

ability and radiance vision but instead employ both simultaneously, much as humans use both chromatic and achromatic information to assess a scene. Thus, at close range, a polarization-sensitive animal can likely use both polarization and radiance cues to obtain a more complete and potentially more discernible view of an object. However, it is unlikely that an animal can combine the two visual modalities to increase sighting distance. Once one modality drops below the threshold for detection, it cannot improve the other modality's sighting distance limit. This is analogous to underwater color vision, which can provide additional information at close range, but does not increase sighting distance because the image of the target at long range generally has the same color as the background due to the effects of the intervening water (i.e. at a great enough distance, all fish in blue water eventually look blue).

While our study is limited in location and number of species, it is the first to combine *in situ* polarization imagery with a realistic model of visual perception that allows us to quantitatively compare the utility of polarization vision versus radiance vision when viewing silvery fish. The results show clearly that silvery fish, while by no means cryptic relative to polarization vision, are nevertheless seen at the greatest distances using radiance information alone. This should be examined in other species, habitats, and especially at viewing angles further from horizontal to determine if there is a situation in which polarization vision can increase detection range. In addition, it is known that various polarization-based haze-reduction algorithms [1] can, in certain situations, increase the sighting distance of any target, silvery or not. Because it is not known whether these algorithms have been implemented by any animal, they were not the focus of this study. However, preliminary modeling of the simplest of these strategies — using the vertical channel to minimize the background light and thus boost achromatic contrast — show some, though often minimal, benefit for two-thirds of the sampled fish (Supplemental information), but at the cost of reducing the sighting distance for the remainder of the fish. Further research should explore whether this

algorithm or other more complex ones are used by extant visual systems.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures and one figure can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.07.030>.

AUTHOR CONTRIBUTIONS

S.J. conceived the study, V.G. and S.P. developed and calibrated the polarization camera, N.J.M. collected the imagery, S.J. and Y.L.G. developed and implemented the visual model, and all interpreted the results and wrote the manuscript.

REFERENCES

1. Cronin, T.W., Johnsen, S., Marshall, N.J., and Warrant, E.J. (2014). *Visual Ecology* (Princeton University Press).
2. Denton, E.J. (1970). On the organization of reflecting structures in some marine animals. *Phil. Trans. R. Soc. B.* 258, 285–313.
3. Jordan, T.M., Partridge, J.C., and Roberts, N.W. (2012). Non-polarizing broadband multilayer reflectors in fish. *Nature Photon.* 6, 759–763.
4. York, T., Powell, S.B., Gao, S., Kahan, L., Charanya, T., Saha, D., Roberts, N.W., Cronin, T.W., Marshall, J., Achilefu, S. *et al.* (2014). Bioinspired polarization imaging sensors: from circuits and optics to signal processing algorithms and biomedical applications: analysis at the focal plane emulates nature's method in sensors to image and diagnose with polarized light. *Proc. IEEE*, 102, 1450–1469.
5. How, M.J., and Marshall, N.J. (2013). Polarization distance: a framework for modelling object detection by polarization vision systems. *Proc R. Soc. B.* 281, 20131632.
6. Cronin, T.W., and Shashar, N. (2001). The linearly polarized light field in clear, tropical marine waters: Spatial and temporal variation of light intensity, degree of polarization and e-vector angle. *J. Exp. Biol.* 204, 2461–2467.
7. Shashar, N., Hagan, R., Boal, J.G. and Hanlon, R.T. (2000). Cuttlefish use polarization sensitivity in predation on silvery fish. *Vision Res.* 40, 71–75.
8. Temple, S., Pignatelli, V., Cook, T., How, M.J., Chiou, T.H., Roberts, N.W. and Marshall N.J. (2012). High-resolution polarisation vision in a cuttlefish. *Curr. Biol.* 22, R121–R122.
9. Roberts, N.W., Porter, M.L., and Cronin, T.W. (2011). The molecular basis of mechanisms underlying polarization vision. *Phil. Trans. R. Soc. B.* 366, 627–637.
10. Bernard, G.D., and Wehner, R. (1977). Functional similarities between polarization vision and color vision. *Vision Res.* 17, 1019–1028.

