

## Sex differences in recombination

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### Abstract

One of the stronger empirical generalizations to emerge from the study of genetic systems is that achiasmate meiosis, which has evolved 25–30 times, is always restricted to the heterogametic sex in dioecious species, usually the male. Here we collate data on quantitative sex differences in chiasma frequency from 54 species (4 hermaphroditic flatworms, 18 dioecious insects and vertebrates and 32 hermaphroditic plants) to test whether similar trends hold. Though significant sex differences have been observed within many species, only the Liliaceae show a significant sexual dimorphism in chiasma frequency across species, with more crossing over in embryo mother cells than in pollen mother cells; chiasma frequencies are unrelated to sex and gamety in all other higher taxa studied. Further, the magnitude of sexual dimorphism, independent of sign, does not differ among the three main ecological groups (dioecious animals, plants, and hermaphroditic animals), contrary to what would be expected if it reflected sex-specific selection on recombination. These results indicate that the strong trends for achiasmate meiosis do not apply to quantitative sex differences in recombination, and contradict theories of sex-specific costs and benefits. An alternative hypothesis suggests that sex differences may be more-or-less neutral, selection determining only the mean rate of recombination. While male and female chiasma frequencies are more similar than would be expected under complete neutrality, a less absolute form of the hypothesis is more difficult to falsify. In female mice the sex bivalent has more chiasmata for its length than the autosomes, perhaps compensating for the absence of recombination in males. Finally, we observe that chiasma frequencies in males and females are positively correlated across species, validating the use of only one sex in comparative studies of recombination.

## Introduction

Observations of sex differences in the amount of recombination at meiosis are common, even among autosomal genes, and date back to the early days of genetics (Morgan, 1912, 1914; Haldane, 1920). These differences can be usefully divided into three types, according to their cytogenetics. First, both sexes may have normal chiasmate meiosis, but with quantitative differences in the number or position of cross-overs (e.g. mice). Second, one sex may have an achiasmate meiosis, with no crossing-over of homologous chromosomes at all (e.g. male fruit flies). Finally, there may be neither independent segregation of nonhomologous chromosomes nor crossing-over in one sex (always the male), as in haplodiploid and parahaplodiploid species (e.g. bees, scale insects). Here, we will be mainly concerned with the evolution of quantitative sex differences in recombination.

Haldane (1922) gave the first general treatment of the problem, advancing the empirical claim that recombination tends to be reduced in the heterogametic sex. Huxley (1928) similarly suggested that whenever a marked sex difference in recombination occurred, it was always the heterogametic sex that had the lower value. Both authors proposed the same explanation: if gender is determined by two or more loci on the sex chromosomes, then selection against intersexes will favour reduced recombination between these chromosomes in the heterogametic sex, and as a pleiotropic effect the recombination of autosomal chromosomes may also be reduced.

These views have been questioned on occasion, both because there are some exceptions to the empirical generalization (e.g. Dunn and Bennett, 1967; Callan and Perry, 1977) and because the proposed explanation cannot account for observed sex differences in hermaphrodites (e.g. Ved Brat, 1966). However, there was no alternative theoretical perspective until Trivers (1988) recently revived the subject, with slightly different empirical claims and a provocative new explanation. According to Trivers, recombination tends to be lower in males than females, as well as lower in the heterogametic sex than the homogametic sex, though he acknowledges that there are many exceptions to these rules. Trivers suggests that both reduced recombination and heterogamety are consequences of selection being more intense in one sex (usually the male) than the other. He argues that reproducing individuals of the sex experiencing more intense selection will, on average, have better combinations of genes than those of the other sex, and so the cost of breaking up those combinations should be higher. Bernstein et al. (1988) counter with an alternative explanation, that rates of recombination tend to be higher in females because oogenesis is associated with higher metabolic rates, and thus more DNA damage, than spermatogenesis; however, they admit to being puzzled by the association with gamety.

Most other theories of recombination can be adapted to predicting sex-specific optimal recombination rates. For example, many theorists believe that the main function of recombination is to reduce linkage disequilibrium (e.g. Felsenstein, 1988; Maynard Smith, 1988; Kondrashov, 1988). As two potentially important sources of linkage disequilibrium are selection and drift, one might expect that the

sex experiencing the more intense selection, or otherwise having the higher variance in reproductive success, should have more recombination. This prediction is exactly opposite to that made by Trivers. Other predictions follow from the various proposed diversity theories of recombination (Williams, 1975; Bell, 1982; Tooby, 1982). Alternatively, sex differences in recombination may be more-or-less invisible to natural selection, the latter determining only the mean value. Simulations by Nei (1969) indicate that sex differences in recombination may have very little effect on population mean fitness.

Information currently available on achiasmate meiosis in no way contradicts Haldane's, Huxley's, and Trivers' empirical claims: we know of 25–30 independent origins of achiasmate meiosis among dioecious animals (A. Burt, unpublished; see Serrano, 1981; Bell 1982; Nokkala and Nokkala, 1986 and references therein) and every time it has evolved in the heterogametic sex, which all but twice is the male (exceptions are Copepoda and Lepidoptera/Trichoptera). Here, we bring together the available data on quantitative sex differences in chiasma frequencies, to further test the strength of the proposed trends and, if possible, to test the various explanations. To this end we also examine the magnitude of sexual dimorphism in chiasma frequency, independent of sign, and look for evidence of compensation between the sexes.

