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Premating reproductive barrier is more efficient than post mating in *Drosophila*

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Abstract: **It has been known since the time of Lamarck and Darwin that the role of isolation is crucial in the process of speciation. The populations which are undergoing evolutionary change must develop certain mechanisms of isolation so that gene flow between the Mendelian populations is prevented. The term "Isolating Mechanisms" was coined by Theodosius Dobzhansky in 1937 for the barriers which are genetically conditioned and impede gene exchange between Mendelian populations. Basically, isolating mechanisms are of two types: reproductive isolation (sympatric populations) and geographical isolation (allopatric populations). The mechanisms of reproductive isolation are again classified into two types: premating and post mating or pre zygotic and post zygotic. Among different means of reproductive isolating mechanisms, sexual or ethological or behavioural isolation is considered as a very important isolating mechanism in animals. Ernst Mayr, the main architect of the biological species concept, claimed that: "if we were to rank the various isolating mechanisms in animals according to their importance, we would have to place behavioural isolation far ahead of all others." The genus Drosophila which is considered as a very good biological model, has been often employed for studies on sexual isolation. The results of these studies have demonstrated that the degree and pattern of sexual isolation among different species vary and have been found very useful to discuss the direction of evolution and phylogenetic relationship among different species which support the claim of Ernst Masyr that sexual or behavioural isolation should be placed far ahead of all other isolation mechanisms.**

Index Terms: **Reproductive isolation, pre and post mating reproductive isolation, *Drosophila***

I. INTRODUCTION

It was remarked by Dobzhansky (1951) that without isolation evolution is not possible. Wagner (1889) discussed in detail the role of isolation in evolution. In modern form, Jordan (1905) elaborated the importance of isolation in evolution. Species and races differ in their genetic constitution and their separate gene pools must remain isolated by certain mechanisms because their interbreeding will remove their differences which will lead to the loss of their identity. Thus, during the process of cladogenesis, the evolving populations must acquire certain mechanisms of isolation in order to prevent free exchange of genes between different gene pools. The term "Isolating Mechanisms" was coined by Theodosius Dobzhansky in 1937 for different agents which alone or in combination impede the flow of genes between different Mendelian populations. There are different types of isolating mechanisms: reproductive isolation operating in sympatric populations and geographic (spatial) isolation operating in allopatric populations. The mechanisms of reproductive isolation are again classified in two types: pre mating and post mating or pre zygotic and post zygotic. Figure 1 depicts different classes of isolating mechanisms. Only gametic isolation is pre zygotic as well as post mating.

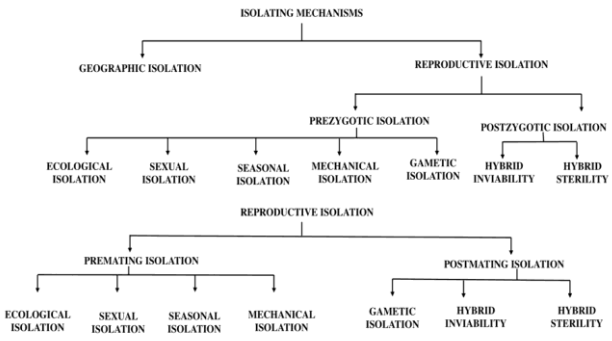

Figure1. Different kinds of isolating mechanisms in animals

The isolating mechanisms are the most important attributes of a species (Mayr 1966). The evolutionary biologists such as Coyne and Orr (2004) have rightly remarked that the speciation is a key process for the evolution of biological diversity and under biological species concept can be viewed as the evolution of reproductive isolation between formerly interbreeding populations. Sawamura (1999) who believes in biological species concept suggested that question how new species evolve

should be substituted by a more answerable question "how reproductive isolating mechanisms are established between populations". With the development of modern genetics in *Drosophila*, interest has been focused on the question of role of reproductive isolating mechanisms in evolution. Nanda and Singh (2011) have demonstrated that the origin of sexual isolation is the central event in the evolution of biological diversity and plays an important role in maintaining biological diversity.

