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# INTERSPECIFIC LABORATORY COMPETITION OF THE RECENTLY SYMPATRIC SPECIES *DROSOPHILA SUBOBSCURA* AND *DROSOPHILA PSEUDOOBSCURA*

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*Abstract.*—*Drosophila subobscura* and *D. pseudoobscura* are closely related species coexisting on the West Coast of North America, which was recently colonized by *D. subobscura*. In competition experiments with overlapping generations, *D. subobscura* is eliminated by *D. pseudoobscura* in a few generations at all four temperatures and two initial frequencies tested. Yet in one-species cultures, *D. subobscura* thrives at all experimental conditions. Single-generation competition experiments reveal lower survivorship and productivity of *D. subobscura* at all temperatures and frequencies. Productivity per female is dependent on the initial frequencies: greater for *D. subobscura* as its initial frequency becomes higher, but lower for *D. pseudoobscura* as its frequency becomes higher. Strains of *D. subobscura* from three disparate geographic origins yield similar results.

*Key words.*—Colonizing species, competition between species, *Drosophila pseudoobscura*; *Drosophila subobscura*, relative fitness.

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Species colonizing new habitats provide natural experiments in evolution, and recent colonizations allow for the study of evolution in action. *Drosophila subobscura*, an endemic Palearctic species, offers the opportunity to study a very recent colonization. It was found for the first time in South and North America in 1978 and 1982, respectively, and thereafter spread very quickly in both hemispheres (Prevosti et al. 1989). The origin of the colonizers is unknown, although there is evidence that the colonization of both hemispheres derives from the same original population (Latorre et al. 1986; Prevosti et al. 1988; Rozas and Aguadé 1991; Mestres et al. 1992; Balanyà et al. 1994).

An important difference between the two hemispheres is the absence in South America of endemic species closely related to *D. subobscura*, whereas several species of the *obscura* group are endemic to North America. *Drosophila pseudoobscura* is the most widespread of the Nearctic *obscura* group species along the West Coast of North America (Buzzati-Traverso and Scossiroli 1955; Prevosti et al. 1989); and it is the only abundant representative of the *obscura* group whose distribution range in North America includes that of *D. subobscura*.

The *obscura* group species are morphologically very similar to one another. They are generalists in their feeding habits (Shorrocks 1982), although the major feeding and breeding resources are unknown (Carson et al. 1956; Spieth 1987).

However, a correspondence analysis, based on drosophilids collected over fermented banana bait in three locations of California, has revealed ecological similarities, expressed as seasonal abundance, between the colonizer *D. subobscura* and the Nearctic members of the *obscura* group (Pascual et al. 1993).

The rapid spread of *D. subobscura* in North America raises the question of whether this species directly competes in nature with the native *obscura* group species. In this paper, we study in the laboratory the competitive ability between *D. pseudoobscura* and *D. subobscura*. If there is significant substrate overlap between the two species, *D. subobscura* might be favored in some laboratory competition experiments, since it outnumbers *D. pseudoobscura* in certain localities or certain seasons. We analyze different temperatures, frequencies, and densities that might favor one or the other species and try intermediate frequencies and temperatures that might facilitate the coexistence of both species in the laboratory. Finally we analyze different fitness components, such as survivorship and productivity, to ascertain which ones, if any, might be responsible for the success of one or the other species in the laboratory experiments.

## Materials and Methods

### *Strains of Flies*

The three *D. subobscura* strains used were collected in Eureka (40°48′N), Davis (38°32′N), and Gilroy (37°N), California, and the *D. pseudoobscura* strain was collected in Gilroy. Both species coexist in all three localities, although at different frequencies since they present an opposite geographical cline of abundance, with *D. subobscura* being more abundant in Eureka (Pascual et al. 1993). Each strain was established with the first-generation progeny of at least 20 wild females and was maintained in the laboratory at 18°C by mass culture. The experiments started immediately after the establishment of the strains.

### *Competition Experiments*

Competition between *D. subobscura* and *D. pseudoobscura* is studied with two kinds of experiments, Type 1 and Type 2 (Ayala 1971; Ayala et al. 1973).

