

Genotype-dependent effect of B-chromosomes on chiasma frequency in *Eyprepocnemis plorans* (Acrididae: Orthoptera)

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Abstract

In order to analyze the effect of B-chromosomes on chiasma frequency, the offspring of different females of the grasshopper *Eyprepocnemis plorans* have been studied. From the comparison between individuals of the different families having a given number of B's and between individuals with different numbers of B-chromosomes within the same family, it can be concluded that the effect of the genetic background on chiasma frequency is greater than that produced by the presence of B's, and that there is a between-families variation in the effect of B-chromosomes which, in addition, is negatively correlated with the chiasma frequency of related individuals without B's. This genotype-dependent effect of B-chromosomes is discussed.

Introduction

The possible effect of B-chromosomes on chiasma frequency has been the subject of a number of studies. Contradictory results have been obtained by different authors even within the same species (see Jones, 1975). It is well known that there are many other factors such as genotype, age and environmental conditions that have an effect on chiasma formation. The different results obtained could be due to the interaction of these factors with B-chromosomes.

Mosaics for numbers of B-chromosomes are probably the best material in which such interactions can be studied (John & Miklos, 1979). However, the low frequency of such individuals has made detailed studies impossible.

The relative effect of B-chromosomes and genetic background on chiasma frequency has been studied here by analyzing the effect of B's between and within families formed by the male offspring of individual females.

Material and methods

Thirty fertilized *Eyprepocnemis plorans* females were collected in a natural population near Daimuz (Valencia, Spain) and maintained in the laboratory in order to obtain pods. After 45 days at room temperature, pods were kept for at least 45 more days at 4 °C and then incubated at 33–35 °C until eclosion of the eggs. The offspring of each female (a 'family') was maintained separately in 50 l cages. 15 days after the appearance of the adult males, testes were fixed in acetic-alcohol 1:3. Squash preparations of the fixed material were stained following the Giemsa C-banding technique described previously (Santos & Giraldez, 1978).

Chiasma frequency was determined in the males of 12 families showing variation for the number of B-chromosomes. Four follicles per individual were analyzed scoring 10 diplotene cells per follicle. No significant differences were found between the follicles of a given individual, and the results are, therefore, given per individual. Only the chiasmata formed by the A-chromosomes were considered.

Results

In the population of Daimuz, three types of B-chromosomes have been described in *E. plorans* (Henriques-Gil *et al.*, 1982). All families reported here were of the B₁ type. One family had also the B₂-chromosome.

Figure 1 shows diplotene cells with different numbers of B-chromosomes.

Table 1 shows the mean chiasma frequency of the 87 analyzed males grouped in families. When the total cell distributions are considered, there is a significant increase in chiasmata per cell with increasing number of B's. However, there are differences in the effect of B-chromosomes when each family is considered separately. From the family analysis, three main observations can be made:

(1) There is a great variation between families in the effect of B-chromosomes on chiasma frequency. For instance, the individuals with one B-chromosome show a statistically higher chiasma frequency

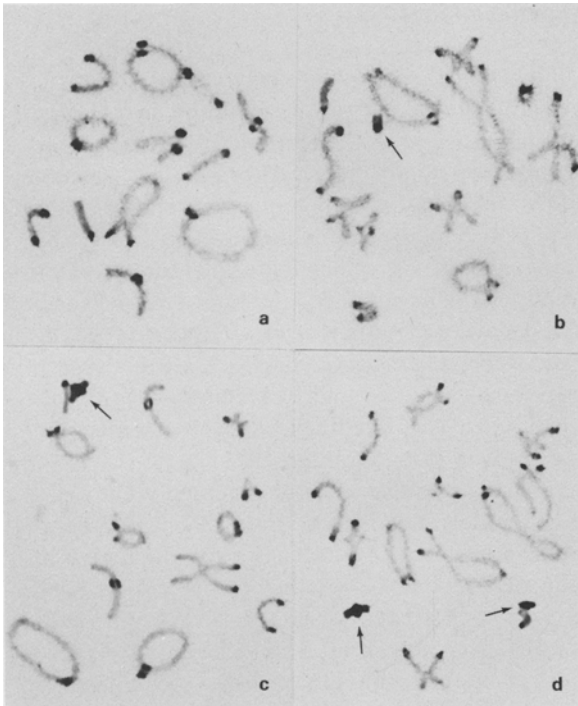


Fig. 1a-d. Diplotene cells with different numbers of B-chromosomes: (a) without B's; -(b) one B; -(c) one B-bivalent; -(d) one B-bivalent and one B-univalent. Arrows identify B-chromosomes.

