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Fluctuating Asymmetry in *Drosophila*: Hybrids are as Stable as Parents

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Abstract: In most of the animals, as per general body plan there is bilateral symmetry for different morphological traits. However, it may get disturbed in the presence of genetic and environmental stresses which results in either increase of developmental noise or decrease of developmental stability. When bilateral symmetry is disturbed in the organism, it is known as fluctuating asymmetry which is defined as subtle differences between left and right sides of a trait. It is considered as an ability of organisms to cope with genetic and environmental stress during development. Developmental instability is most often estimated by fluctuating asymmetry, the right and left side differences in shape, size or number in a single trait across the population. Thus, fluctuating asymmetry is a pattern of developmental instability resulting from perturbations during development which gives rise to imprecise expression of developmental pathways. Because of this reason, it has been used as a measure of individual quality and also as an indicator of environmental as well as genetic stress. It is interesting to mention that even Aristotle observed the regular patterns of bilateral asymmetries in animals such as crayfish, lobsters, and crabs. Fluctuating asymmetry has been investigated in different species of *Drosophila* and interesting findings have been reported. In this article, a study is reported which shows that fluctuating asymmetry in two sibling species of *Drosophila* and their hybrids are similar when different morphological traits were used. Further, the hybrids of *D. ananassae* and *D. pallidosa* are as stable as their parents. And also, the effect of hybridization on FA appears to be sex and trait specific.

Index Terms: Fluctuating asymmetry. *Drosophila*, parental species, hybrids

I. INTRODUCTION

Phenotypic variation is a universal characterstic of living organisms and is observed in a wide variety of traits across the populations and species. Expression of phenotypic variation in a population is influenced by genetic differences among individuals, environmental heterogeneity affecting development and random variations in development (Yampolsky & Scheiner, 1994). In animals including humans, there is a bilateral symmetry of different phenotypic traits. There are subtle differences between left and right sides of a trait known as fluctuating asymmetry which is considered as an indicator of an organism's ability to cope with genetic and environmental

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stresses during development. Pattern of fluctuating asymmetries were also observed by Aristotle in animals like crabs, lobsters and crayfishes. While using various morphological traits, fluctuating asymmetry has been studied in different species of *Drosophila* (Shakarad et al. 2001;Vishalakshi, 2011). When bilateral symmetry is disturbed due to genetic and environmental stresses, it results in increase of developmental noise or decrease of developmental stability. Measurement of fluctuating asymmetry, small nondirectional differences in size between symmetric paired morphological structures is a potentially useful tool for detecting factors that influence developmental instability. Lower values of FA may reflect development that proceeds more precisely, whereas elevated FA values may be due to problems during development that reflect increased developmental instability (Carter et al. 2009). When deviations from normal symmetry in morphological traits occur, the asymmetries may be grouped into three categories: directional asymmetry (DA), antisymmetry (AS) and fluctuating asymmetry (FA) (Van Valen 1962). Directional Asymmetry (DA)- occurs when there is normally greater development of a trait on one side of the plane of symmetry than on the other (Van Valen, 1962). On the other hand, Antisymmetry (AS) occurs when mostly individuals of a population are asymmetric but it is unpredictable which side of an individual shows greater development (Timofeef-Ressovsky, 1934; Graham et al. 1993). Fluctuating asymmetry (FA) is defined as minor random deviations from perfect bilateral symmetry (Ludwig, 1932; Van Valen, 1962). According to Polak (2003), the three kinds of asymmetries in morphological traits are common in natural populations. However, under stressful situations, examples are available which show that there are transitions from one type of asymmetry to the other type: from AS to DA, DA to FA and FA to AS(Graham et al. 1993; Smith et al. 1997; Leany & Klingenberg, 2005). Palmer (1996) has suggested that out of three types of asymmetries, fluctuating asymmetry is used to quantify the developmental instability as it originates due to random fluctuations causing a trait to depart from its normal symmetry during the development, whereas directional asymmetry and antiasymmetry are thought to have unknown genetic basis and consequently are not commonly seen as reflection of developmental perturbations. Fluctuating asymmetry (FA) has been studied in different species of *Drosophila* and varying results are reported (Shakarad et al., 2001; Vishalakshi & Singh, 2006, 2008a,b,c,d,e,2009a,b; Carter et al. 2009). It has also been found that mating success in *D. ananassae* is not correlated with fluctuating asymmetry (Vishalakshi & Singh, 2008a). Banerjee and Singh (2015) observed that iterspecific hybridization does not affect the level of fluctuating asymmetry in the *Drosophila bipectinata* complex involving four species: *D. bipectinata, D. parabipectinata, D. malerkotliana* and *D. pseudoananassae.* It has been reported that evolution of faster development does not lead to increase in fluctuating asymmetry of sternopleural bristle number in *D. melanogaster*. Developmental instability is quantified by the amount of variation among phenotypes that would be produced by the same developmental blueprint under identical genetic and environmental conditions and is most often estimated by fluctuating asymmetry, the right and left side difference in size or shape in a single trait across the population.

