

useful frequencies. The differences between stabilities could be exploited to facilitate one or other of these aspects in particular experiments.

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CHIASMATA HAVE NO EFFECT ON FERTILITY

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SUMMARY

The hypothesis that most gametes are rendered incapable of fertilisation owing to errors of crossing over is examined and found to have no reliable basis. The general high fertility of eggs is sufficient evidence to refute the hypothesis.

1. INTRODUCTION

COHEN (1967-73) has persistently expressed the idea that defects arising from recombination errors during meiosis cause a large proportion of gametes to be incapable of fertilisation. Although this hypothesis could be

tested directly in terms of organisms with external fertilisation, he has adopted an indirect approach of correlating sperm redundancy ($R = \text{sperms: zygotes for one mating}$) with chiasma frequency ($C = \text{mean chiasma count per spermatocyte}$), and claims that the two characteristics are unquestionably highly associated. If this were true, the calculated regression coefficient of R on C permits the explanation that more than a quarter of all chiasmata are so defective as to render sperm infertile, or perhaps that one of the chromatids involved in each cross-over is necessarily sacrificed in the process, representing a strong selection pressure to reduce or eliminate recombination.

2. ARGUMENT

A glance at the data shows that Cohen's correlation is based on a rather peculiar sample: limited to animal species which practise internal fertilisation and overwhelmingly drawn from insects and mammals. Data from these two groups are considered here, sacrificing information from a rotifer and a mite which both have achiasmate spermatogenesis. The insects and mammals provided markedly different regression coefficients according to the figures provided by Cohen (1971, 1973), but subsequent corrections have reduced this heterogeneity to an acceptable level. Fig. 1 shows that the corrected data for these two groups do not overlap, while their regression lines still diverge to some extent and are considerably displaced. An analysis of variance (table 1) shows the significance of the regression coefficients of both insects and mammals, and of their joint regression coefficient. A single regression encompassing all the data such as Cohen drew, however, markedly increases both the regression coefficient and the error variance above those of the joint regression. It thus seems that the overall correlation on which Cohen based his hypothesis is at least in part an artifact of assembling heterogeneous data. Most of the heterogeneity lies in the relative displacement of the two regression lines shown in fig. 1, as explained in the appendix. There is no doubt that it is a genuine difference, for it reflects an obvious difference in the reproductive physiology of the two groups. Mammals transfer larger numbers of sperm at each mating, all of which are expended on a single ovulation of usually 1-10 eggs. Female insects, however, commonly store sperm from one mating so that it may serve to fertilise a large proportion or all of the eggs, say 50-1000, produced in a lifetime. This difference, concerning female physiology and perhaps related to viviparity, largely accounts for the discrepancy of sperm redundancy between the two groups. It precludes any use of the data as a homogeneous sample. Consequently, the data for the mammals and the insects need to be assessed separately before attaching much confidence to their joint regression. Having already corrected the chiasma frequencies to the best of my ability, I propose to consider the reliability of the estimates of sperm redundancy.

Perhaps the only evidence that so many sperm are actually required for fertilisation in mammals comes from mice, where insemination with fewer than 10^6 sperm is held to reduced litter size. In contrast to that, it is clear that virtually all the redundancies over 10^8 , concerning domesticated ungulates (fig. 1, open stars) and primates, are exaggerated. Superovulation in man and sheep leads to an increased litter size without any known need for super-insemination. The commercial practice of artificial insemination