One further motivation for this study is to estimate the correlation between male and female chiasma frequencies across species, thus determining whether the value for one sex is a good indicator of what is happening in the other sex and in the species as a whole. This estimate is important because male meiosis is usually more easily studied than female meiosis, and so comparative surveys of chiasma frequencies tend to only use data for males (e.g. Burt and Bell, 1987; Sharp and Hayman, 1988). There are about 20 times more chiasma frequencies for males in the literature as for females.

### Data and Analysis

Rates of recombination can be measured both by counting chiasmata through the microscope and by crossing marked individuals to construct a linkage map. Counts of chiasmata are available for many more species than are extensive linkage maps, and here we will restrict ourselves to the former. As with any comparative analysis using data from the literature, the quality of estimates varies – for example, in techniques and sample sizes. Actually counting chiasmata in some species is quite straight-forward and in others quite difficult; female mammals are notoriously difficult. For plants, often only metaphase figures are available, whereas counts at the earlier diplotene stage are usually considered more accurate. Perhaps more importantly, the methods used are often different for the two sexes, so that observed differences between males and females may be due to differences of technique rather than real. This problem is particularly acute when the data for the two sexes come from different studies (3 of 6 amphibians and 2 of 4 mammals in our data set).

Perhaps the best measure of recombination to be got from a meiotic spread is the proportion of the genome which recombined. This value can be calculated by measuring the distances between the ends of chromosomes and the nearest chiasma and between neighboring chiasmata, and expressing these as a proportion of the total genome length. For  $n$  bivalents and  $C$  chiasmata, there will be  $n + C$  such distances,  $d_i$ . The proportion of the genome which recombines is then equal to the proportion of pairs of loci which are on different segments:  $P = 1 - \sum d_i^2$ . This value will be a function of the number and size distribution of chromosomes and the number and position of cross overs. Corrections could be made for obviously noncoding fractions of the genome simply by not including them in the calculations.

Unfortunately, this proportion has yet to be reported for any species. Instead, we shall use simple counts of the number of chiasmata, noting that for any given distribution of cross overs along the genome, our measure  $P$  increases monotonically with the number of chiasmata. Ignoring possible sex differences in the position of cross overs will lead to some inaccuracy: for example, Fletcher & Hewitt (1980) observe that males of *Chrysochraon dispar* have slightly more chiasmata per bivalent than females, but that they are terminalized to such an extent that the effective amount of recombination is greater in females. However, quantitative information on the position of chiasmata is available for very few species.

One possible check on the data is to compare sex differences in chiasma frequency and linkage map lengths. Unfortunately, we know of map length data for only three species in our data set, all mammals: *Sminthopsis crassicaudata* (Bennett et al., 1986), mice (Dunn and Bennett, 1967), and humans (Donis-Keller et al., 1987). For *S. crassicaudata* and mice the sex differences in chiasma frequency and map lengths are in the same direction, but not for humans: the cytogenetic data suggest that males have more chiasmata than females (51 vs 43; Lange et al., 1975; Jagiello et al., 1976), but the genetic data indicates they have shorter map lengths (2017 vs 3857 cM; Donis-Keller et al., 1987). Apparently, the female chiasma frequencies are greatly underestimated. This corroborates Chandley's (1988:20) statement that, due to technical difficulties, "accurate counts of chiasmata for the human female still remain to be established." As the problems of getting sufficient appropriate material (oocytes at time of ovulation) are much greater for human females than for other species, this discrepancy is unlikely to be representative of the rest of the data. Indeed, among other organisms for which both chiasma frequencies and extensive genetic maps exist, there is a strong correlation between the two ( $r = 0.85$ ,  $n = 10$ ; A. Burt, unpublished). Here, we have excluded humans from further analysis.

Having decided to use counts of chiasmata at meiosis, there still remains a number of possible indices of recombination. Burt and Bell (1987) defined the excess chiasma frequency as the number of chiasmata per bivalent in excess of one, summed across bivalents. This measure was considered to most accurately reflect selection for recombination, independently of the various constraints on changes in chromosome number and the mechanical role of chiasmata in proper segregation. However, it does not make much biological sense for polyploid and achiasmate species, both of which are represented in our data set. Therefore we use here the

number of chiasmata per autosomal bivalent. Interpretations are also made easier by this choice, since in our data set the chiasma frequency per bivalent is independent of chromosome number ( $r = -0.105$ ,  $n = 54$ ,  $p > 0.4$ ), while excess chiasma frequency is positively correlated with chromosome number ( $r = 0.317$ ,  $n = 54$ ,  $p < 0.02$ ). In any case, choice of index does not affect the conclusions drawn.

Data is available for 54 species of animals and higher plants (Appendix), approximately 0.002% of all known animals and higher plants. Unfortunately, the data set is taxonomically unrepresentative: there are 8 species of acridid grasshoppers, but no other arthropods; 4 *Triturus* newts, but no fish, reptiles, or birds; 22 species in the Liliaceae, but only two dicots. This nonrandomness means that we cannot put much weight on overall trends and must instead look within lower taxa: since we cannot make definitive statements about all animals and higher plants, we shall try to say something about acridid grasshoppers, *Triturus*, and the Liliaceae.

