

DEVELOPMENTAL STABILITY OF INTERSPECIES HYBRIDS AMONG *DROSOPHILA MELANOGASTER*, *D. SIMULANS* AND *D. MAURITIANA* (DIPTERA: DROSOPHILIDAE)

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Abstract

Interspecies hybridization is expected to cause developmental instability (DI) as a consequence of outbreeding depression and genomic stress. The variability of fluctuating asymmetry (FA) of bilaterally symmetrical organs can accompany such stress conditions and change from parental individuals to hybrids. The aims of the present study were to estimate, under laboratory conditions, the degree of prezygotic reproductive isolation among three sibling *Drosophila* species, *D. simulans*, *D. mauritiana* and *D. Melanogaster* and to estimate the effects of interspecies hybridization on wing FA.

The results show that *D. mauritiana* females are the most discriminating toward males from other species, whereas *D. simulans* females are the least discriminating and successfully give progeny of both sexes with both other species. *D. melanogaster* females give only female progeny with males of the other two species.

Interspecies hybridization changes DI, but it is species-, sex-, and trait-specific. Our data support the heterozygosity hypothesis only in the case of the significant decrease of FA in wing width of female hybrids obtained from the *D. simulans* x *D. melanogaster* cross. Most of the obtained hybrids in our experiments show increases in FA due to disturbed coadaptive inter-allelic balances within the genome of each species, which is in favour of the coadaptation hypothesis.

KEY WORDS: fluctuating asymmetry, developmental stability, *Drosophila*, coadaptation, heterozygosity, interspecies hybridization

Introduction

Interspecies reproductive isolation is determined by pre- and postzygotic mechanisms. Complete reproductive isolation would enable rapid divergence into separate genotypic clusters, but reproductive isolation among many taxa considered as "species" is incomplete (DOBZHANSKY, 1937; MAYR, 1963). Hybrid sterility is one of the postzygotic isolation mechanisms, and occurs in the progeny of interspecies mating. It usually affects males first, which is known as "Haldane's rule", with a still unclear genetic background (HALDANE, 1922; COYNE & ORR, 1998).

A large part of the studies of hybrid unfitness deal with sibling *Drosophila* species and reveal the genes responsible for hybrid incompatibility (reviewed in MALLETT, 2006). Crosses among *D. simulans*, *D. mauritiana*, and *D. sechellia* showed that interaction of X and Y chromosomes, and not disbalance of X, is associated with hybrid sterility (COYNE, 1989). Studies of hybrid sterility of *D. pseudoobscura* and *D. virilis* conclude that all chromosomes except Y affect male sterility. Some results obtained with *D. virilis* subgroup showed that the interaction of autosomes with Y chromosomes affects hybrid sterility (HEIKKINEN & LUMME, 1999). Maternal effect was considered as well, in the same paper.

Regardless of the chromosomes involved, the hybridization among individuals from different species and/or populations disturbs the coadapted gene complexes, but also increases heterozygosity in a part of the genome. According to two major hypotheses, the developmental stability of the genotype can be either due to the increase of heterozygosity, and/or is the result of the balanced genetic complexes during species (population) evolution (VOLLESTAD *et al.*, 1999; ALBERT & AUFRAY, 2003).

Interspecies hybridization is expected to cause developmental instability as a consequence of outbreeding depression and genomic stress. The variability of fluctuating asymmetry (FA) of bilaterally symmetrical organs can accompany such stress conditions, and change from parental individuals to hybrids. Numerous studies on different taxa were aimed at revealing the pattern of the DI change in interspecies hybrids (reviewed in ALBERT & AUFRAY, 2003). However, the relative importance of coadaptive gene arrangements and/or heterozygosity regarding DI remains unclear. As each half of the hybrid genome comes from different parental species, the hybrid progeny is expected to have higher heterozygosity and, thus, lower FA than the parental pair, if the heterozygosity hypothesis is true. If the coadaptation hypothesis is true, the FA of the hybrids increases due to the disturbed coadaptive inter-allelic balances within each species' genome.