II. FLUCTUATING ASYMMETRY INDICES

Related to fluctuating asymmetry, there is another measurement i. e. trait size. Trait size for each trait may be measured by the average value of right and left sides [(R+L/2]. To describe the levels of fluctuating asymmetry, different indices have been used (Palmer, 1994; Palmer & Strobeck, 2003). FA1- absolute value of difference in trait size between the right and left sides of the body !(R-L)! FA2-.Relative difference between sides: [Mean/ (R-L) /(R+L) /2]. FA3-a measure of the difference between the two sides of the body in the way in which the components of a meristic trait are arranged or positioned. It was calculated for both sternopleural bristle number and sex comb tooth number. For the sternopleural bristle number, positional fluctuating asymmetry (PFA_B) was calculated as [(Right A/ Right T) –(Left A/Left T)] and for sex comb tooth number ($PFA_{S)}$ as [Right C1/Right C2)-(Left C1/Left C2)]. Different morphological traits used in the study of FA are shown in Figure 1 and the two sibling species are shown in Figure 2. (taken from the thesis of C Vishalakshi submitted under the supervision of the author).

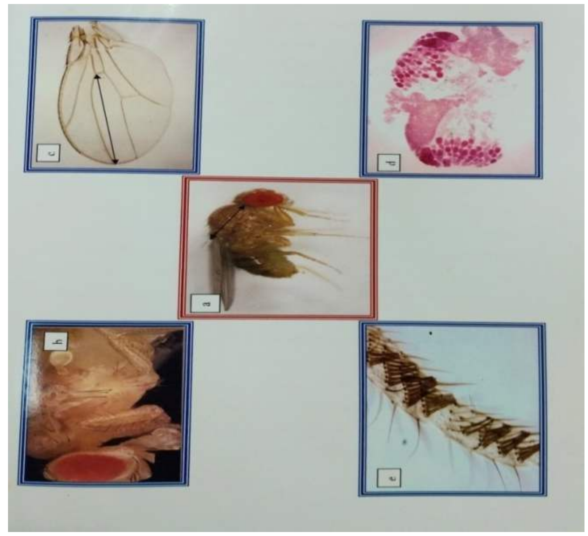

Figure 1. Different morphological traits used in this study: (a) Thorax length (b) sternopleural bristle number (c) Wing length (d) Ovariole number (e) Sex comb tooth number

Figure 2: Two sibling species of *Drosophila:* (a) Female of *D. ananassae* (b) Male of D. ananassae (c) sex comb of *D. ananassae* (d) Female of *D. pallidosa* (e) Male of *D. pallidosa* (f) Sex comb of D. *pallidosa* (Singh 2023).

While using the measurements of trait size and different fluctuating asymmetry indices for different morphological traits, Vishalakshi and Singh (see Vishalakshi, 2011) investigated fluctuating asymmetry in *D. ananassae* and their results demonstrate the following:

1. There is evidence for genetic heterogeneity among the laboratory populations of *D. ananassae* as the trait size for different morphological traits differ significantly among the different geographic strains.
2. The magnitude of FA is higher in sexual traits than non-sexual traits which suggests that sexual traits are better indicator of developmental stress.
3. The levels of FA are similar in mated and unmated flies for different morphological traits in both males and females which suggests that FA could not be used as an ideal phenotypic cue for choosy females and thereby weakens the FA-sexual selection hypothesis.
4. The levels of F A are similar in the flies reared on poor media and on normal media. However, there is significant difference for asymmetry measures in the flies reared at different larval densities for all the traits.
5. The trait size of different morphological traits decreases at higher temperature and decreases at lower temperature.
6. The trait size of different morphological traits decreases in different mutant strains when compared with wild type strains.
7. The levels of FA differ significantly among the hybrids of different selection lines in comparison to their parents. Moreover, the magnitude of F A is lower in hybrids as compared to parents. This decrease in F A levels in hybrids is caused due to increase in heterozygosity.

Thus, fluctuating asymmetry in certain morphological traits in *D. ananassae* is affected by both genetic and environmental stresses but the effect seems to be trait- and sex specific.