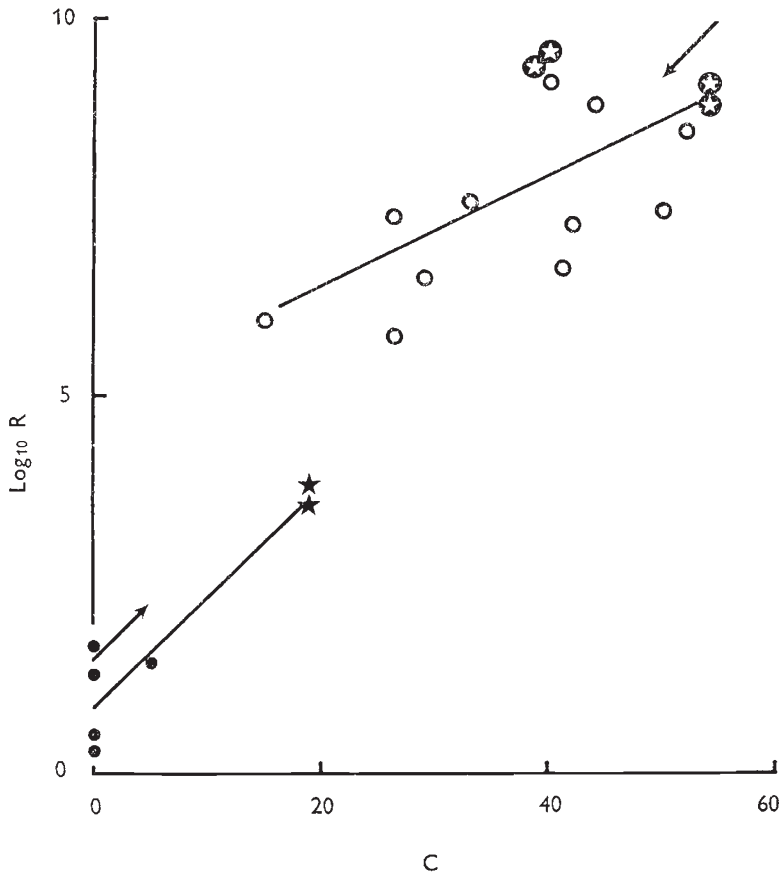


FIG. 1.—Comparison of sperm redundancy (R) with mean spermatocyte chiasma frequency (C) for insects (solid symbols) and mammals (open symbols). Special cases mentioned in the text, locusts and domestic ungulates, are identified by stars. The data are derived from Cohen (1971, 1973, and references cited there) but reduced to a single point for each species and with the following modifications. $R = 2$ for *Drosophila melanogaster* (see text); R is estimated as 20 for *Steatococcus tuberculatus* to allow for possible haploid males among broods of 15 or more embryos (Hughes-Schrader and Ris, 1941); $C = 41$ for guinea-pigs (cf. Meredith, 1969); C is taken as 54 for both sheep and goats (cf. Makino, 1943). The correlation coefficient for the total data shown here ($r = 0.92$) is even higher than that calculated by Cohen (1973), suggesting that these alterations have not imposed a subjective bias. The linear regressions are shown; arrows indicate the position of the overall regression calculated for all the data shown. The corresponding regression coefficients are listed in table 1.

TABLE 1
Regression coefficients (b) and analysis of variance on data in fig. 1

Category	b	Regression M.S.	Error M.S.	t	P
Insects	0.147	10.498	0.274	6.130	<0.01
Mammals	0.074	10.092	0.991	3.191	<0.01
Joint regression	0.089	18.543	0.792	4.839	<0.001
Heterogeneity	—	2.046	—	1.607	<0.2 >0.1
Overall regression	0.156	180.655	1.545	10.812	<0.001

in cattle, sheep and swine depends on the ability to achieve fertilisation with fewer sperm than are normally available. We can reasonably assume the same to be true of goats, not only because of their relationship to sheep and cattle but because all these ungulates form herds with a single dominant male whose sperm production must be unusually high. Since R is given as 4×10^9 for cattle (fig. 1) and use of 2×10^7 frozen sperm is known to give a normal rate of conception, it seems fair to reduce the redundancy estimates for all ungulates by a factor of 100. This adjustment alone, ignoring other defects in the present mammalian data, eliminates the significance of the regression coefficient (table 3). It is likely that other compensations to these sperm redundancy estimates would bring them within the range 10^6 - 10^8 and show no correlation to chiasma frequency.

The significance of the regression coefficient for insects is entirely attributable to the high sperm redundancy estimates obtained for two genera of locusts (fig. 1, black stars). Table 2 shows the figures from which these estimates were derived (Cohen, 1971); in the absence of any experimental details, these figures are highly questionable. The count of

TABLE 2
Data for locusts and possible corrections described in the text

	Original Counts (Cohen, 1971)			R corrected for	
	Sperm	Zygotes	R	total eggs	excess sperm
<i>Locusta</i>	500,000	70	7100	1000	100
<i>Schistocerca</i>	300,000	70	4300	1000	100

70 zygotes appears to be a mistake, for it is virtually identical to the number of eggs laid in a single pod (Norris, 1952). The average number of pods laid by a female is seven in *Locusta* and five in *Schistocerca*. Females of the latter genus continue to lay pods of fertile eggs for their normal life-span when isolated after a single mating, although it is not certain that they lay the normal number of 300 eggs or achieve the normal 70 per cent fertility (Norris, 1954). If, as seems likely, *Locusta* females can similarly lay up to 500 fertilised eggs after a single mating, then R should be reduced to about 10^3 in each case (table 2). There are two reasons for suspecting that the locusts sperm counts may also be misleading. Firstly, locusts mate for a protracted period during which the male can transfer several spermatophores. The first spermatophore forms a plug so that only its sperm have access to the eggs (Parker, 1970), and only they should be counted for this purpose. Secondly, it is possible that these experimental matings were conducted with aged virgin males which, by analogy to the better known case of *Drosophila*, are likely to transfer more sperm than required for total fertilisation. That implies an excess of fertile sperm in each spermatophore, disregarding the hypothetical proportion of infertile ones. Sufficiently aged males of *Drosophila* are reported to transfer several thousand sperm at their first mating, exceeding the total egg production of the female, but transfer progressively fewer at each successive mating to virgin females. This involves a tenfold decrease in sperm counts, while the sperm redundancy estimate falls to 1.3-2.5 depending on female genotype (Peacock and Erickson, 1965; Zimmering and Fowler, 1968). If this situation occurs in