The aims of the present study were: 1) to estimate the degree of prezygotic reproductive isolation among three sibling *Drosophila* species – *D. simulans*, *D. mauritiana* and *D. melanogaster* in laboratory conditions and 2) to estimate the effects of interspecies hybridization on wing fluctuating asymmetry of the obtained hybrids.

Material and Methods

Long established laboratory lines of three *Drosophila* species were used in the present experiments: *D. simulans* (with the eye colour marker "white", provided by N. JUNAKOVIC), *D. mauritiana* (provided by N. JUNAKOVIC), and *D. melanogaster* (Canton-S).

In order to measure the degree of reproductive isolation, individual matings were set between each pair of species, in both directions (both sexes from each species were used in the combinations). This way, nine

combinations were made, including intraspecies crosses. All cultures were reared, and matings were done at 23°C, on the standard medium for *Drosophila* (9% sugar, 10% cornmeal, 2% agar, and 2% yeast, with nipagine as mold inhibitor). Prior to mating, virgin flies were collected and males kept individually, females in groups of five. Individual matings of 100 pairs were done per combination. Pairs were allowed five days to mate, then both wings of parental flies were cut and prepared on a slide to be measured for width and length. The percentage and phenotype of hybrids was recorded with respect to sex and sterility. All viable hybrids were backcrossed to each of the parental species in order to assess hybrid sterility. After such crosses, ovaries from the females that gave no progeny were additionally dissected to determine hybrid dysgenesis.

Fluctuating asymmetry was measured on all of the obtained hybrids, up to 50 individuals. The left and right wings from each fly were cut and prepared on a slide for measurement. The wing length was taken as the distance from the intersection of the third longitudinal vein with the anterior crossvein to the wing tip where the third vein ends. The wing width was taken as the distance between the ends of the second and the fifth longitudinal veins. Measurements were made under a binocular microscope, with a Leica/Cannon Image analysis system. Fluctuating asymmetry (FA) statistics were run according to (PALMER & STROBECK, 2001). All measurements were done twice, and the measurement error was estimated for all samples by the two-way ANOVA on a sample of 30 individuals measured twice. There were significant interactions between the wing size and the individual FA for both length ($MS = 31.079$, $p < 0.001$) and width ($MS = 34.617$, $p < 0.001$), which means that FA has a greater value than the measurement error. To test size dependence of the FA, regressions of the transformed absolute FA on trait size were performed for each sex and trait. The FA_4 index was used as the variance of the difference between the right and left wing sizes ($FA_4 = \text{var}(R-L)$). It is efficient in estimating the between-side variations and is not biased by directional asymmetry (DA). The F-test was used to compare the variabilities in FA_4 between the samples and the sexes.

Results

Interspecies hybridization

The percentage and sex of hybrids obtained from the intra- and interspecies crosses are shown in Tab. I. As expected, the success of intraspecies mating is high, between 87% (*D. melanogaster*) and 92% (*D. simulans*).

The success of interspecies mating varies significantly. Only females appear in the progeny when *D. melanogaster* females are crossed with males of either of the two sibling species and the percentage of hybrids is 26% with *D. mauritiana*, and 36% with *D. melanogaster* males.

Hybrids of both sexes are obtained when *D. simulans* females are crossed with males of two other species, but mating success is higher if they are crossed with *D. mauritiana* males (90%) than with *D. melanogaster* males (24%).

Only males appear in hybrid progeny when *D. mauritiana* females are crossed with males of *D. Melanogaster*, but at a very low percent (3%).

A striking contrast was obtained in the *D. simulans* x *D. mauritiana* and *vice versa* cross: when *D. simulans* females were crossed with *D. mauritiana* males, 90% of the progeny of both sexes was obtained, while the reciprocal cross gave no progeny of either sex.