## Results

### *Correlations*

Across all chiasmata species there is a positive correlation between male and female chiasmata per bivalent ( $r = 0.75$ ,  $n = 54$ ,  $p < 0.001$ ; Fig. 1). This result seems to be fairly robust, as the sign of the correlation is positive in 9 of 11 independent taxa (Table 1). The exceptions are amphibians and Oedipodinae, a subfamily of grasshoppers, though neither are significantly negative.

### *Sexual dimorphism*

Across all species females seem to have more chiasmata than males (paired t-test,  $t = 2.49$ ,  $n = 54$ ,  $p < 0.02$ ). Closer examination of the data shows that this trend holds for *Lilium* (all 8 species,  $p \sim 0.008$ ) and probably Liliaceae genera (all 4 genera have more species with more chiasmata in the female than the male,  $p = 0.0625$ ). However, there is no evidence that the trend applies to other plant taxa or any animal taxon (Table 1). As many species individually show significant sex differences in chiasma frequency (Appendix), this result indicates that there is a large sex  $\times$  species interaction effect. All dioecious species in the data set are male heterogametic (except one species with unknown sex chromosome system), so the absence of a consistent sex difference also indicates that there is no consistent difference between homo- and heterogametic sexes.

### *Ranges*

The magnitude of sexual dimorphism, independent of sign, is given by |male-female|. This is also the range, a measure of dispersion. The idea of sex-specific

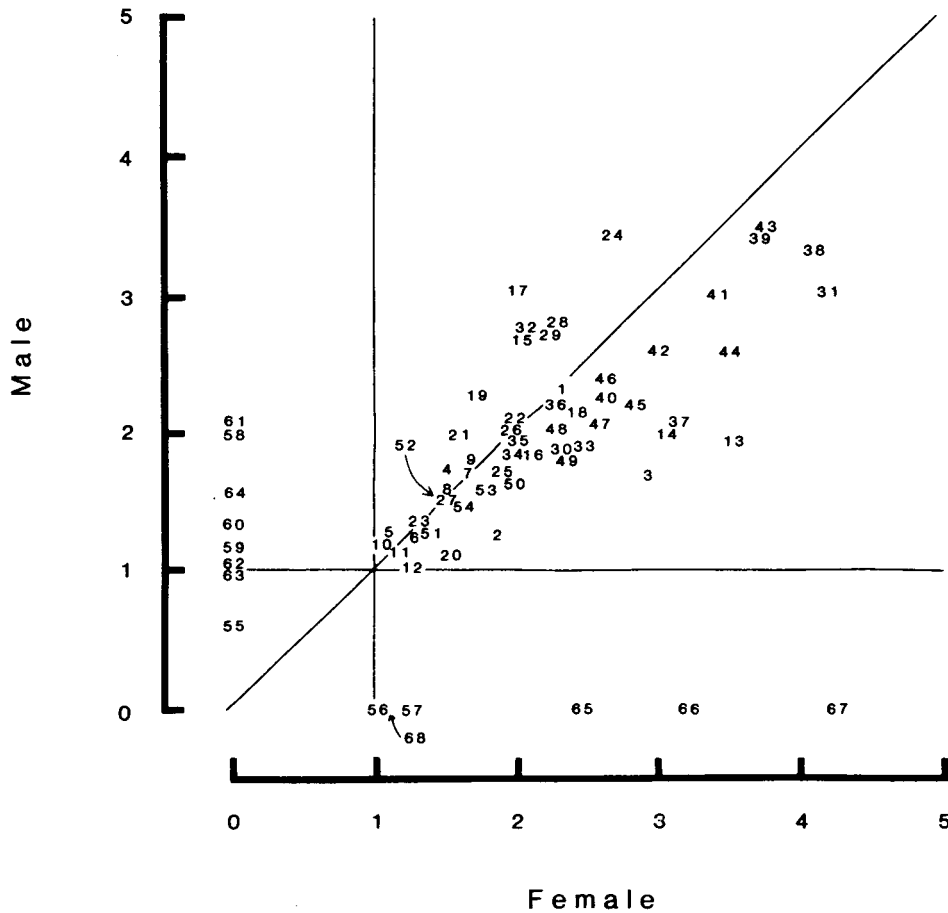


Fig. 1. Male vs female chiasma frequencies per bivalent with line of equality. Numbers refer to species in the appendix. Note the large gap separating chiasmate and achiasmate species: all chiasmate species have at least one chiasmata per bivalent (horizontal and vertical lines).

optima suggests that the magnitude of sexual dimorphism should be correlated with the opportunity for sex differences in selection, and thus presumably in the order

dioecious > hermaphroditic > hermaphroditic  
animals                      plants                      animals

Mean ranges for these groups are  $0.40 \pm 0.102$  (s.e.),  $0.39 \pm 0.055$  and  $0.52 \pm 0.269$  chiasmata/bivalent respectively (Table 1); there is no significant difference among groups ( $F_{2,51} = 0.20$ ), contradicting this prediction.