#### *Type 1*

In one-species populations, Type 1 experiments estimate the carrying capacity (mean number of adults that the system can support), productivity (mean number of new adults emerging weekly in the cultures), and survivorship (mean frequency of surviving adults after one week). In two-species populations this technique, in addition, estimates the point of stable equilibrium between the two species, if they coexist.

Adult flies were introduced into a half-pint culture bottle with a measured amount of food (standard *Drosophila* culture medium); egg laying was allowed for seven days. At the end of the first and each subsequent week, the adult flies in the population were anesthesized, counted by sex and species, and transferred to a new culture with fresh medium. When adult flies began to emerge in the cultures where the eggs had been laid, the flies were collected, counted, and added to the culture containing the adult population on the same day when the adult population was censused. The cultures were discarded seven to eight weeks after the adult flies had been first introduced, depending on the temperature, to make sure that flies from a second generation were not emerging in a given bottle. The populations were maintained at 16°C, 18°C, 20°C, and 22°C, with a light/dark cycle of 12 hours, except for the 20°C experiments, which for practical reasons were performed under constant light. We chose 18°C and 22°C because they are optimal laboratory temperatures for maintaining stocks of *D. subobscura* and *D. pseudoobscura*, respectively (Prevosti et al. 1987). We selected 16°C because *D. subobscura* apparently is better adapted to cool environments, and 20°C because it is an intermediate temperature between the two optima. The two-species populations were started at two different initial frequencies of each species (20% and 80% of *D. subobscura*) and allowed to follow their own course for many generations. The logarithm of fitness of *D. subobscura* relative to *D. pseudoobscura* has been estimated by the slope of the regression of the (logarithm) ratio of the two species through time (Ayala 1969). The regression lines of the experiments have been compared by means of a multiple regression analysis. The residuals fit a normal distribution, as determined with a normal probability plot. The *D. subobscura* strain used in these experiments was from Eureka.

#### *Type 2*

Type 2 experiments measure the change in numbers over a short time interval, which allows many replicates. A specified number of adults were allowed to lay eggs. After one week the survivors were counted giving an estimate of the survivorship. The adults emerging from the culture were then recorded at weekly intervals over the following seven to eight weeks to obtain the complete first-generation progeny, which constitutes the productivity. The populations were started at two different densities (200 and 600 individuals), at three initial frequencies of the two species (20%, 50%, and 80% of *D. subobscura*), and were maintained at two temperatures, 18°C and 22°C. Twelve replicates were carried out for each experimental condition. The data in survivorship and in productivity per female were normalized prior to comparing the differences between species, densities, and temperatures by an ANOVA in the one- and two-species cultures. The probabilities were adjusted by a sequential Bonferroni technique (see Rice 1989), even though the Bonferroni correction may be overly conservative (Simes 1986). Productivity and survivorship probabilities in one- and two-species cultures were analyzed separately.

## Results

Using the serial-transfer Type 1 technique, *D. subobscura* was eliminated from all two-species populations within a short period (Fig. 1). Competitive performance did not increase at 20°C and constant light, although the sexual activity of *D. subobscura* is light dependent (Rendel 1945), while *D. pseudoobscura* can mate in the dark (Wallace and Dobzhansky 1946). The logarithm of the relative fitness was not significantly different between the species for any of the eight

