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Population Significance of High Frequency Recessive Lethals in *Drosophila albomicans*

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Hwei-yu Chang, Shu-Fen Lan and Fei-Jann Lin (1996) Population significance of high frequency recessive lethals in *Drosophila albomicans*. *Zoological Studies* **35**(2): 138-145. The high frequency of recessive lethals on a segment of the 2nd chromosome with high inversion frequency challenged a previously suggested role of chromosome inversions in maintaining sets of coadapted genes in natural populations of *Drosophila albomicans*. A hypothesis to account for the high frequency of both recessive lethals and the inversion heterozygosity is then proposed. After an investigation of natural populations from Wulai and Kuantzuling, Taiwan, it was found that *In(2L)*B_1D_5 heterozygosity reached 0.46 and the recessive lethal frequency related to it reached 0.44. The estimated recessive lethal frequency within this inversion region was 0.37. Since *(2L)*B_1D_5 in *D. albomicans* comprises only a quarter of the 2nd chromosome, the lethal frequency in this chromosomal segment of *D. albomicans* is indeed much higher compared to other *Drosophila* species. The coexistence of high lethality and high inversion heterozygosity is in accordance with our prediction of the trapping effect of inversions for recessive deleterious alleles. The accumulation of recessive lethals causes an increase of inversion heterozygosity, and the genetic load due to the principle of segregation seems to be the real reason for inversion heterosis.

Key words: Chromosomal inversion, Esterases, Lethality, Population genetics.

Mutation introduces deleterious alleles into a population. Natural selection usually lowers the frequencies of deleterious alleles, but it can not effectively remove recessive alleles. According to the concept of mutation-selection equilibrium, recessive deleterious alleles can be maintained in a population and result in an unavoidable genetic load. Interestingly the frequency of recessive lethals varies distinctively among populations, e.g., from 0.11 to 0.45 in *Drosophila melanogaster* (Dobzhansky 1957, Salceda 1967, Yamazaki et al. 1984). The selection pressure of lethal alleles is the same (i.e., the maximum) for every population and there is no evidence to suggest different mutation rates for different populations. Therefore, it is unlikely that variation in recessive lethal frequency can be explained simply by mutation-selection equilibrium. If these populations are not under some unstable or changing conditions, then apparently the lethal frequencies are also affected by other forces. Another possible explanation for this frequency variation among populations is that these populations are not at equilibrium.

Since the discovery of inversions in salivary gland chromosomes of *D. melanogaster* by Sturtevant in 1917, numerous reports have shown that inversions are common in *Drosophila*. Their frequencies vary distinctively among populations (Dobzhansky and Sturtevant 1938). For example, a cosmopolitan inversion, *In(2L)t*, of *D. melanogaster* has heterozygosity values ranging from 0.02 to 0.34 (Sperlich and Pfriem 1986). Since the frequencies of inversions and lethality are both variable among populations, it is of fundamental importance to find stable populations with high frequencies of both inversion as well as lethals, and to investigate whether interaction between them exists.

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D. albomicans was adopted for this study because of the availability of detailed background information on its inversions (Lin et al. 1974, Lin and Chang 1986, Chang et al. 1987, Chang et al. 1988). A 1-year survey of inversions in the Wulai population showed that the $In(2L)B_1D_5$ heterozygosity fluctuated seasonally, and reached 66.1% during the winter (Chang et al. 1987). Heterosis only occurred in winter, so a satisfactory explanation for this phenomenon was sought. We have previously shown that the Wulai population is stable with linkage equilibrium, and both its inversion heterozygosity and lethality are relatively high (Chang and Lin 1995). The purpose of this study is to answer whether or not the coexistence of high lethality and high inversion heterozygosity is due to the trapping effect of inversions for recessive deleterious alleles.

MATERIALS AND METHODS

Flies

Flies of *Drosophila albomicans* were collected from Wulai, Taipei County (in July 1992) and from Kuantzuling, Tainan County, Taiwan (in May and July 1993).

A pure line was used as a chromosome extraction tool, and 2 balancer stocks with esterase markers and the B_1D_5 inversion on the left arm of the 2nd chromosome were used for maintaining recessive lethal alleles. The #0131.5 stock with F^a(N)/F^c(I) had been used in a previous study (Chang and Lin 1995), and the #0300.7 stock with F^a(I)/F^c(N) was newly established. (N) and (I) represent the standard and inverted chromosome arrangements, respectively. F^a and F^c are two *Est-F* alleles which are useful markers for identification during chromosome manipulation. The N chromosome in the #0131.5 stock contains the F^a allele but that in the #0300.7 stock the F^c allele, and likewise the I chromosome in the #0131.5 stock contains the F^c allele but that in the #0300.7 stock the F^a allele.