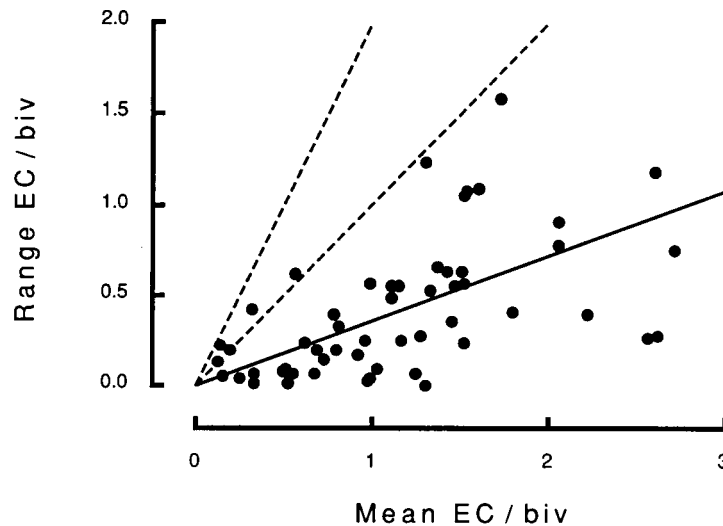
We can also test the idea that sex differences in recombination are neutral. In its strongest form, this hypothesis predicts that species will drift up and down lines of

**Table 1.** Chiasma frequencies per bivalent for males and females. Lettered entries are phylogenetically independent (Burt, 1989). n is the number of species; t refers to paired t-tests; |Diff| is the average magnitude of sexual dimorphism, the mean of the absolute value of the difference between male and female; r is the correlation coefficient for male and female values.

	Taxon	n	$\bar{X}_{ta/bivalent}$		t	Diff	r
			Male	Female			
	All	54	2.05	2.23	2.49*	0.41	0.75***
	Animalia	22	1.77	1.87	0.76	0.42	0.49*
	Platyhelminthes	4	1.74	2.14	1.23	0.52	0.25
a	Trematoda	1	2.31	2.31	–	0.00	–
b	Turbellaria	3	1.56	2.09	1.27	0.69	0.20
	Insecta, Orthoptera, Acrididae	8	1.37	1.33	0.71	0.11	0.89**
c	Eyprepocnemidinae	1	1.28	1.09	–	0.19	–
d	Melanoplinae	1	1.23	1.27	–	0.05	–
e	Gomphocerinae	3	1.69	1.60	3.25	0.09	0.94
f	Oedipodinae	3	1.11	1.16	0.42	0.14	–0.98
	Chordata	10	2.11	2.19	0.33	0.64	0.04
	Amphibia	6	2.27	2.52	0.61	0.81	–0.57
g	Anura	1	1.94	3.52	–	1.58	–
	Urodela	5	2.34	2.32	0.05	0.66	–0.52
h	<i>Salamandra</i>	1	2.00	3.07	–	1.07	–
i	<i>Triturus</i>	4	2.42	2.14	0.89	0.56	–0.50
	Mammalia	4	1.86	1.70	0.75	0.37	0.59
j	Marsupialia	1	2.27	1.70	–	0.57	–
k	Rodentia	1	1.10	1.52	–	0.42	–
l	Primates	2	2.03	1.78	1.67	0.25	1.00
	Plantae, Angiospermae	32	2.25	2.48	2.88**	0.39	0.82***
m	Dicotyledonae, Leguminosae	2	2.38	2.00	1.03	0.39	1.00
	Monocotyledonae	30	2.24	2.51	3.50**	0.39	0.84***
n	Commelinaceae	1	1.70	1.90	–	0.20	–
o	Gramineae	2	1.76	1.74	2.00	0.02	1.00
	Liliaceae	22	2.47	2.81	3.30**	0.49	0.73***
p	<i>Allium</i>	8	2.36	2.44	0.38	0.52	0.50
q	<i>Lilium</i>	8	2.87	3.36	5.93***	0.50	0.89**
r	<i>Tulbaghia</i>	4	2.08	2.47	4.53*	0.39	0.70
s	Orchidaceae	5	1.50	1.63	1.78	0.15	0.84

\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

neutral equilibrium representing isoclines of equal total recombination. The expected magnitude of sex differences can be calculated under this model as follows. Since bivalents are constrained to having at least one chiasma for proper segregation, we shall consider the number of chiasmata per bivalent minus one (i.e. the mean number of 'excess chiasmata' per bivalent). As both male and female excess chiasma frequencies are non-negative, the range is constrained mathematically to being in the interval  $[0, 2m]$ , where  $m$  is the mean of male and female values. The neutral hypothesis claims that all values within this interval are equally likely, and thus that the expectation of the range is equal to  $m$ . In figure 2 we show the range



**Fig. 2.** Range of excess chiasmata per bivalent between sexes versus the mean. Points are mathematically constrained to fall below the top dashed line ( $y = 2x$ ), and are expected by the neutral hypothesis to fall around the lower dashed line ( $y = x$ ). Solid line is the weighted regression fitted through the origin and the bivariate mean ( $y = 0.36x$ ).

of excess chiasmata per bivalent versus the mean. Almost all points fall below the line of equality, indicating that the male and female values are more similar than predicted.

### Compensation

If selection determines only the mean rate of recombination, then the optimal rate for one sex will depend on what the other is doing, and *vice versa*. We test for evidence of such tradeoffs in three situations: achiasmate species, haplodiploid species, and the sex chromosomes.