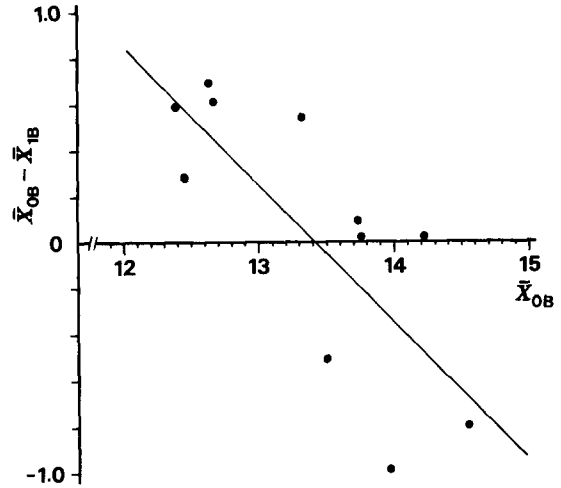


Fig. 2. The effect of one B-chromosome (the difference in chiasma frequency between individuals with 1B and those without B's) plotted against the chiasma frequency of the 0B individuals ($b = -0.60$, $t = 3.53$, $0.01 > p > 0.005$). Eleven families. Cf. Tab. 1.

than those without B's in families SD ($t = 6.37$, $0.001 > p$), F ($t = 4.39$, $0.001 > p$), G ($t = 2.91$, $0.01 > p > 0.001$), JL ($t = 4.55$, $0.001 > p$) and MC ($t = 2.77$, $0.01 > p > 0.001$). There are no significant differences in families C ($t = 0.18$, $p > 0.5$), E ($t = 0.97$, $0.4 > p > 0.2$) and J ($t = 0.11$, $p > 0.5$), and in families H ($t = 3.31$, $0.01 > p > 0.001$), K ($t = 7.52$, $0.001 > p$) and P ($t = 6.26$, $0.001 > p$) the individu-

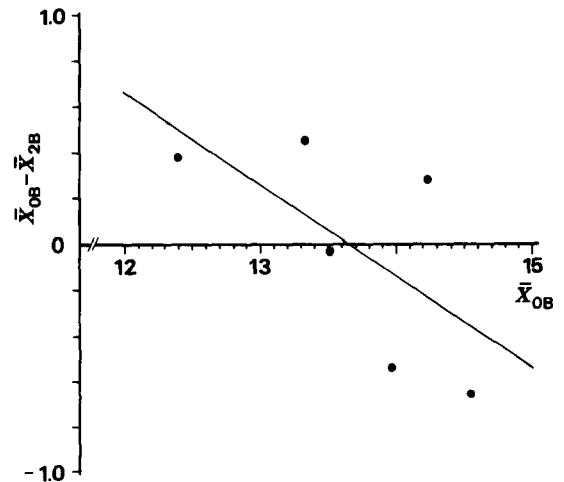


Fig. 3. The effect of two B-chromosomes (the difference in chiasma frequency between individuals with 2B and those without B's) plotted against the chiasma frequency of the 0B individuals ($b = -0.40$, $t = 1.82$, $0.2 > p > 0.1$). Six families. Cf. Tab. 1.

Table 1. The mean chiasma frequency of the 87 analyzed males grouped in families and according to the number of B-chromosomes. T: Family totals considering cell distributions. ^a Individual with 1B₁; ^b individuals with 1B₁ + 1B₂; in the remainder of the cases the B-chromosomes present are of the B₁ type.