All stocks were reared with use of a standard corn meal medium and maintained in an environment of 22 °C and 75% relative humidity throughout the experiment. Newly emerged flies were sexed within 8 hours and kept in separate vials for 3 days before crossing.

Esterase isozyme electrophoresis and chromosome inversion analysis

The esterase isozyme patterns were electrophoretically analyzed as previously described (Chang and Lin 1990). The salivary gland chromosome preparation was also performed as previously described (Lin and Chang 1986). In some cases, both salivary gland chromosomes and isozyme electromorphs were simultaneously analyzed on the same fly (Chang and Lin 1995).

Chromosome extraction

A pure line homozygous for esterases with genotype C^sF^d(N)/C^sF^d(N) was used as a tool for chromosome extraction. *C* and *F* are 2 *Est* loci standing for *Est-C* and *Est-F*, respectively. For chromosome extraction, male flies caught from natural populations were crossed with females of this pure line stock. Their F_1 larvae were subjected to simultaneous analyses of the esterase patterns and chromosome inversions. As soon as 3rd instar larvae appeared in the medium, the wild-caught male was homogenized and its esterase patterns were determined by electrophoresis. The esterase patterns of these F_1 larvae can reveal the genotypes of the 2 chromosomes. If the male is heterozygous for any one of the 2 loci and neither of its haplotypes is the C^sF^d combination, both chromosomes can be extracted (Program I). Alternatively, if the male is homozygous for both loci, or has a C^sF^d haplotype, only one chromosome can be extracted (Program II). The *Est-F* locus was the main marker for chromosome extraction, while the *Est-C* locus was the 2nd marker if the *Est-F* locus was unable to distinguish between the 2 chromosomes from the male.

Program I: Separate pairs (ca. 30 to 40 pairs/captured male) were made from virgin F_1 flies. After F_2 larvae appeared in the medium, the esterase patterns of these F_1 pairs were analyzed. Only the pairs with heterozygotes for the same wild chromosome were saved, others were discarded. The F_2 flies from the 2 kinds of heterozygous pairs were checked for their esterase patterns. If more than 16 flies were checked and no homozygote with the wild chromosome marker was observed, then this wild chromosome was considered to contain a recessive lethal.

Program II: One F_1 male from each wild-caught male was crossed to a C^sF^d(N)/C^sF^d(N) female, and separate pairs were made from the virgin F_2 flies just as in the procedure for the F_1 generation in Program I. The subsequent procedures were the same as Program I with one generation delay and only one kind of heterozygous pair saved for each wild-caught male.

The procedure is summarized in a flow chart (Fig. 1).

Replacement of lethal alleles into balancer stocks

If a chromosome contained a recessive lethal, flies from this stock were crossed with flies from #0131.5 or #300.7 according to their chromosome arrangements and *Est-F* alleles. The lethal allele could then be maintained in a newly formed balancer stock which is heterozygous for both chromosomal arrangement and the *Est-F* locus. About 30 to 40 pairs of F_1 were made, and after the F_2 larvae appeared in the medium, the esterase genotypes of those F_1 flies were checked. Only the correct heterozygous pairs were chosen; others were discarded. The procedure is summarized in a flow chart (Fig. 2).

Complementation test

Lethal alleles maintained in balancer stocks were divided into 2 groups according to whether the location of a lethal was on the N or I chromosomal arrangement. The complementation test was performed by both intra-group (NN, or II) and inter-group (NI) crosses. The same criterion (i.e., 16 flies) was adopted for the crosses between stocks to judge allelism. An example is given in Fig. 3.

