

Journal of Heredity, 2015, 767–768 doi:10.1093/jhered/esv072 Letter to the Editor Advance Access publication August 29, 2015



### Letter to Editor

# Response to May and Delany: We Never Said Wright was Wrong

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We welcome the constructive comments of May and Delany (2015; MD) on our recent review (Allendorf et al. 2015). We appreciate their insightful description of the chromosomal basis of residual tetrasomy and pseudolinkage in salmonid fishes. We have a few clarifications to make that we think will be helpful in our ongoing attempts to understand these fascinating phenomena.

First, it is crucial to recognize that we and MD are in agreement on the major issues involved here. Both residual tetrasomy and pseudolinkage result from pairing and crossover events between homeologous chromosomes stemming from the ancient polyploid event in salmonids. Pseudolinkage occurs in males from a hybrid origin and results from preferential pairing of homeologous chromosome arms from the same parental background followed by alternate disjunction.

MD state that use of a pair of metacentric and acrocentric chromosomes in our figure of residual tetrasomy and use of 2 pairs of metacentrics in our figure of pseudolinkage suggest that we believe residual tetrasomy and pseudolinkage are distinct phenomena. This is incorrect. We used different chromosomal configurations in Figures 1 and 3 to reflect that residual tetrasomy and pseudolinkage occur both between metacentric and acrocentric chromosomes and between pairs of metacentric chromosomes (e.g., Brieuc et al. 2014). We state explicitly in the fourth paragraph of the Pseudolinkage subsection that both phenomena involve crossovers between homeologous chromosomes, but that, in addition, pseudolinkage requires preferential pairing of conspecific homeologs (Allendorf et al. 2015).

MD criticize our use of the term "homeologous." Specifically, they suggest that crossovers on terminal ends of homeologous chromosomes should be considered to result from homologous pairing of homeologous chromosome arms. We agree that crossovers occur here because of near sequence identity, but we believe that referring

to "homologous" crossovers between "homeologous chromosome arms" is misleading and confusing.

It is crucial to recognize that the primary difference between the two models is that in our model crossovers occur between both pairs of homologous chromosomes. In contrast, in the model used by Wright et al., there are no homologous crossovers between the acrocentric chromosomes when there is a pair of metacentric and acrocentric chromosomes, but proper disjunction results from crossovers between homeologs (see Figures 1 and 2, Wright et al. 1983).

Finally, one source of differences in perspective between MD and us is that we have tried to be as general as possible, whereas MD only consider the salmonid literature. We provide evidence for residual tetrasomy and preferential pairing of homeologs from polyploid-derived plant species. We have tried to use general nomenclature and provide a general chromosomal model that applies to other taxa, as well as salmonids.

#### Funding

U.S. National Science Foundation (NSF) (DEB 1258203 to F.W.A.); NSF (DEB 0949053 to W.A.C. and S.L.B); The Danish Council for Independent Research's career program Sapere Aude (12-126687 to M.T.L.); Gordon and Betty Moore Foundation (1453 to J.E.S. and L.W.S.).

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