Dispatches

Sexual Dimorphism: Why the Sexes Are (and Are Not) Different

Sex differences often call sexual selection to mind; however, a new damselfly study cautions on being too hasty, and implicates viability selection in the evolution of male and female colouration.

David Punzalan and David J. Hosken

While males and females obviously differ in their genitalia, sexual dimorphism — differences in male and female physiology, morphology or behavior — often extends far beyond this, and these sex differences have long fascinated biologists. In fact, it was the need to explain the widespread existence of sex-specific trait elaboration that played a key role in Darwin's second major revelation: sexual dimorphism could be attributed to selection arising from differential mating success, or sexual selection [1]. Sexual selection and sexual dimorphism have remained intimately connected ever since, to the extent that sexual dimorphism has at times been used as a proxy of the strength of sexual selection in comparative studies [2]. But there are numerous alternative explanations for sexual dimorphism, most of which invoke sex-specific natural (viability) selection. Fittingly, it was Wallace [3] who was one of the original proponents of ecological causes of sexual dimorphism, asserting that it reflected the operation of viability selection, corresponding to fundamental differences in the niches the sexes occupy. Although Darwin was clearly aware that the sexes could differ for purely ecological reasons, the disagreement was over the generality of each mechanism as a generator of sexual dimorphism [4]. While ecological explanations for dimorphism have received attention both theoretically [5] and empirically [6], it is probably fair to say that, to date, Darwin's thesis has prevailed and sexual selection has dominated the collective mindset. But recent work, including a new paper by Cooper [7], suggests a renaissance of Wallace's idea of ecology generating dimorphism.

Cooper [7] reports on sexual dimorphism in the damselfly *Megalagrion calliphya*. As with many damselfly species, *M. calliphya* exhibits a peculiar twist on the standard sexual dimorphism story: females come in two genetically determined forms — a relatively dull-coloured (green) morph and a brightly coloured (red) morph that closely resembles males of the species. One of the standard explanations for the maintenance of female polymorphism in damselflies is based on a combination of male preference for the female morphs and the costs females incur from male harassment and mating. Although females clearly need males to fulfill the basic needs of reproduction, males harass females so vigorously that excessive attention from males is detrimental to female fitness. Under some ecological circumstances, such as highly male biased sex ratios and high population densities, it is thought that the brightly coloured, red female-morph is selectively favoured because it resembles males and therefore suffers reduced sexual harassment.

Cooper [7] shows this may not be the whole story. She documents female morph ratios in the wild and finds they vary along an altitudinal gradient, with the green morphs far more prevalent at low altitudes, while females are almost exclusively red at high altitudes. However, inspection of the mating rates of each morph did not suggest sexual mimicry was the driver of this pattern. Instead, the clinal variation in female morph frequency is more consistent with a putatively important ecological gradient: solar radiation increases with elevation. The clinal variation is somewhat reminiscent of patterns of insect colour dimorphism [8] and polymorphism [9] attributed to thermoregulation. In the case of *M. calliphya*, however, Cooper hypothesizes that red pigment could be an adaptation to resist the damaging effects of ultraviolet radiation. While the evidence for this is indirect, a combination of laboratory work and field observations yielded data consistent with the hypothesis — red pigment appears to have anti-oxidant properties and the daily numbers of red morphs at mating sites is correlated with the intensity of solar radiation. Males, too, are redder at high elevations, further suggesting red pigmentation has more to do with viability than sexual mimicry. So the puzzle of dimorphism persists, but given the benefits of red pigmentation, the question is probably no longer concerned with explaining the existence of red females, rather it is the persistence of green females that begs explanation. Furthermore, is the female polymorphism the result of an evolutionary 'addition' to a green ancestor or a red one?

The answer to the first question requires testing, but there are a number of plausible explanations involving the viability costs of maintaining bright pigmentation. Resolving the second question is, unfortunately, more difficult. Female polymorphism happens to occur so frequently in this group of insects [10] that it is difficult to guess the ancestral state without more phylogenetic data. Regardless, this highlights another difference between Darwin and Wallace in their macroevolutionary views on sexual dimorphism; *viz* which sex tends to deviate from the ancestral state. Darwin pointed out that the plumage of closely related bird species is often more disparate among males of the species and attributed this to sexual selection. Though some previous studies lend support to the notion that sexual selection frequently generates more marked phenotypic diversification in males, there are also some clear counter examples of rampant sexual dimorphism that are best explained by the phenotypic diversification of females [11].

Ultimately, distinguishing between ecological and sexual causes of sexual dimorphism is not always straightforward because sexual selection is often closely tied to ecology [12] and sexually selected traits are equally associated with ecologically-mediated viability costs. In turn, sex differences in ecology can often be attributed to sexual selection favouring sexually divergent use of resources. Although the distinction is valuable for operational purposes, the line between the two causes is not only blurry, it is somewhat beside the point. Irrespective of the selective mechanisms (be they 'ecological' or 'sexual'), sexual dimorphism reflects the operation of multiple selective factors that, combined, exert sexually antagonistic *net* selection. The most elusive goal for all who study phenotypic evolution, including the phenomenon of sexual dimorphism, is inferring the selective mechanisms that have shaped this pattern of variation. Cooper's study [8] nicely illustrates one way to do so, applying a classic approach of analyzing variation in morph frequencies to the problem of sex-specific polymorphism.