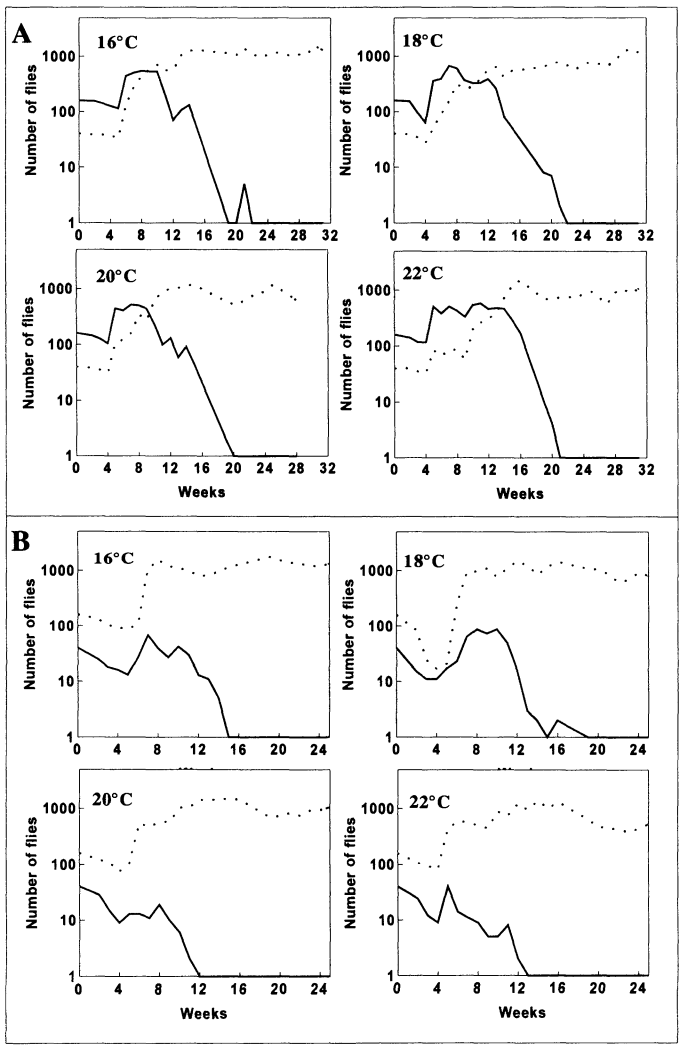


FIG. 1. Results of the competition between *Drosophila subobscura* (solid lines) and *D. pseudoobscura* (dashed lines) at different temperatures. The initial frequency of *D. subobscura* is 80% (A) and 20% (B).

conditions at which competition was studied ($F = 1.46$, $P = 0.1903$), which indicates that over the duration of the experiments the competitive ability of the two species did not vary as a function of temperature and initial frequency. The poor competitive performance of *D. subobscura* cannot be attributed to unsuccessful adaptation to laboratory conditions, as shown by the one-species data (Table 1). In one-species cultures, *D. subobscura* exhibited significantly higher carrying capacity and productivity than *D. pseudoobscura* at 18°C and at 22°C, but similar at 16°C, as shown by the Mann-Whitney *U*-test. Survivorship was similar for both species at all temperatures.

Type 2 experiments were started using the same strains as Type 1. Type 2 cultures were maintained at 18°C and 22°C, the two temperatures at which *D. subobscura* performed best relative to *D. pseudoobscura* in Type 1 experiments. Two densities were investigated, 200 individuals (low density), which was the initial density at which the Type 1 experiments had been started, and 600 individuals (high density), which was close but did not exceed the carrying capacity of either species as revealed by the one-species populations in Type 1 experiments.

In the one-species cultures survivorship was similar between the two species, but was not significantly impacted by temperature or density (Table 2). In the two-species cultures, *D. pseudoobscura* had consistently higher survivorship than *D. subobscura*, and both species performed better at low than at high density. Temperature did not significantly influence survivorship.

The mean number of descendents per female (productivity per female) is plotted for each experimental condition in Figure 2. In monospecific cultures, productivity was similar between both species. In mixed populations the differences in productivity between species were always significant, since *D. pseudoobscura* produced more progeny per female under all conditions. Productivity per female was affected by density, so that more progeny per female were produced at low density in either the one- and two-species cultures. Temperature yielded significant differences only at low density. In the monocultures the productivity of both species was higher at 22°C, and in the two-species cultures *D. subobscura* had higher productivity at 18°C, while *D. pseudoobscura* had higher productivity at 22°C. Differences in productivity among the three initial frequencies were statistically significant in all conditions of density and temperature for both species, except for *D. subobscura* at 22°C and high density. In *D. pseudoobscura* the number of progeny per female was always higher in low frequency cultures, while in *D. subobscura* it was higher in high frequency cultures (Fig. 2). Productivity was thus frequency dependent and showed an opposite trend for the two species.

