

The colorful language of Australian flowers

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The enormous increase in phylogenetic information in recent years has allowed many old questions to be reexamined from a macroevolutionary perspective. We have recently considered evolutionary convergence in floral colors within pollination syndromes, using bird-pollinated species in Australia. We combined quantitative measurements of floral reflectance spectra, models of avian color vision, and a phylogenetic tree of 234 Australian species to show that bird-pollinated flowers as a group do not have colors that are significantly different from the colors of insect-pollinated flowers. However, about half the bird-pollinated flowers have convergently evolved a narrow range of colors with dominant long-wavelength reflection far more often than would be expected by chance. These convergent colors would be seen as distinctly different from other floral colors in our sample when viewed by honeyeaters (family Meliphagidae), birds with a phylogenetically ancestral type of color vision and the dominant avian pollinators in Australia. Our analysis shows how qualitative ideas in natural history, like the concept of pollination syndromes, can be given more precise definition and rigorous statistical testing that takes into account phylogenetic information.

Bird-pollinated flowers are often red.¹ This simple observation fits the concept of pollination syndromes, suites of floral traits thought to have evolved among distantly related species to appeal to and facilitate visits by various classes of pollinators, such as birds, short-tongued bees,

long-tongued bees, moths, and so on. Although this concept has been entrenched in pollination ecology for decades,² the phenotypic traits in pollination syndromes are often described with little more precision than casual observation affords. And although pollination syndromes would be outstanding examples of repeated convergent adaptation due to biotic interaction, quantitative measures and statistical confirmation of convergence are lacking for pollination syndromes, as for most putatively convergent traits.³ These and other deficiencies in the evidence for pollination syndromes have cast doubt on their existence.⁴ We recently rectified 2 of these deficiencies in an examination of floral colors among bird-pollinated Australian angiosperms: we represented colors as they would be perceived by birds rather than by humans, and we used a new analytical technique to quantify the extent of convergent evolution and to test it statistically against null expectations.⁵

Floral color is usually described in the ecological literature by the color categories of human color perception, although it has been appreciated for some time that this approach is inadequate.⁶ In order to treat color in a manner relevant to pollinators (and therefore to pollinator-mediated selection) we quantitatively measured reflectance spectra of flowers and used a model of bird vision that translates these spectra to points in a “color tetrahedron” in which the location a point relative to the 4 vertices of the tetrahedron represents the degree of stimulation of each of the 4 classes of color photoreceptors in avian visual systems. There are 2 classes of bird color vision

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that differ primarily in their sensitivity to violet and UV light.⁷ The violet sensitive type, which is ancestral in the phylogeny of birds, is the visual system of the family Meliphagidae (honeyeaters), the most important avian nectarivores and flower pollinators in Australia.⁸ We modeled both classes of color vision, violet-sensitive and UV-sensitive, in our analysis.

We found that the colors of Australian bird-pollinated flowers were widely distributed in the color tetrahedrons, and not strongly dissimilar overall to the range of color loci found among insect-pollinated flowers. This result tends to support the sceptics of the pollination syndrome concept. However, when floral colors were modeled according to violet-sensitive avian color vision, bird-pollinated flowers were almost evenly divided between 2 discrete regions of the color tetrahedron: an arc corresponding to violet to yellow flowers (using human color categories), and a narrow arm extending toward the red vertex of the tetrahedron. We initially thought that the unoccupied gap between these clusters might have been an artifact of inadequate sampling, but when we augmented our original data set with reflectance spectra from an additional 23 bird-pollinated species, the new species again occupied the violet-yellow arc and the narrow red arm, with a gap between them. Intriguingly, this pattern disappeared when we modeled the spectra in UV-sensitive avian vision. Birds with this type of color vision would not perceive a gap in floral color between the red-arm species and the other species.

