

# What Kaneshiro "really said" about asymmetrical mating<sup>1</sup>

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**ABSTRACT:** We discuss the arguments of Giddings and Templeton (1) regarding Kaneshiro's model of asymmetrical mating. We disagree with these, and discuss the basis of our disagreement. Finally we consider their view that "... universal truths concerning speciation should not be expected."

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Giddings and Templeton (1) (hereafter G & T) have recently published a spirited defense of what Kaneshiro (2,3,4,5) "really said" about asymmetrical mating and directions within phylogenies. In an inordinately long article which argues a small point, these authors defend Kaneshiro and maintain that his model is not a general one. They maintain that Kaneshiro "made explicit" the "essential assumptions" of the model. G & T assert that these are two: "... that these populations are related by founder events with little or no subsequent gene flow, and that the ancestral populations have not been subjected to drastic population bottlenecks since these founder events".

These authors then proceed to argue that when an example appears likely to satisfy these assumptions the Kaneshiro model correctly predicts which population is ancestral and which is derived. They consequently maintain that when a particular example does not support the same model then there is good evidence that one of the supposed assumptions of the model has been violated.

We wish to make a number of points with respect to this paper.

(1) Kaneshiro did not, as Giddings and Templeton (1) argue, make explicit these supposed assumptions. The reader will quickly verify this by simple recourse to the publications quoted, (2,3).

Hence the argument put forward by these authors largely dissolves.

(2) Furthermore the Kaneshiro model as put forward by G & T, has at least one other assumption. G & T remark "Given the 'choosing female' model of courtship common in *Drosophila*, the predicted pattern between ancestral and derived species would be precisely as observed by Kaneshiro in the four picture winged species studied". Hence the authors have contradicted themselves since they earlier remark that there are only two essential assumptions". (One wonders what constitutes "non-essential assumption"?). The latter is an important assumption because, given a "choosing male" system then G & T's logic leads to the opposite of the Kaneshiro prediction.

There is also, some reason to be concerned with the validity of such an assumption. Firstly "choose" is a difficult word and the experimental determination of the whole action of active choice is difficult (4,5). Also the concept that females choose males in many insect groups has been argued to be inappropriate (6). It seems appropriate to consider an interaction system of male-female communication (7,8). Any discussion of asymmetrical evolution should preferably then, be based on such an approach.

(3) G & T (1) are so determined to ensure that the Kaneshiro model works that they indulge in some amazing ad hoc arguing. Consider, for example, the case of populations of *Drosophila pullipes* and *D. grimshawi*. G & T discuss Ohta's (9) results from crosses between these populations which contradict the expectations of Kaneshiro's model. In an acrobatic twist of logic they construe this as support for the Kaneshiro hypothesis "via refinement of the necessary conditions". Surely the results of experiments in which assumptions of the model under test have been violated, cannot be regarded as evidence for that model: they are merely irrelevant. Indeed this is the approach used by

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If the authors whose work is discussed here ever send a suitable reply, it will be printed, but this comment cannot be delayed indefinitely.

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G & T when dismissing the results of Watanabe and Kawanishi (10), Wasserman and Koepfer (1), Markow (12) and Moodie (13).

(4) Since 1976 there have been a number of publications which G & T (1) argue are irrelevant to the Kaneshiro model because they supposedly violate the assumptions. This is simply because these assumptions were not explicitly stated. G & T admit that "The general applicability of the Kaneshiro model depends on whether it should be so narrowly defined as to be of limited use, or, whether it is general enough to apply to previously unresolvable situations". Hence the question is really "How should we define the Kaneshiro model?", not "Have other authors violated the explicitly stated essential assumptions?".

We believe that such a tightly constrained model is of limited use. Consequently we disagree with G & T that the model has the power to clarify previously unresolved situations. The model must be limited to cases in which organisms are amenable to mate choice experiments, where there is asymmetrical mating, where there is "female choosing", and (according to G & T) where there is "good evidence" for founder speciation with no subsequent gene flow and where the ancestral species does not subsequently undergo population bottlenecks. In considering the second limitation there appears to be some confusion as to whether asymmetrical mating results are common. Kaneshiro in his 1976 paper (2) remarked:

"This kind of one-sided mating preference between species has not been reported in any other species group". Yet in 1980 Kaneshiro (3) commented:

"A preliminary search of the literature on ethological isolation between populations of *Drosophila* indicated that one-sided mating preference or asymmetrical isolation is not an uncommon phenomenon".

(5) Giddings and Templeton are quick to dismiss examples of asymmetrical isolation which contradict Kaneshiro's model, often on the basis that they violate one or both of the assumptions. However, they seem unaware of the fact that two of the three laboratory experiments (14,15) which they give in support of his model also violate one of the same two assumptions.

Giddings and Templeton's second assumption clearly states that "the ancestral populations have not been subjected to drastic population bottlenecks since these founder events". However, Arita and Kaneshiro state that the "T79B3 stock (the ancestral population) was established from progeny of a female (our emphasis) collected by K.Y. Kaneshiro on September 15-16, 1975" six years after M55G17 the derived population. It is clear then that the ancestral population in this experiment has in fact suffered a severe bottleneck and subsequent flush in its establishment as an isofemale line, rendering the experiment invalid. Ahearn's study suffers from exactly the same problem and the inclusion of these two examples would appear to be a major oversight on the part of G & T.

G & T finally remark that there is a "growing awareness that speciation is not a monolithic process, but rather a collection of variable processes yielding diverse outcomes". Alternatively we contend that there is considerable evidence of diverse genetical and morphological outcomes of a single process of founder speciation in, for example, Hawaiian *Drosophila* (16). In contrast to G & T we consider that there is a growing realization that critical analyses of many models of speciation reveals substantial weaknesses in theoretical, experimental and field evidences for these (8, 17-22). We suggest that a much more critical approach will result in a rejection of many currently accepted models, and a consequent better understanding of speciation (8, 16). Hence we reject G & T's dictate that "... universal truths concerning speciation should not be expected".

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