Drosophila which belongs to the family Drosophilidae, order Diptera and class Insecta, is an excellent biological model (Singh, 2025). From the time of Thomas Hunt Morgan in the beginning of last century, it has been extensively used in different kinds of studies in biological sciences such as genetics, evolution, behavior, molecular biology, disease biology and ecology. Different kinds of mechanisms of reproductive isolation have been studied in Drosophila by utilizing numerous species belonging to different species groups (Dobzhansky, 1937, 1951;Pattertson& Stone, 1952; Mayr, 1966; Singh, 1997; Powell, 1997; Coyne & Orr, 2004). Although there are different types of reproductive isolating mechanisms in animals shown in Figure 1, the types of reproductive isolating mechanisms which have been studied in detail in Drosophila are: Sexual isolation, gametic isolation, hybrid in viability and hybrid sterility. Sexual or ethological or behavioral isolation is premating isolation and operates among sympatric species. However, the other three are post mating isolation and one important feature is associated with these reproductive isolating mechanisms is that they cause wastage of gametes.

Pre mating reproductive barriers prevent gene flow before transfer of sperm to members of other species. According to Powell (1997), it is primarily due to behavioral divergence, the species do not exchange genes regardless of whether fertile, viable offspring could be produced. Pre mating reproductive isolation has been classified into different kinds: temporal isolation, ecological isolation, mechanical isolation and sexual (behavioral or ethological). Among them, sexual isolation is most important and has been extensively investigated in the genus Drosophila (Patterson & Stone, 1952; Singh, 1997; Nanda & Singh, 2012). The results obtained from different species have clearly demonstrated that there is variation in the results. There are species which show complete sexual isolation. Also, there are species which show incomplete sexual isolation. It has been frequently observed that when two closely related species show incomplete sexual isolation, the pattern of isolation (or mating preference) may be symmetrical (both sided) or asymmetrical (one sided). Singh (1997) has suggested that the mode of mating preference and the degree of sexual isolation are often utilized to discuss the direction of evolution and the phylogenetic relationship among the species.

In the genus Drosophila, there are a large number of cases of asymmetrical (or one-sided) mating preference (ethological isolation). Based on this, different models which are opposite to each other have been proposed. Kaneshiro (1976) studied sexual isolation among certain Hawaiian species of Drosophila belonging to the planitibia subgroup such as *D. differens*, *D. planitibia* and *D. silvistris*. Based on asymmetrical mode of mating preference, he suggested that "The species whose females more often fail to mate with the males of other species is the ancestral species and the species whose females readily accept the males of other species is derived species". This is known as Kaneshiro's model which is based on random genetic drift (founder principle of Mayr (1942) and allopatric mode of speciation. The evolutionary sequence among Hawaiian species of *Drosophila* is: *D. differens* → *D. planitibia* → *D. silvestris* (Figure 2A). A large number of examples are known which support this model.

Watanabe and Kawanishi (1979) studied sexual isolation among three species of the *D. melanogaster* species group: *D. melanogaster*, *D. simulans* and *D. mauritiana* and observed one-sided mating preference. Their suggestion is: "It is the females of derived species which do not mate with males of ancestral species and the species whose females readily accept the courtship overtures of other is ancestral species". Thus, the direction of evolution is just opposite of Kaneshiro's model. This model is based on sympatric mode of speciation. According to Watanabe and Kawanishi, the first step for the initiation of speciation (cladogenesis) is the failure of mating between derived females and ancestral males which is the most crucial change for the creation of new species (Singh, 1997). The evolutionary sequence among these species is:*D. melanogaster* →*D. simulans* → *D. mauritiana* (Figure 2B). In a number of cases, supporting evidence in favour of this model has been found. Both these models were considered by Markow (1981) who is of the opinion that such generalized models cannot be proposed for the whole of genus Drosophila because relationships between the species may depend on ecological and evolutionary history of a group.

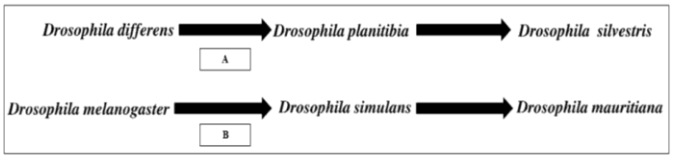

Figure 2. Diagram showing evolutionary sequence between derived and ancestral species based on: (A) Model of Kaneshiro and B) Model of Watanabe and Kawanishi.