We also wished to quantify the degree of convergent evolution that had occurred

among species in the red arm of color space. Convergence has typically been thought of as evolution by many species toward an adaptive optimum, quantified as the *degree* of phenotypic similarity among taxa (using distances in a phenotypic space, for example). But often the *frequency* of convergence, measured by the number of lineages that evolved into a given region of phenotypic space, is more meaningful. Using published phylogenetic information, we assembled a phylogenetic tree for our sample species and used standard techniques to estimate floral colors at internal nodes in the phylogeny, that is, the floral colors of the common ancestors of the extant lineages. With this information, we used a newly developed technique to count the number of lineages that evolved a red floral color (i.e., a position inside the minimum ellipsoid containing all the red-arm species in the color tetrahedron) from a non-red ancestor. These counts of phylogenetic entries into a target region of morphospace provide an index of convergent evolution. We then tested whether this index represented statistically significant convergence compared with null expectations derived from repeated simulations of color evolution according to a random-walk process along the branches of the phylogenetic tree. We found that red-arm colors had evolved independently 31 times among our sample species, while a mean of only 5.5 independent origins would be expected under random-walk evolution, an indication that strong directional selection had shaped the distribution of floral colors

among our sample species. The most likely source of this selection would be from honeyeaters, a family that has influenced the evolution of Australian flowers since the Eocene⁹ and that is currently the dominant group of pollinating birds in Australia.⁸ With their violet-sensitive type of color vision, honeyeaters would see the red-arm floral colors as particularly distinct from the flower colors of other Australian species.

Our methods in this study are broadly applicable to any traits that can be described in a quantitative morphospace, especially when a complex region of morphospace rather than a single point constitutes the putatively convergent state. Indeed, these and other techniques are currently being used to detect convergence in both morphology and mechanical performance in other taxa. We are also looking into global comparisons of bird-pollinated species to determine if intercontinental convergence in flower color occurs when dominant pollinators share similar visual systems. This kind of work is greatly facilitated by the ease of measurement of floral spectra with modern spectrophotometers, models of relevant pollinator vision, and phylogenetic comparative methods to assess potential convergence. With these new measurement tools and analytic tools, the longstanding issue of pollination syndromes can be examined more rigorously and at larger geographic and phylogenetic scales.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

References

1. Raven PH. Why are bird-visited flowers predominantly red? *Evolution* 1972; 26:674; <http://dx.doi.org/10.2307/2407064>
2. Waser NM. Specialization and generalization in plant–pollinator interactions: an historical perspective. In: Plant–pollinator interactions: from specialization to generalization. Waser NM, Ollerton J, eds. Chicago: University of Chicago Press, 2006; 3-17.
3. McGhee G. *Convergent Evolution: Limited Forms Most Beautiful*. MIT Press: London; 2011.
4. Ollerton J, Alarcón R, Waser NM, Price MV, Watts S, Cranmer L, Hingston A, Peter CI, Rotenberry J. A global test of the pollination syndrome hypothesis. *Ann Bot* 2009; 103:1471-80; <http://dx.doi.org/10.1093/aob/mcp031>; PMID:19218577
5. Burd M, Stayton CT, Shrestha M, Dyer AG. Distinctive convergence in Australian floral colours seen through the eyes of Australian birds. *Proc R Soc B: Biol Sci* 2014; 281:20132862; PMID:24573847; <http://dx.doi.org/10.1098/rspb.2013.2862>
6. Kevan PG, Chittka L, Dyer AG. Limits to the salience of ultraviolet: lessons from colour vision in bees and birds. *J Exp Biol* 2001; 204:2571-80; PMID:11511673
7. Hart NS, Hunt DM. Avian visual pigments: characteristics, spectral tuning, and evolution. *Am Nat* 2007; 169(Suppl 1):S7-26; <http://dx.doi.org/10.1086/510141>; PMID:1942609
8. Paton DC, Ford HA. Pollination by birds of native plants in South Australia. *Emu* 1977; 77:73-85; <http://dx.doi.org/10.1071/MU9770073>
9. Barker NP, Weston PH, Rutschmann F, Sauquet H. Molecular dating of the 'Gondwanan' plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. *J Biogeogr* 2007; 34:2012-27; <http://dx.doi.org/10.1111/j.1365-2699.2007.01749.x>