♂ Obtained from a natural population (※ and ◎ indicate 2 alleles for the locus chosen as a marker in this male)

If, for any one of the 2 *Est loci*, its 2 alleles are different from each other (i.e., ※ ≠ ◎), and neither of them is C^sF^d, then → Program I:

♂ ※◎ × ○○ ♀

↓

choose ※○ × ※○ and ○◎ × ○◎

↓ ↓

※※	※○	○○	○○	○◎	◎◎
1/4	1/2	1/4	1/4	1/2	1/4

If both loci are homologous (i.e., ※ = ◎), or there is a combination of $C^sI^{\cdot d}$ (i.e., ◎ = ○), then → Program II:

♂ ※◎ × ○○ ♀

↓

♂ ※○ × ○○ ♀

↓

choose only ※○ × ※○

↓

※※	※○	○○
1/4	1/2	1/4

Fig. 1. Males obtained from a natural population crossed with females of the extraction tool. The experiment should proceed into Program I or Program II according to the esterase genotype of these males. The expected possibility of the appearance of a homozygous offspring from a heterozygous pair is 1/4.

RESULTS

The polymorphic *Est-F* and *Est-C* loci

There are 5 alleles, named F^a, F^b, F^c, F^d, and F^o (i.e., 4 visible variants and a null form), at the esterase *Est-F* locus, and 4 alleles, named C^f, C^m, C^s, and C^n (i.e., 3 visible variants and a null form), at the *Est-C* (Fig. 4). The flies used for

A lethal allele is located on a $(2L)B_1D_5$ arrangement A with a *Est-F* marker *.

If A = N, and * ≠ *c*, then use #0131.5;
if A = I, and * ≠ *c*, then use #0300.7.

$F^*F^d \times F^aF^c$

↓

Choose only: $F^*F^c \times F^*F^c$

Discard other F_1 pairs.

If A = I, and * ≠ *a*, then use #0131.5;
if A = N, and * ≠ *a*, then use #0300.7.

$F^*F^d \times F^aF^c$

↓

Choose only: $F^*F^a \times F^*F^a$

Discard other F_1 pairs.

Fig. 2. Establishment of new balancer stocks to maintain recessive lethals extracted from the natural population.

$l_xF^a+/+F^cl_z \times l_yF^b+/+F^cl_z$

↓

$l_xF^a+/+F^cl_z$	l_xF^a+/l_yF^b+	$l_yF^b+/+F^cl_z$
1/3	1/3	1/3

Fig. 3. Allelism determined by the absence of F^a/F^b genotype in this example of a complementation test. F^a, F^b, and F^c indicate different alleles of *Est-F*; l_x, l_y and l_z indicate lethal alleles; + indicates non-lethal allele.

electrophoresis in Figure 4 were all females from 5 pure lines and 6 balancer stocks, and C^n was not shown on this gel. These balancer stocks were constructed by using lethal alleles extracted from the Wulai population. The genotypic frequencies of both the Wulai and Kuantzuling populations did not statistically deviate from Hardy-Weinberg expectations. The allele frequencies of *Est-F*^{a}, *Est-F*^{b}, *Est-F*^{c}, *Est-F*^{d}, and *Est-F*^{o} for the 158 males from the Wulai population were 0.53, 0.11, 0.27, 0.07, and 0.02, respectively. Those for the 257 males from the Kuantzuling population were 0.57, 0.16, 0.23, 0.03 and 0.01, respectively. The allele frequencies of *Est-C*^{f}, *Est-C*^{m}, *Est-C*^{s}, and *Est-C*^{n} for the 154 males from the Wulai population were 0.42, 0.28, 0.29, and 0.006, respectively. Those for the 257 males from the Kuantzuling population were 0.42, 0.24, 0.34, and 0.001, respectively.

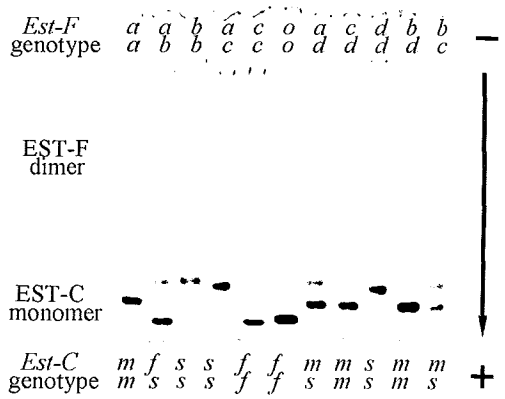

Fig. 4. Electrophoretic variants of the dimer EST-F shown in the upper zone with the genotypes indicated above them, and those of the monomer EST-C in the lower zone with their genotypes indicated below. Symbols *a*, *b*, *c*, *d*, and *o* indicate the 5 *Est-F* alleles, F^a, F^b, F^c, F^d, and *null*; *s*, *m*, and *f* indicate 3 *Est-C* alleles, C^s, C^m, and C^f, respectively.

