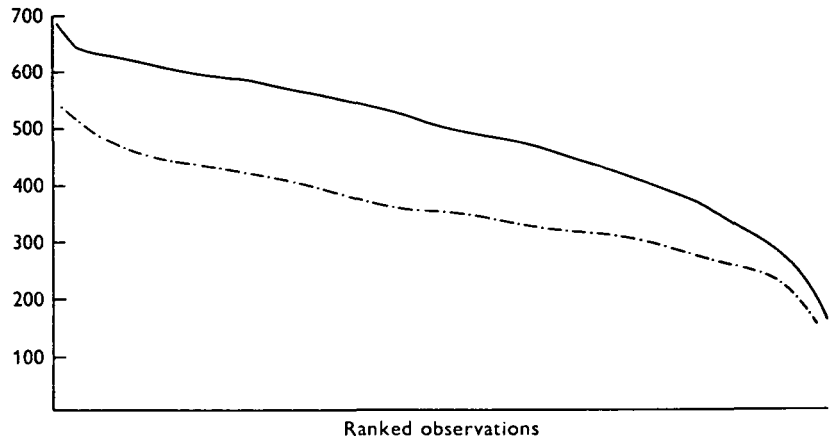

Fig. 2. Distribution of sperm counts (top curve) and progeny counts (bottom curve) from matings of 24-h-old Oregon-R males with 5-day-old Oregon-R females.

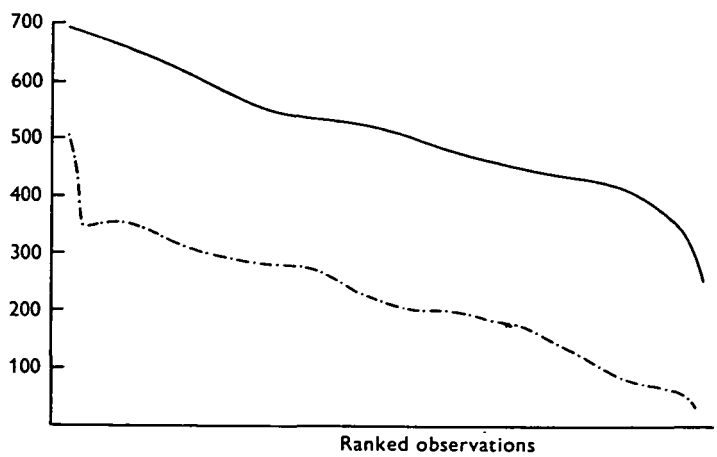

Fig. 3. Distribution of sperm counts (top curve) and progeny counts (bottom curve) from matings of 24-h-old Oregon-R males with 5-day-old *yellow* females.

number of sperm stored in the two kinds of females corresponded closely, 493·9 in Oregon-R females and 515·2 in *yellow* females. Yet, the mean progeny:sperm ratio with Oregon-R females was 0·69 and with *yellow* females 0·43. The three experiments reported by Peacock & Erickson involving matings of Oregon-R males and *yellow* females gave values for mean sperm number and associated progeny:sperm ratios as follows: 134·5 (0·53); 233·9 (0·42); 311·5 (0·39). From the corresponding runs in the present series we

observed: 435·1 (0·38); 542·7 (0·48); 572·8 (0·42). Thus, the progeny:sperm ratios in the present experiments with *yellow* females are in line with those reported by Peacock & Erickson and are extended to higher mean sperm counts.

Peacock & Erickson concluded from these ratios that 50 % of the sperm produced by the male are non-functional. However, the results from the present run with Oregon-R females argue strongly against the validity of extrapolating from progeny:sperm ratios to the proportion of non-functional sperm produced by the male.

The present authors interpret the results as follows: (1) The difference in proportions of non-functional sperm in *yellow* females as compared with Oregon-R females, given that the number of sperm stored in the two kinds of females is the same (or nearly so), suggests that a sperm determined as non-functional (not effecting fertilization) in one female may be determined as functional (effecting fertilization) in another. (2) A sperm is determined as functional or non-functional depending at least in part on the genotype of the female into which the sperm is transferred. If the determination is independent of the genotype of the sperm, then progeny:sperm ratios would reflect the relative efficiencies with which two different females utilize similar batches of sperm. An alternative interpretation immediately suggests itself, namely, the progeny:sperm ratio, which theoretically could vary from 0 to 1·0, reflects the proportion of non-functional sperm determined in the female and results from an interaction between the genotype of the female and the genotype of the sperm.

Investigations are underway to determine if the non-functional sperm inferred from progeny : sperm ratios are related to the unequal recovery from the male of reciprocal gametic products where such inequalities originate at or are critically related to events occurring at meiosis, i.e. meiotic drive (Novitski & I. Sandler, 1957; Zimmering & Perlman, 1962; Sandler, L. & Novitski, 1957; Lindsley & L. Sandler, 1958; L. Sandler, Hiraizumi & I. Sandler, 1959).

SUMMARY

When Oregon-R males of *Drosophila melanogaster* were mated with *yellow* females, counts of stored sperm and of progeny recovered from comparable females gave a progeny:sperm ratio of 0·5. These results are in excellent agreement with those obtained by Peacock & Erickson (1965) from similar crosses which led them to suggest that 50 % of the sperm produced by the male are non-functional. On the other hand, under otherwise very similar conditions, departures toward a ratio of 1·0 (approximately 0·65–0·85) were observed from matings of Oregon-R males (brothers of the above) and Oregon-R females in the present experiments. These results argue strongly against the validity of extrapolating from progeny:sperm ratios to the proportion of non-functional sperm produced by the male. The present authors interpret the results as follows: a sperm is determined as functional or non-functional depending at least in part on the genotype of the female into which the sperm is transferred. If the determination is independent of the genotype of the sperm, then progeny:sperm ratios would reflect the relative efficiencies with which two different females utilize similar batches of sperm. Alternatively the progeny:sperm ratio which theoretically could vary from 0 to 1·0 reflects the proportion of non-functional sperm determined in the female and results from an interaction between the genotype of the female and the genotype of the sperm.

The relationship of the non-functional sperm inferred from progeny : sperm and meiotic drive is to be determined.

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