In species where one sex has an achiasmate meiosis, one might expect the other to have a higher than average chiasma frequency to compensate. Chiasma frequencies for species in which one sex is achiasmate are available for 13 species (Appendix). The rate of recombination in the chiasmate sex is to be compared to that of the same sex of a fully chiasmate species. Note that for two such comparisons to be independent, they must involve different parts of the phylogeny – a comparison between a Lepidopteran and an Orthopteran is not independent of a comparison between another Lepidopteran and another Orthopteran (see Burt, 1989 for discussion). In our data set there are three such ‘phylogenetically independent’ comparisons between an achiasmate species and a fully chiasmate species: *Neorhabdocoela* (Turbellaria, nos. 55 vs 3 in Fig. 1), Insecta (56–64 vs 5–12) and *Fritillaria* (Liliaceae, 65–67 vs 37). In no case is there any indication of compensation.



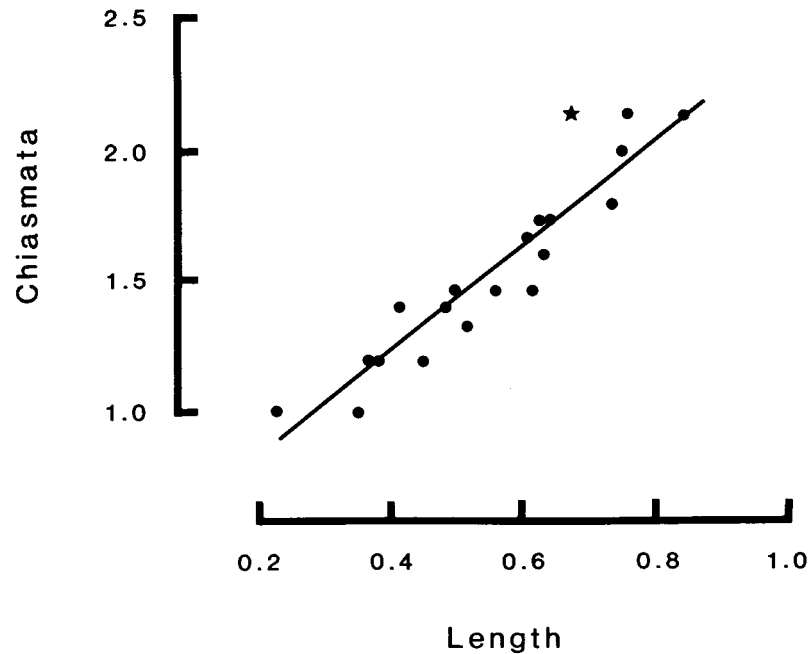


Fig. 3. Chiasma frequency as a function of chromosome length (arbitrary units) in female mice. Regression line is for autosomes only (circles;  $r = 0.95$ ). The sex bivalent (star) has significantly more chiasmata for its length than the autosomes. Chromosome length (from idiograms of oocyte chromosomes) and chiasma frequencies (mean of 15 oocytes) from Jagiello & Fang (1987).

Data are also available for one haplodiploid species, the parasitic wasp *Aphytis mytilaspidis* (Rossler and DeBach, 1973, no. 68 in Fig. 1). Again there is no indication of compensation compared to wholly sexual insects (Fig. 1).

Finally, in species with strongly dimorphic sex chromosomes the X (or Z) has a haplodiploid mode of inheritance and one can test for compensation by comparing chiasma frequencies of the sex bivalent to those of autosomes in the homogametic sex. The only data available on chiasma frequencies for individually identifiable bivalents in the homogametic sex are for mice (Jagiello and Fang, 1987). In figure 3 we plot chiasma frequency as a function of chromosome length and observe that the X bivalent has significantly more chiasmata at meiosis than the autosomes ( $t = 3.4$ ,  $p < 0.01$ ). This observation supports the notion of compensation.

### Discussion

The strong empirical generalizations for the occurrence of achiasmate meiosis in dioecious species do not hold for quantitative sex differences in chiasma frequency: chiasma frequencies do not differ consistently between homo- and heterogametic

sexes, nor between males and females, outside the Liliaceae. Dunn and Bennett (1967) come to similar conclusions, based on many fewer species, in their review of sex differences in genetic map lengths. These results suggest that the two types of sex differences require different explanations.

Early accounts of sexually dimorphic rates of recombination suggested that recombination might be lower in the heterogametic sex as a result of selection against crossing over between the sex chromosomes in this sex (Haldane, 1922; Huxley, 1928). Bell (1982) notes that this cannot be a complete explanation for achiasmatic meiosis: White (1976) estimates that it has evolved some 8 times in the Mantodea, yet in each instance males were XO heterogametic, so crossing over between sex chromosomes could not have been possible in males anyway. Here we conclude that the explanations of Haldane and Huxley also cannot satisfactorily account for observed quantitative sex differences in chiasma frequency.