The possible effect of the population from which the experimental strains originated has been tested analyzing two other *D. subobscura* strains, one from Davis and one from Gilroy. All the experiments comparing the three strains were maintained at 18°C, since productivity of *D. subobscura* from

TABLE 1. Mean and standard error for population parameters in continuous (Type 1) one-species cultures. *N* is the carrying capacity, or average number of adults; productivity is the number of newly emerged adults per culture; survivorship is the percent surviving adults after one week.

| | *D. subobscura* | | | *D. pseudoobscura* | | |
|---|---|---|---|---|---|---|
| | *N* | Productivity | Survivorship (%) | *N* | Productivity | Survivorship (%) |
| 16°C | 1268 ± 76 | 328 ± 37 | 73.7 ± 1.7 | 1203 ± 35 | 380 ± 35 | 72.0 ± 2.8 |
| 18°C | 1231 ± 59 | 402 ± 41 | 76.8 ± 2.5 | 874 ± 57 | 287 ± 31 | 69.3 ± 3.4 |
| 20°C | — | — | — | 960 ± 70 | 296 ± 32 | 71.1 ± 2.6 |
| 22°C | 981 ± 82 | 354 ± 41 | 73.9 ± 5.1 | 785 ± 51 | 246 ± 26 | 71.5 ± 2.3 |

TABLE 2. Differences in survivorship and productivity per female between *D. subobscura* and *D. pseudoobscura* at low and high density and low and high temperature. An ANOVA was performed on normalized data; the factors considered are species, density, and temperature. In the two-species cultures a nested analysis within initial frequency is used to estimate significance. D = initial density.

| Factor | Conditions | | One-species | | Two-species | |
|---|---|---|---|---|---|---|
| | | | Survivorship | Productivity | Survivorship | Productivity |
| Species | D = 200 | 18°C | −0.096 | 0.732 | −0.098* | −7.197** |
| | | 22°C | −0.039 | 1.430 | −0.146** | −9.437** |
| | D = 600 | 18°C | −0.001 | 0.008 | −0.192** | −2.059** |
| | | 22°C | 0.003 | −0.136 | −0.129* | −1.732** |
| Density | *subobscura* | 18°C | 0.044 | 1.291 | 0.183** | 0.828** |
| | | 22°C | −0.023 | 4.168** | 0.170 | 0.419** |
| | *pseudoobscura* | 18°C | 0.139** | 0.567 | 0.089** | 5.966** |
| | | 22°C | 0.019 | 2.602** | 0.187** | 8.124** |
| Temperature | *subobscura* | D = 200 | 0.062 | −3.018** | 0.023 | 0.395** |
| | | D = 600 | −0.005 | −0.141 | 0.010 | −0.014 |
| | *pseudoobscura* | D = 200 | 0.119* | −2.320** | −0.025 | −1.845* |
| | | D = 600 | −0.001 | −0.285 | 0.073 | 0.313 |

* $P < 0.05$, ** $P < 0.001$ (Bonferroni-corrected probabilities).

Eureka in the two-species populations was higher at 18°C than at 22°C. The mean survivorship and the productivity per female, for each strain separately, are given in Table 3. For any density or initial frequency, no differences have been detected among strains as shown by an analysis of variance of the normalized data. The probabilities have been adjusted by a sequential Bonferroni technique.

## DISCUSSION

*Drosophila pseudoobscura* in the laboratory outcompetes *D. subobscura* at all temperatures and at all initial frequencies tested, with *D. subobscura* being completely eliminated in two to four generations in the serial-transfer Type 1 experiments. Yet, in one-species cultures, both species do quite well, and *D. subobscura* scores as well as or better than *D. pseudoobscura* at all temperature regimes and with respect to the three parameters measured: carrying capacity, productivity, and survivorship. As revealed by the serial-transfer Type 2 experiments, the survivorship and productivity of *D. subobscura* is severely affected in the two-species populations at all temperatures and densities analyzed.