Undoubtedly, the sexes are often subject to very different selection, and in light of this, one might wonder why sexual dimorphism is not even more frequent. One possibility is that a common genetic architecture underlying sexually homologous traits limits the independent evolution of the sexes [13]. However, these intersex genetic correlations are expected to break down over time and some open questions in this field are concerned with the degree to which these correlations might constrain the evolution of dimorphism and/or adaptation [14,15]. Sexual dimorphism almost inevitably reflects past sexually antagonistic selection, but whether it reflects resolved (intralocus) sexual conflict is debatable and has only recently begun to be investigated in any detail [16,17].

We have learned a lot since Darwin and Wallace famously disagreed about the primacy of selective mechanism generating sexual dimorphism, but in some ways old debates continually bubble away beneath the surface, only to rear up and reignite from time to time. We should certainly be aware that sexual dimorphism is not a carte blanche indicator of sexual selection, and equally sexual dimorphism may not mean sexual conflicts are resolved. In short, there is still a lot to learn and it seems the long-standing interest in sexual differences is likely to continue for some time yet.

References

1. Darwin, C. (1874). The Descent of Man; and Selection in Relation to Sex, 2nd edn (New York, NY: Crowell).
2. Barraclough, T.G., Harvey, P.H., and Nee, S. (1995). Sexual selection and taxonomic diversity in passerine birds. Proc. R. Soc. Lond. B *259*, 211–215.
3. Wallace, A.R. (1889). Darwinism: an Exposition of the Theory of Natural Selection with Some of its Applications, 2nd edn. (London, UK: MacMillan).
4. Andersson, M. (1994). Sexual Selection. (Princeton, NJ: Princeton University Press).
5. Slatkin, M. (1984). Ecological causes of sexual dimorphism. Evolution *38*, 622–630.
6. Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. *64*, 419–461.
7. Cooper, I.A. (2010). Ecology of sexual dimorphism and clinal variation of coloration in a damselfly. Am. Nat. *176*, 566–572.
8. Kingsolver, J.G. (1983). Thermoregulation and flight in *Colias* butterflies: elevational patterns and mechanistic limitations. Ecology *64*, 534–545.
9. de Jong, P.W., and Brakefield, P.M. (1998). Climate and change in clines for melanism in the two-spot ladybird, *Adalia bipunctata* (Coleoptera, Coccinellidae). Proc. R. Soc. Lond. B *265*, 39–43.
10. Fincke, O.M. (2004). Polymorphic signals of harassed female odonates and the males that learn them support a novel frequency-dependent model. Anim. Behav. *67*, 833–845.
11. Kunte, K. (2008). Mimetic butterflies support Wallace's model of sexual dimorphism. Proc. R. Soc. Lond. B *275*, 1617–1624.
12. Emlen, S.T., and Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. Science *197*, 215–222.
13. Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution *34*, 292–305.
14. Cox, R.M., and Calsbeek, R. (2009). Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. Am. Nat. *173*, 176–187.
15. Poissant, J., Wilson, A.J., and Coltman, D.W. (2010). Sex-specific genetic variance and the evolution of sexual dimorphism: a systematic review of cross-sex genetic correlations. Evolution *64*, 97–107.
16. Harano, T., Okada, K., Nakayama, S., Miyatake, T., and Hosken, D.J. (2010). Intralocus conflict unresolved by sex-limited trait expression. Curr. Biol. *20*, 2036–2039.
17. Bonduriansky, R., and Chenoweth, S.F. (2009). Intralocus sexual conflict. Trends Ecol. Evol. *24*, 280–288.

Centre for Ecology and Conservation, University of Exeter, Cornwall campus, Penryn, Cornwall TR10 9EZ, UK.
E-mail: D.Punzalan@exeter.ac.uk

DOI: 10.1016/j.cub.2010.09.067

Vascular Lumen Formation: Negativity Will Tear Us Apart

Functional blood vessels are essential for vertebrate development, but how endothelial cells initiate lumen formation during vasculogenesis is not known. A new study now reveals that electrostatic repulsion is key.

Renée M. Robbins and Greg J. Beitel*

Establishing patent blood vessels is an essential milestone for developing vertebrates, but exactly how cord-like clusters of endothelial cells create a lumen during vasculogenesis has not been established. Several sialomucins, including CD34 and the podocalyxin-like protein PODXL, localize to presumptive lumenal faces, which suggests that they might assist in lumen formation [1–3]. Sialomucins are transmembrane proteins that are extensively glycosylated and modified with sialic acid on their extracellular domains [3]. Although there are multiple possible functions for sialomucins in lumen formation [3,4], an appealing and almost 30-year-old hypothesis is that the negatively charged sialic acid creates electrostatic repulsion that helps separate the lumenal faces [5–7]. In a study published in this issue of *Current Biology*, Strilić *et al.* [8] now provide strong support for this hypothesis using an impressive combination of *in vivo* and *in vitro* approaches, ranging from pharmacological treatments of embryos to atomic force microscopy to a clever new cell adhesion assay.

This group previously showed that, during vasculogenesis, the mouse