The only consistent sex difference observed was that in the Liliaceae there are more chiasmata formed in the embryo mother cells (female) than in the pollen mother cells. It is difficult to relate this observation to the various theories because the relevant plant population biology is unknown. For example, while among animals the variance in reproductive success tends to be higher in males than in females (Clutton-Brock, 1988), the only direct study on a plant gave ambiguous results. Meagher (1986) studied seeds collected from known female parents of *Chamaelirium luteum*, a dioecious lily, and estimated paternity using genetic markers; he found that variance in the number of mates was higher for males than females ( $F_{58, 68} = 7.7$ ). However, in a study of established seedlings, from which both the mothers and the fathers were estimated, variance in the number of mates and the number of progeny was higher among females than among males ( $F_{136, 183} = 3.15$  and  $F_{136, 183} = 4.19$  respectively; Meagher and Thompson, 1987). Similarly, several diversity theories of recombination emphasize the importance of dispersal patterns (e.g. Williams, 1975; Bell, 1982; Tooby, 1982), and so one could derive predictions from any differential dispersal of genes transmitted through pollen and ovules. While one would expect that genes transmitted through pollen should be scattered further than those through ovules, since they have an extra round of dispersal, nevertheless established seedlings of *C. luteum* were found significantly closer to their father than to their mother (8.9 vs 10.1 m; Meagher and Thompson, 1987).

Thus it is not clear how well any particular theory based on sex-specific costs and benefits can account for the trend in the Liliaceae. In any case, no such theory seems to account in any obvious way for the considerable variance in sexual dimorphism outside this family. Further, the very idea of sex-specific optima suggests that the magnitude of sexual dimorphism should be correlated with the opportunity for sex differences in selection. To test this idea we compared dioecious animals, plants, and hermaphroditic animals; the absence of a significant difference among these groups contradicts the hypothesis. Indeed, it is rather difficult to imagine how any selective differences might account for the large sex differences observed in some Platyhelminthes. Perhaps an alternative approach is required.

*Are sex differences in recombination neutral?*

To now we have assumed that selection on recombination determines a simple individual optimum and that sex differences in recombination are due to sex differences in this optimum. The repair theory of Bernstein et al. (1988) is a particularly clear example of this type of theory. However, it is also possible that selection determines only the population mean recombination rate (analogous to determining a 50:50 sex ratio) and that individual optima will depend on what others in the population are doing. In the present context, the optimum for males may depend on the females' rate of recombination, and *vice versa*. Theories of linkage disequilibrium decay fit this mold well.

Suppose there is linkage disequilibrium (l.d.) among the males of a population, but not the females. Then, since the sexes contribute equally to the next generation, recombination in females will have no effect on population l.d. On the other hand, if l.d. is equal in the two sexes, then the mean amount of recombination in the two sexes will determine the rate of decay; sex differences *per se* will have no effect. Thus, if the function of recombination is to reduce l.d., then the potential for sex-differential optima of recombination is restricted to instances where there are sex differences in the amount or pattern of l.d. Furthermore, one can divide the l.d. in a population at time of reproduction into the fraction which was created in that generation, and the remainder, which is a holdover from all previous generations. Only the former can differ consistently between the sexes, due to sex-specific epistasis or selection: just as the sexes start each generation with equal gene frequencies (assuming a large zygote population), so they start with equal l.d. (This need not be so: one can imagine a meiotic system in the heterogametic sex in which recombinant chromosomes segregate with one type of sex chromosome and parental chromosomes with the other. Other mechanisms can be imagined for haplodiploid and monogenous species. However, we know of no example.) At equilibrium, when the l.d. created by selection equals that destroyed by recombination, the l.d. created in one generation between unlinked loci will be only one half the total l.d.; for more closely linked loci, this fraction will be correspondingly lower.

Thus, if recombination functions to reduce linkage disequilibrium, then there is unlikely to be strongly dimorphic selection pressures between the sexes. Indeed, Nei's (1969) simulation study of recombinational load using different fitness matrices for the two sexes found only very slight effects of sex differences in recombination on population mean fitness – too small, he suggests, to be selected. These very slight differences in optima may be swamped by other factors, such as differences in the mechanical cost of chiasmata or historical contingencies. For example, if there is selection on the population for increased recombination, then whichever sex has more additive genetic variance for rates of recombination may respond more, and thus the sexes may diverge over time. The absence of a consistent sex difference across species would not be mysterious, but expected.

In its strongest form, this theory suggest that sex differences in recombination are invisible to natural selection and that species will drift up and down lines of neutral

equilibria representing isoclines of equal total recombination. This does not seem to be an accurate description of the data, as the chiasma frequency of males and females is much more similar than this hypothesis would lead one to predict (Fig. 2).

A slightly modified theory suggests that sex differences are more-or-less neutral only in the region of the line of equality, affecting mean fitness only at some distance away. Such a situation may arise, for example, if the mechanical or physiological costs of crossing over increase with increasing numbers of cross-overs. To test this modified theory we take a different tack.

The neutral theory of sex differences predicts that experimental manipulations of recombination in one sex will result in selection for compensation by the other. Unfortunately, this prediction is difficult to assess at the moment: we are not aware that any such experiment has been done, and interpreting comparative relations in terms of tradeoffs is notoriously difficult, as recent experience with the cost of reproduction has demonstrated (Bell and Koufapanou, 1986). For example, the positive correlation of male and female chiasma frequencies across species (Fig. 1, Table 1) may seem to contradict the prediction of compensation, but actually is to be expected simply if the between-species variance in mean chiasma frequency is greater than the variance in sexual dimorphism. The most relevant comparisons are those which appear to be a 'natural experiment' – a seemingly randomized effect, if not actually manipulated. Here we consider three such situations: achiasmate species, haplodiploid species, and the sex chromosomes.