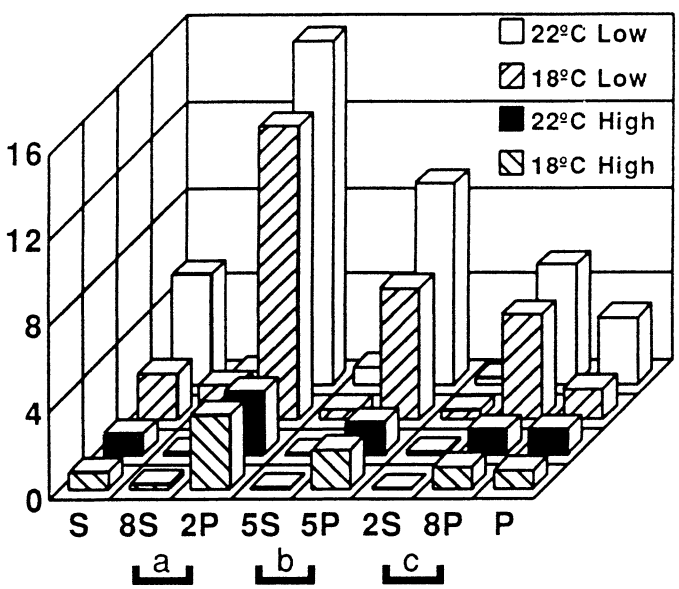


FIG. 2. Mean number of progeny per female in Type 2 experiments at different temperatures (18°C and 22°C), initial densities (high = 600 and low = 200 individuals) and frequencies (a = 80%, b = 50%, and c = 20% *Drosophila subobscura*). S = *D. subobscura* and P = *D. pseudoobscura*.

The poor competitive performance of *D. subobscura* with respect to *D. pseudoobscura* may be attributable to several factors. The larval development of *D. subobscura* is three to nine days shorter than that of *D. pseudoobscura* at 13°C and 18°C, but two days longer at 23°C (Orengo and Prevosti 1994). Because no differences between temperatures were detected in our results, the rate of development is unlikely to account for the outcome of the competition in this case. Negative effects of larval diffusible metabolites have been demonstrated for various *Drosophila* species (e.g., Weisbrot 1966; Joshi and Thompson 1995), including *D. subobscura* competing with different autochthonous Chilean species (Budnik and Cifuentes 1989). Orengo and Prevosti (1994) found that *D. subobscura* was less viable than *D. pseudoobscura* in either monospecific or mixed larval cultures. However, each species increased its viability in the mixed larval cultures and thus larval metabolites cannot explain the marked decrease in the productivity of *D. subobscura*. Considerable variation in fecundity between strains, between females, and from one day to the next was observed in *D. subobscura* (Nogués 1976) and *D. pseudoobscura* (Nickerson and Druger 1973). These authors reported higher values in the mean daily egg production per female, earlier and longer lifetime egg production, and longer lifespan for *D. pseudoobscura* than for *D. subobscura*. These factors could explain the rapid increase of *D. pseudoobscura* in Type 1 experiments. Productivity in *D. subobscura* increases with initial frequency, while in *D. pseudoobscura* it is inversely related to initial frequency. A few *D. pseudoobscura* in the cultures are enough to decrease greatly the number of progeny per female of *D. subobscura*. Thus adult interspecific interactions are more important in *D. subobscura*, while intraspecific interactions are limiting the number of progeny in

TABLE 3. Mean survivorship and productivity per female for the two species in competition and *D. subobscura* in single-species experiments. The *D. subobscura* data are for three strains from different geographic origins. Standard errors are given in parentheses.

| | | | Survivorship | | | Productivity | | |
|---|---|---|---|---|---|---|---|---|
| Density | Species | Frequency | Eureka | Davis | Gilroy | Eureka | Davis | Gilroy |
| 200 | *subobscura* | 80% | 0.897 (0.017) | 0.872 (0.019) | 0.855 (0.021) | 1.717 (0.247) | 0.801 (0.236) | 1.543 (0.401) |
| | *pseudoobscura* | 20% | 0.925 (0.018) | 0.910 (0.031) | 0.948 (0.015) | 12.980 (1.640) | 9.315 (1.087) | 11.645 (0.791) |
| 600 | *subobscura* | 80% | 0.701 (0.025) | 0.721 (0.044) | 0.714 (0.031) | 0.198 (0.049) | 0.453 (0.102) | 0.420 (0.032) |
| | *pseudoobscura* | 20% | 0.829 (0.023) | 0.878 (0.024) | 0.850 (0.024) | 3.557 (0.402) | 3.794 (0.368) | 4.155 (0.550) |
| 600 | *subobscura* | 20% | 0.561 (0.042) | 0.590 (0.073) | 0.530 (0.072) | 0.023 (0.016) | 0.075 (0.028) | 0.110 (0.061) |
| | *pseudoobscura* | 80% | 0.822 (0.010) | 0.855 (0.023) | 0.848 (0.030) | 1.051 (0.119) | 1.044 (0.080) | 1.238 (0.191) |
| 200 | *subobscura* | 100% | 0.854 (0.036) | 0.798 (0.036) | 0.797 (0.038) | 2.113 (0.444) | 2.407 (0.659) | 2.363 (0.691) |
| 600 | *subobscura* | 100% | 0.810 (0.026) | 0.802 (0.040) | 0.749 (0.025) | 0.822 (0.103) | 1.335 (0.165) | 0.919 (0.118) |