III.SIBLING SPECIES

There are two sibling species: *D. ananassae* and *D. pallidosa* (Singh, 2023). *D. ananassae* is a cosmopolitan and domestic species, but *D. pallidosa* is endemic to certain Islands such as Samoa in South Pacific and Fijii. Both these species are phylogenetically closely related and are sympatric in distribution. In nature, they remain reproductively isolated by means of ethological (sexual or behavioural) isolation. However, they hybridize in the lab and produce fertile hybrids. Although the genetic basis of developmental stability is not fully understood, it is thought that genetic coadaptation and heterozygosity levels are the two main causal genetic agents associated with sustaining developmental stability in organisms (Alibert et al., 2003; Pertoldi et al., 2006). It is expected that in hybrids, the developmental stability may decrease due to breakdown of coadapted genetic complexes and alternatively there may be an increase in the level of developmental stability levels as a result of increase in the level of heterozygosity but it depends on degree of divergence in the genetic systems controlling development in hybridizing taxa (Alibert et al. 1997;Careira et al. 2008).The most widely used parameter of developmental stability is fluctuating asymmetry i.e. subtle random deviation from ideal bilateral symmetry which may result due to the inability of self regulatory mechanisms to stabilize development in the face of environmental perturbations (Van Valen, 1962;Careira et al., 2008). It has been demonstrated that interspecific hybrids have either decreased or increased developmental stability as compared to parents (Leany et al., 1985; Ross & Robertson, 1990; Lamb et al., 1990; Markow & Ricker, 1991; Blows &Sokolowaski, 1995; Hutchingson & Chevecrud, 1995; Alibert et al., 1997) which provides indirect evidence that epistatic interaction may be important in controlling the degree of fluctuating asymmetry (Leany & Klingenberg, 2005).

IV. FLUCTUATING ASYMMETRY IN TWO SIBLING SPECIES AND THEIR HYBRIDS

Vishalakshi and Singh (2009a) studied fluctuating asymmetry in two sibling species: *D. ananassae* and *D. pallidosa* and their hybrids while using the six morphological traits mentioned above. In the absence of post zygotic isolation, hybrid sterility in F1 and F2 generations between these two species permitted these authors to separate the effect of two hybridizations events that is heterozygosity (which may result in decreased level of FA in F1 hybrids) and breaking of coadapted gene complexes in subsequent generations (which may result in increased levels of FA in F2 or F3 generations) of interspecific hybrids. In view of the above facts, these authors studied the effects of hybridization between these two sibling species on the degree of F A in different morphological traits mentioned above. The results of these experiments have shown that: the trait size of different morphological traits differed significantly among parental species and their hybrids of different generations in both sexes. However, the levels of fluctuating asymmetry of different morphological traits were similar in parental species and their hybrids of different generations in males (except SCTN) and in females (except for WL and W/T ratio). These results are interpreted in terms of developmental stability as a function of a balance between the level of heterozygosity and the disruption of coadapted gene complexes. Thus, the interspecific hybrids of *D. ananassae* and *D. pallidosa* are developmentally as stable as their parents. Further, the effect of hybridization on FA appears to be sex and trait specific (Vishalakshi & Singh, 2009a).

CONCLUSION

It is interesting to mention that even Aristotle observed the regular patterns of bilateral asymmetries in animals such as crayfish, lobsters, and crabs. When bilateral symmetry is disturbed in the organism, it is known as fluctuating asymmetry which is defined as subtle differences between left and right sides of a trait. It is considered as an ability of organisms to cope with genetic and environmental stress during development. Developmental instability is most often estimated by fluctuating asymmetry, the right and left side differences in shape, size or number in a single trait across the population. Thus, fluctuating asymmetry is a pattern of developmental instability resulting from perturbations during development which gives rise to imprecise expression of developmental pathways. Because of this reason, it has been used as a measure of individual quality and also as an indicator of environmental as well as genetic stress.

Fluctuating asymmetry has been studied in different species of *Drosophila* and varying results have been reported. In this article, the results of F A study done on a pair of sibling species and their hybrids are described briefly. The results of these experiments have shown that: the trait size of different morphological traits differed significantly among parental species and their hybrids of different generations in both sexes. However, the levels of fluctuating asymmetry of different morphological traits were similar in parental species and their hybrids of different generations in males (except SCTN) and in females (except for WL and W/T ratio). These results are interpreted in terms of developmental stability as a function of a balance between the level of heterozygosity and the disruption of coadapted gene complexes. Thus, the interspecific hybrids of *D. ananassae* and *D. pallidosa* are developmentally as stable as their parents. Further, the effect of hybridization on FA appears to be sex and trait specific. Thus, it may be suggested that interspecific hybrids which managed to reach the adult stage may have conceived as compatible combinations of parental genomes which might be sufficiently different at loci involved in the development of a trait as to generate differences observed between two parental species and among the parental species and their hybrids and this may be correlated with the similar levels of developmental stability of hybrids with the parental species (Vishalakshi & Singh, 2009a).

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