



REPLY TO ROSENTHAL ET AL.:

Both premating and postmating isolation likely contributed to manakin hybrid speciation

Alfredo O. Barrera-Guzmán^a, Alexandre Aleixo^b, Matthew D. Shawkey^c, and Jason T. Weir^{a,d,e,1}

In a recent letter to the editor, Rosenthal et al. (1) object to our proposal (2) that evolution of a unique male crown color in the avian hybrid species *Lepidothrix vilasboasi* might generate premating reproductive isolation from its parental species. Rosenthal et al.'s (1) key argument, derived from a narrow class of theoretical models of sexual selection (3), is that trait divergence might facilitate species collapse upon secondary contact rather than prevent it. We agree that species collapse is a distinct possibility, especially if female preferences have not yet diverged. Divergence of female preference is currently untested, as we make clear in our paper (2), and is the focus of ongoing research.

A broader question than the one raised by Rosenthal et al. (1) is whether premating isolation in and of itself is ever sufficient to prevent species collapse upon secondary contact. While there do appear to be specific scenarios in which premating isolation is sufficient (4), we argue that even high levels of assortative mating facilitated by divergence in song, plumage, and other secondary sexual characters are generally insufficient to prevent species collapse without the evolution of postmating isolation (5, 6). Simulations with strong assortative mating in the absence of postmating isolation result in species collapse within secondary contact zones, but premating and postmating isolation can work jointly to generate greater reproductive isolation than postmating isolation alone (6). In our paper (2) we argue that *L. vilasboasi* likely possesses moderate levels of both pre- and postmating isolation. Any premating isolation generated by the different male

crown colors of *Lepidothrix* manakins probably helps to reinforce reproductive isolation generated by postmating isolation, a scenario that Rosenthal et al. (1) do not dispute.

L. vilasboasi has a small geographic range (~400-km long by 250-km wide) which, given its likely current geographic contact with the parental species (following an initial allopatric phase), should have been strongly affected by introgression if reproductive isolation were absent. We see no evidence of introgression of the brilliant white and opalescent crown colors of the parent species into the geographic range of *L. vilasboasi*, and our genomic analyses indicate that *L. vilasboasi* individuals from across their geographic range possess consistent genomic proportions derived from both parental species, as expected if they are reproductively isolated. Well-documented hybrid species like the Italian sparrow show similar patterns of consistent genomic proportions (7). The question now arises whether levels of postzygotic isolation are sufficient to prevent species collapse in secondary contact, or whether the combined effect of both pre- and postmating isolation is at play (see ref. 8). Given the young ages of the three species involved, it seems likely that postmating isolation will have evolved to only moderate levels and that premating isolation driven by the unique crown colors of these species might also be very important in maintaining species distinctions. However, the role of premating isolation driven by crown-color differences in contributing to speciation will remain speculative until female preferences are better understood in this system.

- 1 Rosenthal GG, Schumer M, Andolfatto P (2018) How the manakin got its crown: A novel trait that is unlikely to cause speciation. *Proc Natl Acad Sci USA* 115:E4144–E4145.
- 2 Barrera-Guzmán AO, Aleixo A, Shawkey MD, Weir JT (2018) Hybrid speciation leads to novel male secondary sexual ornamentation of an Amazonian bird. *Proc Natl Acad Sci USA* 115:E218–E225.

^aDepartment of Ecology and Evolutionary Biology, University of Toronto, Toronto, M5S 3B2 ON, Canada; ^bDepartment of Zoology, Museu Paraense Emílio Goeldi, Belém, Pará 66040-170, Brazil; ^cDepartment of Biology, University of Ghent, 9000 Ghent, Belgium; ^dDepartment of Biological Sciences, University of Toronto Scarborough, Toronto, M1C 1A4 ON, Canada; and ^eDepartment of Ornithology, Royal Ontario Museum, Toronto, M5S 2C6 ON, Canada

Author contributions: A.O.B.-G., A.A., M.D.S., and J.T.W. wrote the paper.

The authors declare no conflict of interest.

Published under the [PNAS license](#).

¹To whom correspondence should be addressed. Email: jason.weir@utoronto.ca.

Published online April 18, 2018.

- 3 Servedio MR, Bürger R (2014) The counterintuitive role of sexual selection in species maintenance and speciation. *Proc Natl Acad Sci USA* 111:8113–8118.
- 4 Servedio MR, Boughman JW (2017) The role of sexual selection in local adaptation and speciation. *Annu Rev Ecol Syst* 48:85–109.
- 5 Hudson EJ, Price TD (2014) Pervasive reinforcement and the role of sexual selection in biological speciation. *J Hered* 105:821–833.
- 6 Pulido-Santacruz P, Aleixo A, Weir JT (2018) Morphologically cryptic Amazonian bird species pairs exhibit strong postzygotic reproductive isolation. *Proc Biol Sci* 285:20172081.
- 7 Elgvin TO, et al. (2017) The genomic mosaicism of hybrid speciation. *Sci Adv* 3:e1602996.
- 8 Cooney CR, Tobias JA, Weir JT, Botero CA, Seddon N (2017) Sexual selection, speciation and constraints on geographical range overlap in birds. *Ecol Lett* 20:863–871.