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Correspondence Evidence for meiotic sex in bdelloid rotifers

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In their study of genetic exchange in the bdelloid rotifer *Adineta vaga*, Debortoli *et al.* [1] conclude that the patchwork pattern of allele sharing among three individuals in the genomic regions they examined is “...unlikely to arise in cases of PTH (*Oenothera*-like) meiosis since haplotypes are transferred as entire blocks...” and therefore that “Genetic exchange among bdelloid rotifers is more likely due to horizontal gene transfer than to meiotic sex.” This assumes without justification that horizontal gene transfer (HGT) in bdelloids precludes the sexual transmission of entire haplotypes, for which we have reported evidence in the bdelloid *Macrotrachela quadricornifera* [2]. And it does not consider the contribution to such a patchwork pattern that would result from conversion and subsequent outcrossing, even in *Oenothera*-like systems.

Moreover, the group of three individuals studied by Debortoli *et al.*, in which the shared sequences are considerably diverged, is not well suited to the detection of sex in a population that may include numerous distinct *Oenothera*-like haplotypes. For that purpose, one should employ individuals whose shared sequences are identical or nearly so in order to enrich for direct descendants of the F1 from a cross. Otherwise, subsequent outcrossing could replace the shared haplotypes with others, removing the evidence for transmission of entire haplotypes. It is therefore important to note that in the group of three individuals we studied the shared sequences were either identical or very nearly so, allowing us to observe the specific and unusual pattern of sharing expected for *Oenothera*-like meiosis. To explain the presence of such

closely related individuals among the six members of the mitochondrial clade we sampled, we drew upon the proposal of Tucker *et al.* [3] that the rapid extinction of obligately asexual *Daphnia pulex* is driven by the uncovering of recessive deleterious mutations by gene conversion. In bdelloids, occasional outcrossing would restore heterozygosity, increasing fitness and the relative abundance of descendants of recent outcrossing, while other lines would continue to suffer clonal erosion, reflecting an advantage of sex of possible importance in other systems as well.

Debortoli *et al.* suggest that the pattern of sharing we observed in *M. quadricornifera* may have been produced by HGT of long segments at multiple sites throughout the genome, rather than by transmission of entire haplotypes. But this takes no account of our discussion of this possibility, showing that even with massive HGT and implausible restrictions on the direction and source of transfers it would be highly unlikely.

Whether bdelloid rotifers evolved without meiosis or instead engage in sexual reproduction with meiotic segregation of entire parental haplotypes bears on fundamental questions regarding the evolutionary advantage of sex. While awaiting full genome sequencing of the allele-sharing individuals of *M. quadricornifera*, present evidence argues for the occurrence in bdelloid rotifers of sexual reproduction with *Oenothera*-like meiosis.

REFERENCES

1. Debortoli, N., Li, X., Eyers, I., Fontaneto, D., Hespels, B., Tang, C.Q., Flot, J.-F., and Van Doninck, K. (2016). Genetic exchange among bdelloid rotifers is more likely due to horizontal gene transfer than to meiotic sex. *Curr. Biol.* 26, 723–732.
2. Signorovitch, A., Hur, J., Gladyshev, E., and Meselson, M. (2015). Allele sharing and evidence for sexuality in a mitochondrial clade of bdelloid rotifers. *Genetics* 200, 581–590.
3. Tucker, A.E., Ackerman, M.S., Eads, B.D., Xu, S., and Lynch, M. (2013). Population-genomic insights into the evolutionary origin and fate of obligately asexual *Daphnia pulex*. *Proc. Natl. Acad. Sci. USA* 110, 15740–15745.