Speciation in South Pacific Populations of *Drosophila ananassae*

Speciation in South Pacific populations of *D. ananassae* was studied by Futch (1966) who found light and dark forms of this species. The light form was identified as *D. palidosa* (Bock & Wheeler, 1972) on the basis of sexual isolation and differences in sex comb tooth numbers. The dark form is cosmopolitan species *D. ananassae* described by Doleschall in 1858. However, both these species are crossable in the laboratory producing fertile offspring of both sexes and possess identical male genitalia. It has been suggested that these two species which are sympatric in natural populations of Samoa and Fijii Islands and maintain their independent status of species just by ethological isolation are said to be in the statunascendi (in the process of speciation). Ethological isolation has been studied

tested between light and dark forms (Futch, 1966) and between D. ananassae and D. pallidosa (Futch, 1973; Singh & Singh, 2020). Futch (1973) designated these two species as sibling species (morphologically similar and reproductively isolated).

Futch (1966) tested sexual isolation between light and dark forms of *D. ananassae* from Samoa and observed asymmetrical pattern of mating preference. The degree of sexual isolation is strong with dark males but the mating was found to be random with light males. The dark form is cosmopolitan species *D. ananassae* and light form is *D. pallidosa* described by Bock and Wheeler (1972). Both these species have been called as sibling species (Futch, 1973). Light females discriminate against the dark males whereas dark females' mate with both the males randomly. This relationship between light and dark forms of *D. ananassae* supports the Watanabe and Kawanishi's model. Thus, light form (*D. pallidosa*) should be considered as derived whereas dark form (*D. ananassae*) as ancestral. Based on this, there is ancestral and derived relationship between dark form (*D. ananassae*) and light form (*D. pallidosa*).

There is another study of sexual isolation by Singh and Chatterjee (1985) among various laboratory strains of *D. ananassae*. These authors employed five isofemale lines of different geographic origins in their experiments which spent varying number of generations in the lab. The pattern of mating varied in different experiments: no isolation, symmetrical isolation and asymmetrical isolation. The strains which had spent more than 12 years showed asymmetrical isolation with the strains of recent origin which did not show isolation between them. Females of older strains discriminate against the males of strains of recent origin. The older strains were considered as derived and the strains of recent origin were considered as ancestral. Since the females of derived strains discriminate against the ancestral males, this relationship fits well with the model of Watanabe and Kawanishi. Nanda and Singh (2011) reported the origin of sexual isolation within *D. ananassae* due to founder effect. A large number of strains were used and different drift lines were passed through flush-crash cycles for twenty generations. In a number of crosses, asymmetrical isolation was found which extends evidence for the origin of behavioural isolation due to founder effect within *D. ananassae*.

There are recent studies on pre mating and post mating reproductive isolation in *Drosophila* (Matute, 2010; Jennings et al. 2014; Syed et al. 2017; Hsu et al. 2024; Jerrett et al. 2025). There is a report of reinforcement of post mating prezygotic isolation between D. yakuba and its endemic sister species *D. santomea*. This is an interesting example in which natural selection has promoted the evolution of stronger interpopulation genetic barriers that act after mating but before fertilization (Matute, 2010). Based on the study of allopatric populations D. montana, Jennings (2014) have shown that incipient reproductive isolation among populations can be driven by different contributions of both premating and post mating prezygotic barriers occurring between different populations pairs and without the evolution of postzygotic barriers. Syed et al. (2017) presented evidence in *D. melanogaster* that allopatric populations under elevated sexual conflict show assortative mating indicating premating reproductive isolation. Hsu et al. (2017) found that replicated evolution experiments provide valuable insights into the mechanisms of speciation and the rapid emergence of premating reproductive isolation during temperature adaptation extending evidence for incipient ecological speciation. Jarrett et al. (2025) have shown that populations subject to divergent selection evolved stronger reproductive isolation as compared to populations which evolved in similar environments which is consistent with ecological speciation theory and it is based on meta-analysis of 34 experimental speciation studies on arthropods, yeast and vertebrates.

These examples from different *Drosophila* species as well as the same species geographic strains provide evidence that premating barriers are more effective than post mating. Further, these examples also support the claim of Mayr "if we were to rank the various isolating mechanisms in animals according to their importance, we would have to place behavioural isolation far ahead of all others". Thus, it is primarily due to behavioural divergence, the species do not exchange genes regardless of whether fertile, viable offspring could be produced (Powell, 1997).

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REFERENCES

Bock, I.R. & Wheeler, M.W. (1972). The Drosophila melanogaster species group. Univ. Texas Publ. 7, 1-102.

Coyne, J.A. & Orr, H.A. (2004). Speciation. Sinaur Assoc., Inc. Publ. Sunderland, MA, USA.