Table I. Percentage, sex and phenotype of hybrids obtained from intra- and interspecies crosses among laboratory populations of *D. melanogaster*, *D. simulans* and *D. mauritiana*.

| | | Males | | |
|---------|------------------------|--------------------------------------------------|----------------------------|------------------------------------------------|
| | | <i>D. melanogaster</i> | <i>D. simulans</i> | <i>D. mauritiana</i> |
| Females | <i>D. melanogaster</i> | 87 | 39 (females only dysgenic) | 26 (females only dysgenic) |
| | <i>D. simulans</i> | 24 (both sexes, males sterile, females dysgenic) | 92 | 90 (both sexes, males sterile females fertile) |
| | <i>D. mauritiana</i> | 3 (males only sterile) | 0 | 91 |

Sterility is present in all hybrid males, and all hybrid females are dysgenic except those from matings between *D. simulans* females with *D. mauritiana* males.

Fluctuating asymmetry of hybrids

A comparison of the FA variability for wing length and width *between parents and hybrids* is given in Tab. II. There is no significant difference in the FA of wing width between male hybrids and their fathers in either of the combinations that gave males in high percentages (*D. simulans* x *D. mauritiana* and *D. simulans* x *D. melanogaster*). The FA variance for wing length was significantly higher in hybrids of *D. simulans* x *D. melanogaster* cross, but significantly lower when *D. simulans* females were crossed with *D. mauritiana* males. Regarding trait, the opposite was obtained for females: a significant decrease of the FA in wing width of female hybrids is obtained in the *D. simulans* x *D. melanogaster* cross, whereas female hybrids from the *D. simulans* x *D. melanogaster* and *D. simulans* x *D. mauritiana* crosses have significantly higher FA for wing length and width, respectively, than their mothers. The majority of the obtained hybrids show an increase in FA, but it is not significant.

Data on FA obtained for "mothers" and "fathers" in a specific cross can tell about the FA difference between the sexes within and between the species. *Within* a species, the FA is higher in males than in females for both traits, and there is no significant FA variability *between* the species for either sex or any trait.

The comparison of FA variability *between hybrids* from combinations of different species is presented in Tab. III.

Hybrid females have on average significantly higher wing length FA than wing width FA, and wing width FA is less variable among hybrids. Hybrid females from the *D. simulans* x *D. mauritiana* cross have the highest FA both for the wing width and length. The lowest FA for wing length is obtained in the hybrid females from *D. simulans* x *D. melanogaster* cross, and for wing width in hybrid females from the *D. melanogaster* x *D. mauritiana* cross.

Hybrid males were obtained only in 3 combinations, but in FA analysis only male hybrids from *D. simulans* x *D. mauritiana* and *D. simulans* x *D. melanogaster* are included. A few males (3) were obtained in the progeny of the third cross, which was too small a sample to be analyzed. The obtained FA₄ index for hybrid males is

Table II. The comparison of average FA4 index ($FA_4 = \text{var}(R-L)$) of wing width and length in hybrids and parent of the corresponding sex. The first written species in cross is *mother*, the second is *father*.

(F= F-statistics; n.s. – non significant ($p > 0.5$); ** $p < 0.01$; *** $p < 0.001$).

| FEMALES | | | | | | | |
|-----------------------------------------------|---------|---|-------------|---------|--------|---|-------------|
| LENGTH | | | WIDTH | | | | |
| | FA4 | F | | FA4 | F | | |
| <i>D. simulans</i> x <i>D. melanogaster</i> | | | | | | | |
| mothers | 0.00084 | ↑ | 1.7036*** | mothers | 0.0012 | ↓ | 1.8493*** |
| hybrids | 0.00049 | | hybrids | 0.0006 | | | |
| <i>D. simulans</i> x <i>D. mauritiana</i> | | | | | | | |
| mothers | 0.00152 | | 1.4189 n.s. | mothers | 0.0004 | ↑ | 2.4672** |
| hybrids | 0.00217 | | hybrids | 0.0009 | | | |
| <i>D. melanogaster</i> x <i>D. simulans</i> | | | | | | | |
| mothers | 0.00082 | | 1.241 n.s. | mothers | 0.0006 | | 1.3464 n.s. |
| hybrids | 0.00101 | | hybrids | 0.0009 | | | |
| <i>D. melanogaster</i> x <i>D. mauritiana</i> | | | | | | | |
| mothers | 0.0009 | | 1.0236 n.s. | mothers | 0.0004 | | 1.2931n.s. |
| hybrids | 0.0009 | | hybrids | 0.0006 | | | |
| MALES | | | | | | | |
| LENGTH | | | WIDTH | | | | |
| | FA4 | F | | FA4 | F | | |
| <i>D. simulans</i> x <i>D. melanogaster</i> | | | | | | | |
| fathers | 0.0008 | ↓ | 1.4906* | fathers | 0.0011 | | 1.0664 n.s. |
| hybrids | 0.0011 | | hybrids | 0.0012 | | | |
| <i>D. simulans</i> x <i>D. mauritiana</i> | | | | | | | |
| fathers | 0 | ↑ | 1.7646* | fathers | 0.0011 | | 1.2438 n.s. |
| hybrids | 0.0009 | | hybrids | 0.0014 | | | |