The comparison of chiasmate and achiasmate species is the least satisfactory of the three. On the one hand, the fact that achiasmy is only ever observed in one sex supports the prediction of compensation. (Christensen's (1961) study of hermaphroditic enchytraeid annelids is often cited as the one example of achiasmate meiosis in both sexes. Subsequent study indicated that spermatogenesis in these worms is in fact chiasmate (Christensen 1980).) On the other hand, there is no indication of compensation in the chiasma frequencies of the recombining sex (Fig. 1). However, this result may simply indicate that an achiasmate meiosis reflects selection for reduced recombination, which is also acting on the other sex.

Haplodiploidy seems a more promising natural experiment to test the hypothesis, for it is less likely that this genetic system has evolved and is maintained by selection for reduced recombination. Unfortunately, data is available for only a single species (*Aphytis mytilaspidis*), and this exists in both sexual (haplodiploid) and asexual (automictic) forms (Rossler & DeBach 1973). It appears, then, that there has been selection for reduced recombination in this particular species, and so it is perhaps not surprising that there is no indication of compensation in the females' chiasma frequency (Fig. 1). Comparable data on more haplodiploid species would be of interest.

The final example is a comparison of chiasma frequencies of the sex chromosomes and the autosomes in the heterogametic sex. In female mice the sex chromosomes have more chiasmata for their length than the autosomes (Fig. 3), perhaps compensating for the much lower levels of recombination in the male. Alternative explanations for this observation seem possible, for the absence of

recombination in males is not the only difference between the sex chromosomes and the autosomes. Perhaps most importantly, the X-chromosome is hemizygous in the male, resulting in lower mutation rates (Cavalli-Sforza and Bodmer, 1971; Miyata et al., 1987), greater sensitivity to founder events (Templeton, 1987), faster rates of evolution (Charlesworth et al., 1987), and perhaps altered rates of I.d. production. One possible test to distinguish these theories would be to look at achiasmatic species: the theory of compensation predicts that in such species there should be no difference between sex chromosomes and autosomes in the homogametic sex; theories based on the hemizygous nature of the X-chromosome in the heterogametic sex predict differences as large as those in chiasmatic species.

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## Appendix

*Sex differences in chiasma frequency*

No. is the number used in Fig. 1; Gender system (h-hermaphroditic; d-dioecious, with sex chromosome system; amphibians from Sims et al. 1984 and Duellman & Trueb 1986); n is the haploid number of autosomes; Xta freq is total number of chiasmata formed on these bivalents; Diff indicates whether the author(s) claim there is a real sex difference (y=yes; n=no; those in parentheses are not based on a statistical test); Com. are numbered comments, listed as the bottom; Ref refers to numbered entries in the bibliography.

Taxon No.	Gender system	Ploidy	n	Autosomes	Diff	Com.	Ref.
				Male	Xta freq	Female	
<b>CHIASMATE SPECIES</b>							
Platyhelminthes: Trematoda							
1	h	2	14	32.3	32.3	n	1 10
Platyhelminthes: Turbellaria							
2	h	2	10	12.5	18.6	(y)	14
3	h	2	7	11.8	20.4	y	2 40
4	h	2	3	5.2	4.5	-	3 27
Insecta: Orthoptera: Acrididae							
5	d-XO/XX	2	11	14.1	12.0	y	4 5
6	d-XO/XX	2	11	13.5	14.0	n	4 8
7	d-XO/XX	2	8	13.6	13.1	n	4 24
8	d-XO/XX	2	8	12.6	12.1	y	4 12
9	d-XO/XX	2	8	14.4	13.2	y	4 20
10	d-XO/XX	2	11	13.1	11.6	y	4 12
11	d-XO/XX	2	11	12.3	12.9	y	4 12
12	d-XO/XX	2	11	11.3	13.7	y	4 41
Chordata: Amphibia							
13	d-XY/XX	2	13	25.2	45.7	-	15, 51
14	d-??/??	2	12	24.0	36.8	-	29
15	d-XY/XX	2	12	32.3	24.5	-	5 19, 28
16	d-XY/XX	2	12	22.0	25.0	(y)	49
17	d-XY/XX	2	12	36.5	24.0	y	49