Doleschall, C.L (1858). Drdeleijdrage tot de kennis der dipteren fauna van Nederlandsh Indie. Natuurk. Tijdschr. Ned.-Indie, 17, 73-128.

Dobzhansky,Th., (1937, 1951). Genetics and the Origin of Species, Columbia University Press, New York,

Futch, D.G. (1966). Speciation in South Pacific populations of Drosophila ananassae. Univ. Texas Publ. 6615, 79-120.

Futch, D.G. (1973). On the ethological differentiation of *Drosophila ananassae* and *Drosophila pallidosa* in Samoa. Evolution. Evolution, 27, 456-467.

Hsu, SK., Lai, WY., Novak, J. et al. Reproductive isolation arises during laboratory adaptation to a novel hot environment. Genome Biol 25, 141 (2024). https://doi.org/10.1186/s13059-024-03285-9

Jarrett, B.J.M., Downing, P.A. & Svensson, E.I. (2025). Meta-analysis reveals that phenotypic plasticity and divergent selection promote reproductive isolation during incipient speciation. Nat Ecol Evol 9, 833–844 (2025).

https://doi.org/10.1038/s41559-025-02687-7

Jennings, J.H., Snook, R.R. and Hoikkala, A. (2014), Reproductive isolation among allopatric *Drosophila montana* populations. Evolution, 68: 3095-3108. https://doi.org/10.1111/evo.12535

Jordan, K., (1905). Der Gegensatzzwischengeographischerundnicht geographischer Variation. Zeits. Wiss Zool., 83, 151-210.

Kaneshiro, K.Y. (1976). Ethological isolation and phylogeny in the planitiobia subgroup of Hawaiian Drosophila. Evolution, 34, 437-444.

Markow, T.A. (1981).Mating preferences are not predictive of the direction of evolution in experimental populations of Drosophila. Science, 213, 1405-1407.

Matute, D.R. (2010). Reinforcement of Gametic Isolation in Drosophila (2010) PLOS Biology, 8 (3) e1000341. https://doi.org/10.1371/journal.pbio.1000341

Mayr, E,, (1942). Systematics and the Origin of Species. Columbia University Press, New York.

Mayr, E., (1966). Animal Species and Evolution. The Belknap Press of Harvard University Press, Cambridge.

Nanda, P. & Singh, B.N., (20011). Origin of sexual isolation in Drosophila ananassae due to founder effects. Genetica, 2011, 139, 779-787.

Nanda, P. & Singh, B.N. (2012). Behavioural reproductive isolation and speciation in Drosophila. J. Biosci., 37, 1-16.

Patterson, J.T. & Stone, W.S. ((1952). Evolution in the Genus Drosophila. Macmillan Company, New York.

Powell, J.R. (1997). Progress and Prospects in Evolutionary Biology: The Drosophila Model. Oxford University Press, New York.

Sawamura, K., (1999). The origin of reproductive isolation: Biological mechanisms of genetic incompatibility. In The Biology of Biodiversity (ed. Kato, M.), Springer-Verlag, Tokyo. pp. 3-19.

Singh, B.N. (1997). Mode of mating preference and the direction of evolution in Drosophila. Ind. J. Exp. Biol., 35, 111-119.

Singh, B.N. (2025). .Drosophila: an excellent biological model. In: Flies in Science and Forensics (ed. Omkar),
Taylor& Francis, UK, pp. 94-104.

Singh, B.N. & Chatterjee, S. (1985). Symmetrical and asymmetrical sexual isolation among laboratory strains of *Drosophila ananassae*. Canad. J. Genet. Cytol., 27, 405-409.

Singh, R. & Singh, B.N. (2020). Intra- and interspecific sexual isolation in two sibling species of Drosophila: *D. ananassae* and *D. pallidosa*. Ethol. Ecol. Evol., 32, 572-579.

Syed, Z.A., Chatterjee, M., Samant, M.A. et al. (2017). Reproductive isolation through experimental manipulation of sexually antagonistic coevolution in Drosophila melanogaster . Sci Rep 7, 3330 https://doi.org/10.1038/s41598-017-03182-1

Wagner, M. (1889). Die Entstehung der ArtendurchraumlicheSonderang (Basel: Beno Schwalbe)

Watanabe, T.K. & Kawanishi, M. (1979). Mating preference and the direction of evolution in Drosophila. Science, 205, 906-907.

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