significantly higher in males from the *D. simulans* x *D. melanogaster* cross for wing length than for the males from the other cross. However, their FA for wing width does not differ.

Table III. The comparison of FA4 index ($FA_4 = \text{var}(R-L)$) for wing width and length between hybrids of each sex. The first written species in cross is *female*, the second is *male*. (F= F-statistics; n.s. – non significant ($p > 0.5$); ** $p < 0.01$; *** $p < 0.001$).

| FEMALES | | | | |
|--------------------------------------------------|----------|-------------|----------|-------------|
| LENGTH | | | WIDTH | |
| hybrids from the cross | FA4 | F | FA4 | F |
| <i>D. simulans</i> x <i>D. melanogaster</i> | 0.000492 | 4.4109*** | 0.000643 | 1.3652* |
| <i>D. simulans</i> x <i>D. mauritiana</i> | 0.002170 | | 0.000877 | |
| <i>D. simulans</i> x <i>D. melanogaster</i> | 0.000492 | 2.0709*** | 0.000643 | 1.3401*** |
| <i>D. melanogaster</i> x <i>D. simulans</i> | 0.001019 | | 0.000861 | |
| <i>D. simulans</i> x <i>D. melanogaster</i> | 0.000492 | 1.7683*** | 0.000643 | 1.1647 n.s. |
| <i>D. melanogaster</i> x <i>D. mauritiana</i> | 0.000870 | | 0.000552 | |
| <i>D. simulans</i> x <i>D. mauritiana</i> | 0.002170 | 2.1299*** | 0.000877 | 1.0188 n.s. |
| <i>D. melanogaster</i> x <i>D. simulans</i> | 0.001019 | | 0.000861 | |
| <i>D. simulans</i> x <i>D. mauritiana</i> | 0.002170 | 2.4943*** | 0.000877 | 1.5901** |
| <i>D. melanogaster</i> x <i>D. mauritiana</i> | 0.000870 | | 0.000552 | |
| <i>D. melanogaster</i> x <i>D. simulans</i> | 0.001019 | 1.1711 n.s. | 0.000861 | 1.5608*** |
| <i>D. melanogaster</i> x <i>D. mauritiana</i> | 0.000870 | | 0.000552 | |
| MALES | | | | |
| hybrids from the cross | FA4 | F | FA4 | F |
| <i>D. simulans</i> x <i>D. melanogaster</i> | 0.001131 | 1.3092* | 0.001389 | 1.202 n.s. |
| <i>D. simulans</i> x <i>D. mauritiana</i> | 0.000864 | | 0.001156 | |

Discussion

Interspecies hybridization

Pre-reproductive isolation between species, including *Drosophila*, results from the events which tend to prevent copulation (courtship behavior, mating choice), while post-reproductive isolation occurs after copulation and includes sperm competition, cytoplasmic incompatibility, reduced fitness of hybrids (COYNE & ORR, 1997).