locusts, their sperm redundancy should fall at or below 100—which would nullify the regression calculated from the present insect data (table 3). More refined estimates of sperm redundancy in locusts would need to consider the possibility of physiological polyspermy and a known low incidence of parthenogenesis. Even ignoring these factors, we cannot rely on the present locust data, for there is no evidence that R has been adequately estimated and some justification for suspecting that it has not.

The preceding arguments suggest that sperm redundancies do not exceed 10^2 for insects, but lie in the range of 10^6 - 10^8 for mammals. Table 3 shows the consequence of modifying the data in the way advocated here. The regression of R on C is not significant for either group and there is no possibility of obtaining a single regression which accommodates both groups. The joint regression is still significant, however, implying either that the data contain something to be explained or that there are still enough uncompensated defects to create a bias. My own observations on natural

TABLE 3

Regression coefficients (b) and analysis of variance on modified data (R for ungulates and insects reduced as in text)

Category	b	Regression M.S.	Error M.S.	t	P
Insects	0.055	1.442	0.272	2.301	<0.1 > 0.05
Mammals	0.040	2.984	0.750	1.995	<0.1 > 0.05
Joint regression	0.043	4.349	0.617	2.655	<0.02 > 0.01
Heterogeneity	—	0.078	—	0.355	<0.8 > 0.7

matings of axolotls and artificial fertilisations with native frogs tend to support the latter explanation: estimates of R are less than 500 and probably less than 100 for both species, although their chiasma frequencies are *c.* 60 and 25 respectively (cf. Wickbom, 1945).

Calculations of sperm redundancy depend upon the implicit assumption that all available eggs are fertile. Yet eggs are also meiotic products and so should have experienced much the same recombination errors postulated for sperm. Cohen (1973) briefly considers this but then evades the issue by further postulating that any oocytes which carry cross-over errors are aborted prior to ovulation as "oocyte atresia". He provides no independent support for such an assumption. Oocyte atresia seems only to be characteristic of mammals and then mainly affects oocytes prior to their first meiotic division, during a period when the "interpolation/deletion" errors which he envisages should be potential rather than actual. For that reason, I suppose oocyte atresia is probably irrelevant even in mammals and should be ignored, just as Cohen correctly ignores the atresia of spermatocytes when calculating sperm redundancy. It would be patently ridiculous to equate insect nurse cells with redundant oocytes in this context, for nurse cells segregate by mitotic divisions from the oocyte before it even begins meiosis. Despite that, Cohen (1973) attempts to fortify his sperm redundancy data with a few cases of supposed egg redundancy, calculated on this entirely different basis which has dubious relevance for mammals and is certainly spurious for insects. I contend that it would be illogical to exclude any category of gamete redundancy or to calculate it on a unique basis, when preparing data intended to demonstrate a dependency on chiasma frequency. Egg redundancy is obviously pertinent to this argument, and must be

calculated as eggs : zygotes, the reciprocal of fertility. Incidental observations on natural and artificial fertilisations convince me that the fertility of eggs is usually greater than 90 per cent during the normal breeding season for several species of sea-squirts, sea-urchins, amphibians and birds, and is over 70 per cent in most laboratory insects. Egg redundancy thus approximates to the minimum value of one, as is assumed in the present estimates of sperm redundancy. Even if this were only approximately true, and the chiasma frequencies only roughly known to occupy the range 7-100, the two characteristics are so obviously not correlated that we can reject their hypothetical association out of hand.

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STATISTICAL APPENDIX

By KENNETH MATHER

The regression of log R on C

The relation between sperm redundancy (R) and chiasma frequency (C), as shown by the observations set out in fig. 1, can conveniently be considered in three parts, the relation within the insects (I), the relation within the mammals (M) and the relation between the groups (G). In the first two of these parts the relation is measured by the coefficients of regression of R (or to be more precise of $\log_{10} R$) on C presented by Dr Wallace in his table 1, viz. $b_I = 0.147$ and $b_M = 0.074$ for insects and mammals respectively. Dr Wallace further shows that these two regression coefficients do not differ significantly and so may be replaced by a common estimate of regression within the groups, $b_J = 0.089$. We may also note that the remainder, or