*D. pseudoobscura*. Lower fecundity and viability of *D. subobscura* due to adult interspecific interactions in the two-species populations are suggested by observations from cactophilic colonizing species (Krebs and Barker 1991), in which exclusion resulted after a few generations in Type 1 experiments.

Laboratory cultures containing two species represent simplified artificial conditions that force the larvae of different species into close proximity with each other. The extent to which larvae of these species compete for a shared substrate in nature, however, is unknown. Although both species have been reared in small numbers from a great variety of similar substrates, the major breeding resources of *D. subobscura* and *D. pseudoobscura* remain unidentified. There are no communities sampled in which both species are common; rather, the relative abundances of the two species (i.e., their frequencies among all Drosophilids) are negatively correlated (Pascual et al. 1993). Until the early 1980s, *D. pseudoobscura* was the most abundant *Drosophila* species in natural habitats in the western United States, except in hot deserts, in mountains at high elevations, and in the humid forests of the Pacific Coast from San Francisco Bay northward (Dobzhansky 1965). It is in this humid area that *D. subobscura* now has its most flourishing populations. *Drosophila pseudoobscura* is present only at low densities in human-modified environments (Dobzhansky 1965), whereas *D. subobscura* has been extensively collected in the backyards of houses and urban parks in different localities of the West Coast of North America. Microhabitat differences in nature are not inconsistent with our laboratory results in that the colonization success of *D. subobscura* may not reflect enhanced competitive activity relative to *D. pseudoobscura*. At the time when we collected the flies used in our experiments, the two species had coexisted for only a short time; only about 10 years had elapsed since *D. subobscura* had colonized these localities. It is, of course, possible that *D. subobscura* may be evolving over time an increase in competitive ability as a result of its interaction with *D. pseudoobscura*, as observed in the laboratory between *D. simulans* and *D. funebris* (Mitchell and Wallace 1991).

Perhaps common breeding substrates do not exist for *D. subobscura* and *D. pseudoobscura*, so that in the wild there is no larval competition between the two species. Some effort should be devoted to searching for *D. subobscura* breeding resources in North America. If it can be shown that there is no substrate overlap between these two species, this could account for the colonizing success of *D. subobscura*. The nature and scope of ecological interactions between these two species in North America, and the evolutionary implications of those interactions, remain to be determined.

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# POLYMORPHISM REGENERATION FOR A NEUTRALIZED SELFISH B CHROMOSOME

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*Abstract.*—Long-run evolution of B chromosomes is mainly made up by an evolutionary arms race between these selfish genetic elements and the standard genome. The suppression of B drive is one of the clearest expressions of genome defense against B chromosomes. After drive neutralization, the B is condemned to extinction unless a new variant showing drive can emerge and replace it. This paper reports the first empirical evidence for the substitution of a neutralized B variant by a new selfish B variant. Such a polymorphism regeneration has recently taken place in a natural population of the grasshopper *Eyprepocnemis plorans*.

*Key words.*—B chromosomes, *Eyprepocnemis plorans*, parasitic, selfish.

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The most widely accepted evolutionary view of B chromosomes states that they are selfish genetic elements. That is, they usually show drive mechanisms (Jones 1991) that enable their persistence in natural populations despite their detrimental effect on individuals that carry them. The standard selfish theory predicts that a B chromosome polymorphism will reach equilibrium between two counteracting forces: B drive and detriment to individual fitness (Jones 1985; Shaw and Hewitt 1990; Beukeboom 1994). However, the emergence of drive-suppressor genes in the A genome may upset this equilibrium, making the B chromosome neu-

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