D. simulans, *D. mauritiana* and *D. melanogaster* are sibling species of the *melanogaster* group. *D. simulans* and *D. melanogaster* are cosmopolitan species and they overlap in nature, while *D. mauritiana* is endemic to Mauritius. Data of the structural gene, DNA, and chromosomal variability show that *D. mauritiana* and *D. simulans* are close relatives, with *D. melanogaster* being distant, although the phylogeny is not completely clear (LACHAISE *et al.*, 1986; LEE & WATANABE, 1987).

Our results show that *D. mauritiana* females are most discriminating towards males of other species. *D. simulans* females are least discriminating and give progeny of both sexes successfully with both other species, and *D. melanogaster* females give female progeny only, according to Haldane's rule, with both other species.

Hybrid sterility and inviability have been noticed in crosses between *D. melanogaster* and *D. simulans* since the work of STURTEVANT (1920), and this pair of species has contributed much to our knowledge of genetic mechanisms of reproductive isolation (reviewed in SAWAMURA, 2000). In our study, a high percentage of progeny was obtained from the *D. simulans* x *D. melanogaster* parental cross. In literature, the progeny from *D. simulans* females crossed with *D. melanogaster* males is either easily obtained or scarce, and with low viability (COYNE, 1992; CARRACEDO *et al.*, 1998). A possible explanation of the difference in the results obtained is the history of the lines and populations used in the experiments. Although *Drosophila* is suitable for work under laboratory conditions, the results obtained on hybridization could be rather biased if extrapolated to natural conditions. In addition to laboratory lines of both species used in the present paper, we also tested the first generation from natural populations of these species for reproductive success and got a very low (0-2%) number of progeny with *D. simulans* females crossed with *D. melanogaster* males (STAMENKOVIĆ-RADAK, unpublished data). However, *D. melanogaster* females from natural populations gave progeny with *D. simulans* males in a variable number (0-40%), depending on the population distance. To understand the reproductive isolation and, furthermore, speciation among *Drosophila* species, it is important to pay more attention to populations of the species taken from the wild, from both sympatric and allopatric conditions (MALLET, 2005).

In our study, when *D. simulans* females were crossed with *D. mauritiana* males, 90% of the progeny of both sexes was obtained, while the reciprocal cross gave no progeny. CIVIETTA & SINGH (1998) obtained a similar result. *D. mauritiana* females did not give any progeny with *D. simulans* males, but they obtained males in the reciprocal cross. In *Drosophila*, the courtship song (vibration of the male's wing) is known to be species specific (TOMARU *et al.*, 2000). Some genes can act as the "reservoir" of the species specific behavior during courtship (GREENSPAN & FERVEUR, 2000; KYRIACOU, 2002). This can explain the variability in the mating success depending on the sex of the parental species.

Developmental stability (DI) of hybrids

In interspecies hybridization, the interaction of two different genomes affects the phenotypic variability of hybrids, including fertility and viability. Experimental and comparative evidence indicates that hybrid infertility evolves more rapidly in mammals and *Drosophila* (RICE & CHIPPINDALE, 2002). One aspect of studying the fitness of interspecies hybrids is developmental instability as a consequence of a genomic clash, such as hybridization (LAUNDRY *et al.*, 2007). Developmental instability refers to processes that are reflected in an individual's inability to withstand environmental and genetic perturbations to produce a bilaterally symmetrical phenotype (PERTOLDI *et al.*, 2006). The increased variability in fluctuating asymmetry (FA) would reflect DI (DONGEN, 2006).

Our data show the stability of FA within species for both traits, though in the male progeny of *D. simulans* x *D. melanogaster* the FA is generally higher than in the females. In hybrids, we might expect DI to increase as a result of the disruptions of genome coadaptation. Alternatively, we might expect DI to decrease because of increased heterozygosity (ALBERT & AUFFRAY, 2003). A few studies tested the relationships between outbreeding and DI through FA. In insects, experimental studies involved several *Drosophila* species and different quantitative traits (MARKOW & RICKER, 1991; CIVETTA & SINGH, 1998; GUPTA, 1978; ORR, 1990), and with natural populations only two studies were done within *Apis* (SMITH *et al.*, 1997) and *Solenopsis* (ROSS & ROBERTSON, 1990). Increased or not, FA variability was obtained in all those experiments on the interspecies hybridization of insects.