The chromosomal inversion heterozygosity of *In(2L)B$_1$D$_5$* and the 2nd chromosome lethality in natural populations

The survey of the 2 populations (Wulai, July 1992; Kuantzuling, May and July 1993) of *Drosophila albomicans* showed that the inversion heterozygosity of *In(2L)B$_1$D$_5$* ranged from 0.43 to 0.48, that there is no significant difference among samples, and that the average weighted value based on sample size is 0.46 (Table 1). Among the 119 chromosomes extracted from the Wulai population in July, there were 62 N chromosomes and 57 I chromosomes. Twenty-five of the 62 N chromosomes and 24 of the 57 I chromosomes carried lethals. Among the 94 chromosomes extracted from the Kuantzuling population in July, there were 22 N chromosomes and 72 I chromosomes. Ten of the 22 N chromosomes and 34 of the 72 I chromosomes carried lethals. There is no significant difference between the lethalities of the N and I chromosomes. The frequency of recessive lethal alleles in the B_1D_5 region of the 2nd chromosome is 0.41 for the Wulai population and 0.47 for the Kuantzuling population, there is no significant difference between these 2 samples, and the average weighted value based on sample size is 0.44 (Table 1).

The loss of lethal alleles during maintenance

Fifty 2nd chromosomes with recessive lethal alleles were extracted from the Wulai population and maintained in balancer stocks. Examination based on the same criterion showed that after 20 generations 16% (8/50) of the lethal alleles had been lost. Forty-four 2nd chromosomes with recessive lethal alleles extracted from the Kuantzuling population were not put into balancer stocks, but maintained in stocks mixed with the C^sF^d(N) chromosome instead. Four generations later, 23% (10/44) of the recessive lethal alleles had been

Table 1. Chromosomal inversion heterozygosity of *In(2L)B$_1$D$_5$* and the 2nd chromosome lethality in *Drosophila albomicans* natural populations

Locality	Time	Inversion heterozygosity, with sample size in parentheses	Lethality, with sample size in parentheses
Wulai	July 1992	0.48 (90)	0.41 (119)
Kuantzuling	May 1993	0.44 (34)	—
	July 1993	0.43 (52)	0.47 (94)
Average (weighted)		0.46 (176)	0.44 (213)

lost. Twelve percent of the recessive lethal alleles located on the I chromosome arrangement were lost, while 55% (6/11) of those located on the N chromosome arrangement were lost.

Complementation test

A complementation test was performed by using 39 balancer stocks, each of which contained a chromosome with a recessive lethal allele extracted from the Wulai population. The balancer stocks were divided into 2 groups according to the chromosome arrangement of the lethal allele to be tested. In a total of 445 crosses, 204 were within-group crosses (i.e., N vs. N, or I vs. I) and 241 were between-group crosses (i.e., N vs. I). Three pairs of lethal alleles were found in the within-group crosses (i.e., allelism = 0.015), but none was found in the between-group crosses (i.e., allelism = 0).

DISCUSSION

Compared to our previous survey in 1989 (Chang and Lin 1990), the present study found no new allele of the *Est-F* locus in the Wulai *Drosophila albomicans* population. Basically, the *Est-F* allele composition has remained unchanged during the past several years. Furthermore, the Kuantzuling population, which had not been studied before, showed similar allelic compositions of both the *Est-F* and *Est-C* loci as those in the Wulai population. In fact, in our previous report, no genetic differentiation was detected among the *Est-F* allelic frequencies of *D. albomicans* collected from the Fenglin, Jiuntou, Shitou, and Wulai populations. These results indicate that the local populations of *D. albomicans* in Taiwan are probably homogeneous through time and spatial distribution.

The high, but expected, Hardy-Weinberg heterozygosity of $In(2L)B_1D_5$ found in the Wulai and Kuantzuling populations of *Drosophila albomicans* (Table 1) is consistent with previous studies (Chang et al. 1987, Chang and Lin 1995). In fact, the frequency of $In(2L)B_1D_5$ in the Wulai population has not significantly changed since 1977, indicating that the population is probably at equilibrium. This view is further supported by the linkage equilibrium between *Est-F* and $In(2L)B_1D_5$ (Chang and Lin 1995). These 2 genetic markers, esterase and inversion, apparently indicate that the large and stable Wulai population is a suitable population for studying the interaction of inversion and lethality.

