# Digest: Mechanisms of assortative mating and ecological speciation

Spencer J. Ingley[1,2,3,4] and Gil G. Rosenthal[5,6]

[1]Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27514

[2]North Carolina Museum of Natural Sciences, Raleigh, NC 27601

[3]Department of Biology, Duke University, Durham, NC 27708

  [4]E-mail: sjingley@gmail.com

[5]Department of Biology, Texas A&M University, College Station, Texas 77843

[6]Centro de Investigaciones Científicas de las Huastecas "Aguazarca", Calnali Hidalgo 43230, Mexico

The origin of species has long held the attention of students of biology, yet elements of this process have remained enigmatic. Of specific interest to many has been the role of assortative mating in speciation (Bolnick and Fitzpatrick 2007). Assortative mating, which occurs when individuals prefer mates who possess characteristics similar to their own, has been recognized as a critical component of speciation despite a general lack of understanding of the underlying mechanisms that drive this pattern. In this issue, Greenway et al. employ cutting-edge experimental approaches in a unique study system to provide a fascinating and robust test of alternative mechanisms that can give rise to assortative mating, providing valuable insight into this fundamental process which generates biodiversity on our planet.

Greenway et al. test three alternative mechanisms hypothesized to contribute to assortative mating: condition dependence, "magic" traits, and reinforcement. Models invoking condition-dependent mechanisms posit that the expression of signals used during mate choice is indicative of an individual's degree of local adaptation (Weissing et al. 2011). This does not require divergence in mating preferences among populations because assortative mating results from the reduced expression of traits that are putatively indicative of heritable correlates of viability, which should be reduced in both maladapted immigrants and hybrids. "Magic" trait mechanisms hinge on mating preferences or cues that are correlated with ecological traits under divergent selection (Servedio and Kopp 2012). Finally, reinforcement can drive assortative mating through direct selection on mating preferences to reduce costly hybridization with maladapted individuals from divergent populations. During reinforcement, divergent ecological traits can be co-opted as mating signals, resulting in patterns similar to magic trait mechanisms, though these preferences should be pronounced only in zones where the opportunity to hybridize is high.

A key to Greenway et al.'s success—which allowed them to clear an obstacle that has limited work in this area in the past—was their ability to experimentally disentangle the alternative hypotheses described above. The authors used computer-generated animations to control for natural trait covariation found in live-bearing fish that occur either in extreme (toxic sulfide-rich water) or benign environments. Using *anyFish* (Veen et al. 2013; Ingley et al. 2015), a novel animation platform for creating controlled behavioral stimuli for fish studies, Greenway et al. created fish animations that differed only in body shape, reflecting either differences in locally adaptive traits (e.g., head size) or body condition (e.g., due to differences in nutritional state). They presented these animations to live fish from several populations that either occurred in close proximity to or a great distance from divergently adapted populations. Females failed to show a preference for condition-dependent traits, and indeed only preferred local head shape when there was potential for gene flow between ecologically divergent populations, consistent with classic reinforcement models.

These findings add to the growing evidence that condition-dependence of male traits is of limited relevance to mate-choice evolution (Ryan and Cummings 2013), and potentially challenge the importance of true magic traits during speciation. Rather, they suggest that adaptive traits may merely be co-opted as mating signals during the reinforcement process. This work also highlights a
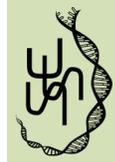
broader conceptual problem related to magic traits. While magic traits require that mating traits be correlated with ecological adaptation, this requirement is not sufficient. Equally important is the ability to identify the forces that give rise to divergent preferences that ultimately facilitate assortative mating. Future research will need to focus more on the factors shaping mating preferences, in addition to simply studying the cues upon which those preferences act.

## LITERATURE CITED

Bolnick, D. I., and B. M. Fitzpatrick. 2007. Sympatric speciation: models and empirical evidence. Ann. Rev. Ecol. Evol. Syst. 38:459.

Ingley, S. J., M. Rahmani Asl, C. Wu, R. Cui, M. Gadelhak, W. Li, J. Zhang, J. Simpson, C. Hash, T. Butkowski, et al. 2015. anyFish 2.0: an open-source software platform to generate and share animated fish models to study behavior. SoftwareX 3–4:13–21.

Ryan, M. J., and M. E. Cummings. 2013. Perceptual biases and mate choice. Ann. Rev. Ecol. Evol. Syst. 44:437–459.

Servedio, M. R., and M. Kopp. 2012. Sexual selection and magic traits in speciation with gene flow. Curr. Zool. 58:510–516.

Veen, T., S. J. Ingley, R. Cui, J. Simpson, M. R. Asl, J. Zhang, T. Butkowski, W. Li, C. Hash, J. B. Johnson, et al. 2013. anyFish: an open-source software to generate animated fish models for behavioural studies. Evol. Ecol. Res. 15:361–375.

Weissing, F. J., P. Edelaar, and G. S. van Doorn. 2011. Adaptive speciation theory: a conceptual review. Behav. Ecol. Sociobiol. 65:461–480.

Associate Editor: K. Moore
Handling Editor: M. Noor