The interspecies hybridization studied here changes developmental stability, but it is species-, sex-, and trait-specific. The sex of the parental species influences the FA variability of hybrids, so the results differ between reciprocal crosses, where males and females from each of the species are combined in a cross. The genetic incompatibilities that produce hybrid sterility and also DI of the hybrids are typically asymmetric: an allele from species A will produce hybrid sterility in the genetic background of species B, but the alternate allele at the same locus from species B will not necessarily produce hybrid sterility in the genetic background of species A (JOHNSON, 2000).

Furthermore, traits differ in the level of FA, which is confirmed by our results concerning wing length and width. There is a relationship between the degree of developmental stability of a character and the extent to which this character affects the fitness of the organism (PALMER & STROBECK, 1986; CLARKE, 1998). Both the functional significance of the character and the adaptive significance differ. The insect wing, and perhaps more the relative ratio between the width and the length, has many properties associated with locomotion, mating, etc., which makes it a target of selection.

Hybrid progeny is expected to have higher heterozygosity, and thus lower FA than the parental pair, if the heterozygosity hypothesis is correct. Our data support this hypothesis only in the case of the significant decrease of FA in wing width of female hybrids obtained from the *D. simulans* x *D. melanogaster* cross, when compared to their mothers.

If the coadaptation hypothesis is true, the FA of hybrids increases due to disturbed coadaptive inter-allelic balances within the genome of each species. Most of the hybrids obtained in our experiments show an increase in the FA but it is non-significant. Only female hybrids from the *D. simulans* x *D. melanogaster* and *D. simulans* x *D. mauritiana* crosses showed significantly higher FA for wing length and width, respectively, than their mothers. It is possible, but not clear, that selection reduces asymmetry in viable offspring. This may be explained by a higher selection pressure on the stability of the hybrids (BOURGUET, 2000). Again, it is the sex and origin of parental species that affect the extent of the negative effects of the genomic break-down on fitness.

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РАЗВОЈНА СТАБИЛНОСТ ХИБРИДА ИЗМЕЂУ ВРСТА
DROSOPHILA MELANOGASTER, *D. SIMULANS* И *D. MAURITIANA*
(DIPTERA: DROSOPHILIDAE)

МАРИНА СТАМЕНКОВИЋ-РАДАК, ИВАНА КОСИЋ, ГОРДАНА РАШИЋ,
НИКОЛАЈ ЈУНАКОВИЋ И МАРКО АНЂЕЛКОВИЋ

Извод

Очекивано је да хибридизација између врста узрокује развојну нестабилност као последицу аутбридинг депресије и геномског стреса. Варијабилност флукутирајуће асиметрије билатерално симетричних органа може пратити такве услове стреса и мењати се између родитеља и хибридног потомства.

Циљ рада је процена степена презиготне репродуктивне изолације између три сестринске врсте *Drosophila simulans*, *D. mauritiana* и *D. melanogaster*, у лабораторијским условима и да сагледа ефекте хибридизације на флукутирајућу асиметрију крила.

Резултати показују да су женке *D. mauritiana* најдискриминативније према мужјацима друге две врсте, док су женке *D. simulans* најмање дискриминативне и успешно дају потомство оба пола са мужјацима друге две врсте. Женке *D. melanogaster* дају само женско потомство са мужјацима друге две врсте.

Међуспецијска хибридизација мења развојну стабилност, специфично за врсту, пол и особину. Резултати иду у прилог хипотези хетерозиготности само у случају значајног смањења флукутирајуће асиметрије за ширину крила хибрида женског пола из укрштања *D. simulans* x *D. melanogaster*. Већина добијених хибрида показује повећање флукутирајуће асиметрије услед разбијања коадаптивних геномских комплекса поједине врсте, што иде у прилог коадаптивној хипотези.

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