Family	0B		1B		2B		3B	
	Male	Xta per cell	Male	Xta per cell	Male	Xta per cell	Male	Xta per cell
C	2	13.78 ± 0.14	1	13.25 ± 0.12				
	3	13.98 ± 0.15	6	14.28 ± 0.16				
	4	13.98 ± 0.15	8	14.48 ± 0.13				
	5	13.30 ± 0.15	9	13.10 ± 0.13				
	T	13.76 ± 0.08	T	13.78 ± 0.08				
SD	3	12.80 ± 0.13	1	13.78 ± 0.15				
	7	12.43 ± 0.13	2	13.93 ± 0.14				
	8	12.50 ± 0.15	4	12.63 ± 0.15				
	10	12.88 ± 0.14	5	13.05 ± 0.13				
	T	12.65 ± 0.07	T	13.34 ± 0.08				
E	1	13.40 ± 0.12	2	14.08 ± 0.14				
	4	14.58 ± 0.13	3	14.10 ± 0.15				
	5	13.18 ± 0.12	9	13.75 ± 0.12				
	6	13.80 ± 0.13	13	13.43 ± 0.13				
	T	13.74 ± 0.08	T	13.84 ± 0.07				
F	2	12.83 ± 0.14	1	13.43 ± 0.18				
	4	12.53 ± 0.11	3	13.15 ± 0.10				
	T	12.68 ± 0.08	T	13.29 ± 0.11				
G	1	12.33 ± 0.13	2	12.65 ± 0.17				
	6	12.45 ± 0.11	3	12.80 ± 0.13				
	7	12.98 ± 0.14	4	12.60 ± 0.11				
	9	12.10 ± 0.12	5	12.90 ± 0.13				
	T	12.46 ± 0.07	T	12.74 ± 0.07				
H	4	13.05 ± 0.16	6	12.75 ± 0.14	5	13.48 ± 0.15		
	7	13.98 ± 0.15	8	13.25 ± 0.13				
	T	13.51 ± 0.12	T	13.00 ± 0.10	T	13.48 ± 0.15		
J	7	14.33 ± 0.11	1	14.13 ± 0.14	4	14.25 ± 0.16		
	8	14.75 ± 0.12	2	14.15 ± 0.13	12	15.08 ± 0.17		
	9	13.88 ± 0.11	3	14.33 ± 0.12	13	14.20 ± 0.16		
	14	13.95 ± 0.12	5	14.38 ± 0.15				
	T	14.23 ± 0.06	T	14.24 ± 0.07	T	14.51 ± 0.10		
K	10	14.63 ± 0.13	4 ^a	13.43 ± 0.16	1 ^b	13.80 ± 0.16		
	11	14.48 ± 0.11	5	13.80 ± 0.13	9 ^b	14.03 ± 0.13		
			8	13.70 ± 0.15				
	T	14.55 ± 0.09	T	13.64 ± 0.09	T	13.91 ± 0.10		
JL	1	12.33 ± 0.13	2	12.93 ± 0.13	12	12.25 ± 0.13		
	10	12.48 ± 0.12	8	13.05 ± 0.14	14	13.30 ± 0.12		
	T	12.40 ± 0.09	T	12.99 ± 0.10	T	12.78 ± 0.11		
MC	6	13.33 ± 0.16	4	14.20 ± 0.14	2	13.78 ± 0.12	5	14.85 ± 0.15
	T	13.33 ± 0.16	T	13.86 ± 0.10	T	13.78 ± 0.10	T	14.85 ± 0.15
P	4	13.65 ± 0.13	2	12.48 ± 0.15	8	13.73 ± 0.14	13	13.75 ± 0.14
	5	14.28 ± 0.14	12	13.48 ± 0.15	11	13.25 ± 0.14		
	T	13.96 ± 0.10	T	12.98 ± 0.12	T	13.49 ± 0.10	T	13.75 ± 0.14
N			4	13.55 ± 0.16	1	14.15 ± 0.15	2	14.35 ± 0.15
			5	14.50 ± 0.15	3	14.65 ± 0.18	6	15.03 ± 0.22
			10	13.73 ± 0.13	9	13.53 ± 0.12	8	14.70 ± 0.18
			T	13.93 ± 0.09	T	14.11 ± 0.10	T	14.69 ± 0.11
Total cell distributions		13.39 ± 0.03		13.52 ± 0.03		13.82 ± 0.05		14.54 ± 0.08
		t ₁₋₀ = 3.29*		t ₂₋₁ = 5.59*		t ₃₋₂ = 7.66**		

* . - 0.005 > p > 0.001

** . - 0.001 > p

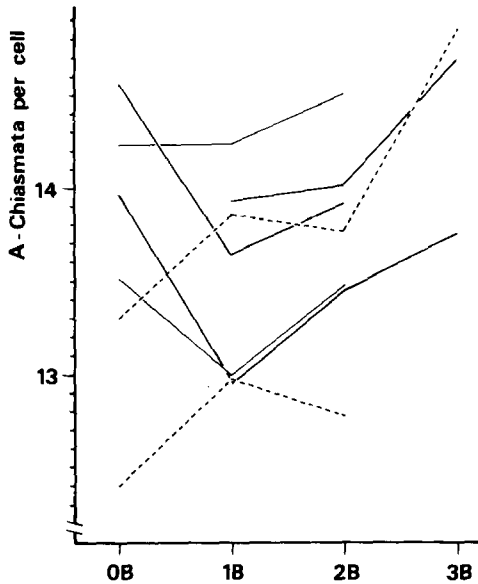


Fig. 4. Variation in chiasma frequency with respect to the number of B-chromosomes within the families having more than 1B.

als with one B-chromosome show a significantly lower frequency than those without B's.