According to chromosome extraction program I (for esterase heterozygotes), both chromosomes of the male can be extracted. However, only one chromosome can be extracted by using program II (for esterase homozygotes). In order to avoid the loss of a large proportion of chromosomes, the 2nd genetic marker *Est-C* locus was adopted to complete chromosome extraction. Only 6.8% of the chromosomes could not be extracted with 2 esterase markers instead of a 27.5% chromosome loss if only 1 marker was used for chromosome extraction.

The lethality associated with the B_1D_5 region of the 2nd chromosome is 0.44 (Table 1). This B_1D_5 region comprises only about one quarter of the 2nd chromosome. However, the average lethality of the entire 2nd chromosome of *Drosophila melanogaster* is 0.48 (Tano 1971), for *D. willistoni* it is 0.42 (Pavan et al. 1951, Prout 1952), and for *D. pseudoobscura* 0.28 (Dobzhansky 1957, Dobzhansky and Spassky 1963). Compared with these *Drosophila* species, the lethality on the 2nd chromosome of *D. albomicans* within or near the B_1D_5 region is relatively high.

There are 2 possibilities that could lead to overestimating of lethality. First, since lethality was determined by using 16 flies, it could be overestimated due to sampling error. In order to determine the effect of sampling error on lethality determination, the distribution of the order of the 1st appeared homozygote was plotted (Fig. 5). According to the regression ($y = 18.435\ e^{(-0.182\,x)}$),

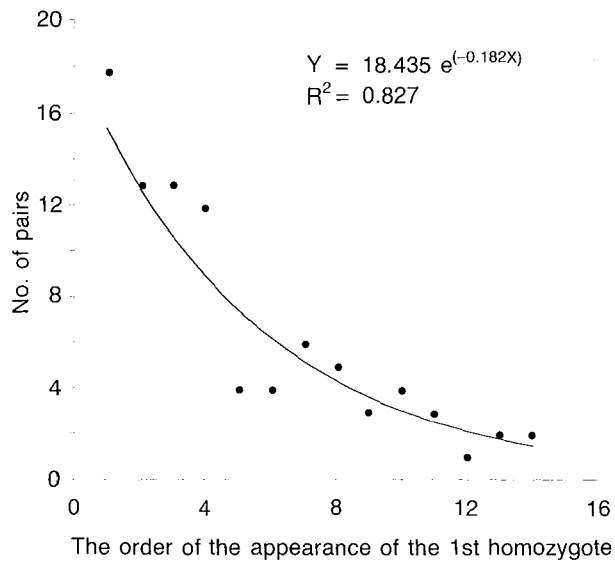

Fig. 5. The distribution of the order for the appearance of the 1st homozygote in F_2 progeny.

the confidence level of this criterion is 0.95. Thus, the effect of sampling on the value of lethality was very small. Second, overestimation of lethality could be due to linkage. Among the lethal alleles maintained in balancer stocks, 16% were lost after 20 generations. These 16% vanished alleles include the misjudged ones and those recessive lethal alleles outside the inversion loop. Our present results show that if the lethal alleles extracted from the Kuantzuling population are not kept in balancer stocks immediately, 55% of the lethal alleles located on the N chromosome arrangement are lost after 4 generations. Alternatively, only 12% of the lethal alleles located on the I chromosome arrangement were lost after the same period of time. These results indicate that an inversion loop could effectively maintain lethal alleles in our balancer stocks, whereas the allele located outside the inverted region could be lost. If alleles possibly misjudged or located outside the B_1D_5 region are excluded, the corrected lethality would become 0.37, which is still relatively high for only one quarter of the 2nd chromosome.

Few reports have evaluated the relationship between chromosomal inversions and lethality in natural populations (Yamazaki et al. 1984, Kim and Sung 1991). However, their study populations were not stable, according to the changing frequencies through time. In the present study, among the 241 between-group crosses no allelism was found, but 3 pairs were found among the 204 within-group crosses. These results indicate that N and I chromosomes can be differentiated by their accumulation of different sets of lethal alleles. This phenomenon may simply be due to heterozygous inversion inhibiting recombination within the inverted region. Therefore, lethal alleles accumulated within this region on the N chromosomes are different from those within the same region on the I chromosomes. The accumulation of different lethal alleles may also result in inversion heterosis in the winter population at Wulai (Chang et al. 1987), because inversions may trap recessive deleterious alleles and cause higher mortality of homozygotes than of heterozygotes. This result does not rule out the possibility that inversions may maintain a set of coadapted genes by the aid of recombination inhibition (Dobzhansky 1951) and result in heterosis. However, it is hard to explain why the coadapted genes only worked in winter but not in summer.