18	T. marmoratus	d-XY/XX	2	12	25.7	29.0	-	19, 34	
Chordata: Mammalia									
19	Sminthopsis crassicaudata (Marsupialia)	d-XY/XX	2	6	13.6	10.2	(y)	1	
20	Mus musculus (Rodentia)	d-XY/XX	2	19	20.9	28.9	y	23	
21	Macaca mulatta, nemestrina (Primates)	d-XY/XX	2	20	39.6	31.7	-	7, 11, 22	
22	Papio papio (Primates)	d-XY/XX	2	20	41.5	39.6	-	6, 7, 22	
Angiospermae: Dicotyledonae: Leguminosae									
23	Trigonella foenum graecum	h	4	16	21.3	21.1	(n)	7, 44	
24	Vicia faba	h	2	6	20.6	16.0	(y)	16	
Angiospermae: Monocotyledonae									
Commelinaceae									
25	Rhoco discolor	h	2	6	10.2	11.4	-	6	
Gramineae									
26	Hordeum vulgare	h	2	7	13.9	13.7	(n)	2	
27	Secale cereale	h	2	7	10.7	10.6	n	9	
Liliaceae									
28	Allium cepa	h	2	8	22.4	17.9	y	17	
29	A. consanguineum	h	2	8	21.9	17.5	y	17	
30	A. flavum	h	2	8	14.9	18.8	(y)	46	
31	A. macranthum	h	4	14	42.3	58.7	(y)	46	
32	A. nigrum	h	2	8	21.9	16.9	y	17	
33	A. pallens	h	2	8	15.0	19.4	(y)	46	
34	A. paniculatum	h	2	8	14.6	16.0	(y)	46	
35	A. ursinum	h	2	7	13.8	14.1	(y)	46	
36	Endymion nonscriptus	h	2	8	17.7	18.2	n	52	
37	Fritillaria meleagris	h	2	12	24.8	37.8	(y)	13	
38	Lilium hansonii	h	2	12	40.0	49.0	-	4	
39	L. henryi	h	2	12	41.2	44.4	(y)	13	
40	L. longiflorum	h	2	12	27.3	31.5	(y)	13	
41	L. martagon	h	2	12	36.3	41.0	(y)	13	
42	L. pardalinum	h	2	12	31.2	36.9	(y)	13	
43	L. regale	h	2	12	41.8	45.0	(y)	4, 13	
44	L. sargentiae	h	2	12	31.2	42.0	(y)	13	
45	L. speciosum	h	2	12	26.4	33.9	-	3	
46	Tulbaghia acutiloba	h	2	6	14.4	15.8	(y)	47	
47	T. leucantha	h	2	6	12.4	15.5	(y)	47	

48 <i>T. pulchella</i>	h	2	6	12.2	13.7	(y)	47
49 <i>T. violacea</i>	h	2	6	11.0	14.3	(y)	47
Orchidaceae							
50 <i>Cypripedium cordigerum</i>	h	2	10	16.4	19.7	(y)	32
51 <i>Eppactis consimilis</i>	h	2	20	25.8	27.1	(y)	30
52 <i>E. latifolia</i>	h	2	20	30.7	29.1	(y)	30
53 <i>Listera ovata</i>	h	2	17	26.9	30.3	y	48
54 <i>Neottia listeroides</i>	h	4	20	29.3	31.1	(y)	31
ACHIASMATE SPECIES							
Platyhelminthes: Turbellaria							
55 <i>Mesostoma ehrenbergii</i> (Neorhabdocoela)	h	2	5	3.0	0.0		37, 38
Insecta							
56 <i>Thericles whitei</i> (Orthoptera)	d-XO/XX	2	8	0.0	8.2		10 50
57 <i>Drosophila melanogaster</i> (Diptera)	d-XY/XX	2	4	0.0	5.0		10 43
58 <i>Allogamus auricollis</i> (Trichoptera)	d-ZW/ZZ	2	30	60.0	0.0		10 25
59 <i>Glyptotaelius pellucidus</i> (Trichoptera)	d-ZW/ZZ	2	30	35.0	0.0		10 26
60 <i>Antheraea assamensis</i> , <i>compta</i> (Lepidoptera)	d-ZW/ZZ	2	15	20.0	0.0		10 18
61 <i>Bombyx mori</i> (Lepidoptera)	d-ZW/ZZ	2	28	58.0	0.0		10 21
62 <i>Byblia lithyia</i> (Lepidoptera)	d-ZW/ZZ	2	17	17.4	0.0		10 33
63 <i>Ephestia kuehniella</i> (Lepidoptera)	d-ZW/ZZ	2	30	30.0	0.0		10 45
64 <i>Philosamia ricini</i> (Lepidoptera)	d-ZW/ZZ	2	14	22.0	0.0		10 39
Angiospermae: Monocotyledonae: Liliaceae							
65 <i>Fritillaria amabilis</i>	h	2	11	0.0	27.0		35, 36
66 <i>F. japonica</i>	h	2	11	0.0	35.2		35, 36
67 <i>F. koidzumai</i>	h	2	12	0.0	51.0		35, 36
HAPLODIPLOID SPECIES							
Insecta: Hymenoptera							
68 <i>Aphytis mytilaspidis</i>	d	2	5	0.0	5.5		42
Comments							

1-Female chiasma frequency given only as "not significantly different from the male".

2-Male chiasma frequencies at metaphase I; female value at diplotene.

3-Chiasma frequencies inferred from verbal descriptions.

4-Sex bivalent in females cannot be distinguished from at least some autosomes; assumed it had the mean chiasma frequency.

5-Male chiasma frequency for subspecies *cyreni*; female value for ssp. *apuanus*.

6-Not clear if the male chiasma frequency included the sex bivalent; subtracted 0.5 to get the autosomal chiasma frequency.

7-Induced polyploid.

8-Assumed  $n = 8$  (Ved Brat 1966 does the same).

9-Some male meiosis is abnormal, leading to unbalanced pollen.

10-Haploid numbers and chiasma frequencies for dioecious achiasmata species include the sex bivalent.