(2) The effect of B's (the difference in chiasma frequency between individuals with 1B or 2B and those without B's) is negatively correlated (Figs. 2 and 3) with the chiasma frequency of the 0B individuals. The regression coefficients of B effect on chiasma frequency are $b = -0.60$ ($t = 3.53, 0.01 > p > 0.005; r^2 = 0.58$) for the effect of 1B and $b = -0.40$ ($t = 1.82, 0.2 > p > 0.1; r^2 = 0.45$) for 2B. In the families in which the individuals with 0B have low chiasma frequency, the presence of one or two B-chromosomes leads to an increase of chiasma frequency. No effect or even a decrease is produced in those families in which the individuals without B's show a higher chiasma frequency.

(3) Figure 4 shows diagrammatically the chiasma frequency variation with respect to the number of B-chromosomes in the families where individuals with more than one B occur: there is no consistent cumulative dosage effect of B-chromosomes within families.

Discussion

From the results shown in Table 1, comparison can be made at two levels: (1) Between families with

a given number of B's: as all individuals were subject to the same environmental conditions, these differences would be mainly due to genotypic differences; (2) Between individuals with different numbers of B's within the same family. In this case, the genotypic differences between the members of the same family are lower and differences in chiasma frequency will be mainly due to the B-chromosomes.

From these comparisons it can be concluded that both genotype and number of B's have an effect on chiasma frequency but the former is larger. For instance, the maximum difference between families with 0B is 2.15 (K and JL) whereas the maximum difference between individuals with 0 and 1B within the same family is 0.98 (P).

Probably the most important conclusion is that the effect of B-chromosomes depends on the genetic background of the individuals carrying them. This conclusion can be derived from the correlations shown in Figures 2 and 3.

In the Acrididae, the effect of B-chromosomes on chiasma frequency has been studied by several workers. An absence of effect has been found by Stephens and Bregman (1972) and John and Freeman (1975), whereas in other cases an increase of the mean chiasma frequency has been observed (John & Hewitt, 1965; Hewitt, 1976; Fletcher & Hewitt, 1980; Camacho *et al.*, 1980). In most cases, a between-individual variation has been observed, i.e., the increase in chiasma frequency associated with the presence of B-chromosomes does not mean that individuals with B's have in all cases higher chiasma frequencies than those without them in the same population.

As far as we know, the interaction between genotype and B-chromosomes has not been studied in this species. There are cases in which B-chromosomes seem to have a different effect on chiasma frequency depending on the population studied (*Myrmeleotettix maculatus*: John & Hewitt, 1965; *Phaulacridium vittatum*: John & Freeman, 1975; Westerman & Dempsey, 1977; *Eyprepocnemis plorans*: Camacho *et al.*, 1980 and this study). These differences could be explained in terms of variation in the genetic background among populations. There is also the possibility of B-chromosome differences between populations. However, as in *Myrmeleotettix maculatus* (John & Hewitt, 1965) the results of this study (Table 1, family K) indicate

that different B-chromosome types (B₁ and B₂) have a similar effect on chiasma frequency. The two B types studied here differ in the length of the euchromatic region, having the same C-heterochromatic amount (Henriques-Gil *et al.*, 1982). This agrees with the results of Ward (1973) who reported that the heterochromatic regions of the B-chromosome of maize seem to be responsible for most of its effect on recombination.

In wheat and in rye-wheat hybrids, a variation in the effect of rye B-chromosomes depending upon the A-chromosome constitution has been reported (Viegas, 1979 and 1980; Romero & Lacadena, 1980). In these cases it was suggested that rye B-chromosomes could carry both asynaptic and post-synaptic genes decreasing and increasing effective pairing, respectively. However, in *E. plorans* the possibility of the effect of B-chromosomes being due to the heterochromatin and the difficulty in establishing a relationship between effect and B-dosage are not easily explained under this hypothesis.

Nevertheless, the presence in both *Triticinae* and *Acrididae* of a genotype-dependent effect of B-chromosomes on chiasma frequency suggests that this phenomenon can be of a widespread occurrence.

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