Although the within-group allelism is indeed higher than that of the between-group as predicted, the 0.015 allelism is much lower than in some natural populations as well as in laboratory-maintained populations (Salceda 1967, Yamazaki et al. 1986). This can easily explain why heterosis does not exist in the large summer population, a fact which can not be explained by the coadapted gene hypothesis. Under the condition of high lethality and equal numbers of N and I chromosomes, the extremely high heterozygosity (0.66) in winter (Chang et al. 1987) indicates small-population and inbreeding effects. Begon et al. (1985) have shown the accumulation of limited recessive lethals with high allelism in a population after a bottleneck. But the within-group low allelism indicates a large stable population. This conflict suggests that there was more than one population at Wulai in winter. Heterosis was found within each small subpopulation because of the high lethality.

A hypothetical scenario was proposed in our previous study (Chang and Lin 1995), but it did not explain the maintenance of variability after a single population underwent flush-crash cycles. An improved scenario is stated here based on new findings.

Hypothetical process:

1. Inverted (I) chromosomes occur in a population as heterozygotes (NI) at low frequency.
2. During the winter, population size decreases and many small sub-populations are formed. Within each sub-population, bottleneck effects occur, and the frequency of heterokaryotypes increases due to inbreeding depression. Inbreeding depression is a genetic load for an outbreeding diploid bisexual population because of an unavoidable accumulation of recessive deleterious alleles in the gene pool.
3. During the summer, all sub-populations merge into a large population and the increased heterokaryotypic frequency influences the lower I chromosome frequency relatively more than the higher N chromosome frequency. Therefore, the I chromosome frequency increases.
4. More sub-populations contain the I chromosomes during the following winter. The frequency change continues until the frequencies of N and I chromosomes became even.
5. The cycles of winter subtraction and summer expansion are repeated year after year. The selection pressure in winter causes partitioning of lethal loci on N and I chromosomes, and, therefore, the differentiation of these 2 chromosome groups. Recessive lethal alleles within the inversion region remain heterozygous. The

inversion heterozygosity increases due to the increase of recessive lethals on both chromosome arrangements.

6. Allelism of lethality is kept low because different winter sub-populations keep different recessive lethal alleles. Natural selection can not keep the total lethality of the inverted region at low frequencies anymore because of the protection of the inversion heterozygotes.

According to our hypothesis, both chromosomal structure (i.e., inversion) and populational structure (i.e., patchy small winter sub-populations) are necessary to cause high lethality and low allelism in *D. albomicans* natural populations. This hypothesis may explain the high variation of inversion frequencies among different populations in other species if they do not have repeated subtraction-expansion cycles. It can also explain the "cage effect" of losing inversions in large population cages (Inoue and Watanabe 1992).

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紅果蠅(*Drosophila albomicans*)高頻率隱性致死因子之族群意義

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紅果蠅(*Drosophila albomicans*)第二對染色體左臂具有高頻率逆位的B_1D_5區段，也同時擁有較高的致死因子頻率。這個事實讓我們開始質疑以往認爲染色體逆位有扣住一組組彼此配合良好的基因之功能。本文提出一個“陷阱”假說來解釋爲何族群中會同時存在高隱性致死因子頻率與高異結合逆位頻率。本文報告烏來和關仔嶺兩地的紅果蠅自然族群之染色體逆位$In(2L)B_1D_5$的平均異結合型比率高達0.46，而隱性致死因子的頻率則高達0.44，估算確實位於逆位區段的隱性致死因子的頻率爲0.37。由於B_1D_5區段僅佔第二對染色體的四分之一，相較於其它果蠅種類，其頻率顯然是高出許多。根據陷阱假說，隱性致死因子的累積是造成異結合型頻率增高的原因，而異結合型的自由分離(Principle of segregation)與配子的重組所導致的遺傳負荷(Genetic load)才是染色體逆位異結合型優勢(Heterosis)的眞正原因。高隱性致死因子頻率與高染色體逆位頻率的共存符合這個假說的預期。

關鍵詞：染色體逆位，酯酶，致死因子頻率，族群遺傳。

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