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Response to Signorovitch *et al.*

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Signorovitch *et al.* [1] comment that an *Oenothera*-like meiosis [2] could produce a pattern similar to what we observed in our study of natural isolates of the bdelloid rotifer *Adineta vaga*, which we attributed to horizontal gene transfers (HGTs) [3]. Indeed, our HGT hypothesis appears at first sight difficult to conciliate with their observation of a congruent pattern of allele sharing at four large loci possibly located on different chromosomes [4]. However, one might imagine conditions under which massive horizontal gene transfer between bdelloid individuals could produce such a pattern, notably if the individuals involved had previously lost most of their heterozygosity because of their exposure to frequent desiccation (which produces DNA double-strand breaks [5]). In the published *A. vaga* genome the loss of heterozygosity due to large-scale gene conversion events or break-induced replication covers only about 10% of the genome [6], but this percentage may be much higher in environmental isolates that often experience desiccation. Besides, if an *Oenothera*-like mode of meiosis occurs in bdelloids frequently enough to be detected in a single sampling of 29 individuals (as in [4]), one would expect males and meiosis to be observed at least occasionally, and instances of congruent allele sharing across loci should turn up frequently in genetic surveys. This was not the case in [3]: among the 82 *A. vaga* individuals sequenced for four nuclear markers, no trio of individuals presented congruent patterns of shared sequences at different loci. For these reasons, and in the absence of any direct evidence for an *Oenothera*-like meiosis in bdelloids, we still consider inter-bdelloid HGTs a more parsimonious explanation for our results.

Clearly, additional multilocus surveys of allele sharing in bdelloid populations will be required to solve the puzzling discrepancy between our observations

and those of Signorovitch *et al.*, as well as to determine the mechanism and frequency of genetic exchange among bdelloids. A completely assembled bdelloid genome sequence would also allow us to test the hypothesis of an *Oenothera*-like mode of meiosis: one prediction of this model is that pairs of colinear telomeric regions should be detected (see Figure 6 in [3]). Besides, one might imagine that several distinct mechanisms mediate genetic exchange in bdelloids, possibly in a genus or clade-specific fashion (notably, the uneven chromosome numbers of *Philodina rosela* and *Habrotricha tridens* mentioned in [4] do not seem compatible with the *Oenothera* model, in which there should be an equal number of α and β chromosomes [2]). Whatever the outcome, this is an exciting time for rotiferology, as upcoming population genomic surveys will allow us to unravel and quantify how bdelloid rotifers, which were until recently dubbed “ancient asexual scandals” [7], actually exchange genetic information.

REFERENCES

1. Signorovitch, A., Hur, J., Gladyshev, E., and Meselson, M. (2016). Evidence for meiotic sex in bdelloid rotifers. *Curr. Biol.* 26, R754–R755.
2. Golczyk, H., Massouh, A., and Greiner, S. (2014). Translocations of chromosome end-segments and facultative heterochromatin promote meiotic ring formation in evening primroses. *Plant Cell* 26, 1280–1293.
3. Debortoli, N., Li, X., Eyers, I., Fontaneto, D., Hespels, B., Tang, C.Q., Flot, J.-F., and Van Doninck, K. (2016). Genetic exchange among bdelloid rotifers is more likely due to horizontal gene transfer than to meiotic sex. *Curr. Biol.* 26, 723–732.
4. Signorovitch, A., Hur, J., Gladyshev, E., and Meselson, M. (2015). Allele sharing and evidence for sexuality in a mitochondrial clade of bdelloid rotifers. *Genetics* 200, 581–590.
5. Hespels, B., Knapen, M., Hanot-Mambres, D., Heuskin, A.C., Pineux, F., Lucas, S., Koszul, R., and Van Doninck, K. (2014). Gateway to genetic exchange? DNA double-strand breaks in the bdelloid rotifer *Adineta vaga* submitted to desiccation. *J. Evol. Biol.* 27, 1334–1345.
6. Flot, J.-F., Hespels, B., Li, X., Noel, B., Arkhipova, I., Danchin, E.G.J., Hejnol, A., Henrissat, B., Koszul, R., Aury, J.-M., *et al.* (2013). Genomic evidence for ameiotic evolution in the bdelloid rotifer *Adineta vaga*. *Nature* 500, 453–457.
7. Schwander, T. (2016). The end of an ancient asexual scandal. *Curr. Biol.* 26, R233–R235.

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