

RESEARCH HIGHLIGHTS

To colour a bird: The evolution of carotenoid-based colouration in passerines is shaped by sexual selection, ecology and life history

Beatriz Willink^{1,2}  | Meng Y. Wu² 

¹Department of Zoology, Stockholm University, Stockholm, Sweden

²Department of Biological Sciences, National University of Singapore, Singapore, Singapore

Correspondence

Beatriz Willink

Email: beatriz.willink@zoologi.su.se

Funding information

Vetenskapsrådet, Grant/Award Number: 2019-06444

Handling Editor: Mariano Rodriguez-Cabal

Abstract

Research Highlight: Delhey, K., Valcu, M., Dale, J., & Kempenaers, B. (2022). The evolution of carotenoid-based plumage colours in passerine birds. *Journal of Animal Ecology*, <https://doi.org/10.1111/1365-2656.13791>. Carotenoids, a class of colour pigments, are responsible for red, yellow and orange hues in nature. They play an important role in visual animals, and specially birds, where dietary carotenoids can act as honest sexual signals. Long-standing interest in the function of carotenoid-based colours has led to different hypotheses for their evolutionary drivers. Yet, comparative studies testing the generality of these hypotheses have been previously limited in phylogenetic scope or resolution. In a recent study, Delhey et al. (2022) combined sexual dichromatism, life history and environmental data to investigate the evolution of carotenoid-based colouration in the largest avian radiation, the passerines (Order: Passeriformes). The authors show that the expression of carotenoid-based colours depends on environmental availability, dietary content and body size. They also show that red carotenoids are more often evolutionarily and metabolically derived, and suggest different colours are favoured by natural and sexual selection. These findings shine new light on commonly held hypotheses of carotenoid-colour evolution and contribute to our understanding of how phenotypic diversity evolves.

The astonishing diversity of bird colour patterns has drawn the attention of sexual selection researchers for decades (Cooney et al., 2019; Read, 1987). Of the various pigments that can colour feathers, carotenoids are of special interest as they are among the traits that act as honest sexual signals (Gray, 1996; Olson & Owens, 1998). Carotenoids can have immune functions (McGraw & Ardia, 2003) and may be sensitive to oxidative stress (Costantini & Møller, 2008). Carotenoid-based colouration may therefore convey reliable information about the health of a prospective mate (von Schantz et al., 1999). Unlike other pigment types (e.g. melanins and porphyrins), carotenoids are not synthesized by most animals, and must be acquired with food (Toews et al., 2017). It is thus also hypothesized that carotenoid-based colours may indicate foraging

ability (Endler, 1980), or at least may be constrained by environmental availability and dietary intake (Biard et al., 2006). While experimental work is key to unravelling the mechanisms behind these different hypotheses, a comparative approach can provide insights about their generality. Previous studies have applied phylogenetic comparative methods to study the evolution of avian carotenoid colouration. However, these studies have focused on relatively small clades (e.g. Mahler et al., 2003), or conducted family-level analyses, bearing limited phylogenetic resolution (Olson, 2006). A recent study by Delhey et al. (2022) investigates enduring question about the evolution of carotenoid-based pigmentation, using a species-level phylogeny of passerines, the largest bird radiation worldwide.

Delhey et al. (2022) collated a vast dataset including plumage colouration, carotenoid dietary content, and ecological variables from various databases and previous studies. The authors then analysed these data to reveal broad evolutionary patterns addressing three main questions. First, how do the different carotenoid-based colours evolve? Carotenoids can produce both yellow and orange-red colouration. In birds, it is largely assumed that yellow colouration is produced by carotenoid deposition in feathers, with little or no chemical modification, whereas red colouration requires multiple metabolic reactions of the dietary carotenoids (Prum et al., 2012). Delhey et al. (2022) examined the length of metabolic pathways leading to yellow and red colouration and confirmed that red colouration more often requires metabolically derived pigments. Consequently, red colours could evolve by modifying previously acquired yellow carotenoids, and are therefore expected to arise in lineages that already display yellow signals. By comparing the marginal likelihoods of independent vs correlated evolution models, this study strongly supports previous findings of yellow colouration preceding the evolution of red (Figure 1a; Ligon et al., 2016; Prum et al., 2012). However, Delhey et al. (2022) also show that yellow is more often lost after red has evolved than vice versa.

This novel result suggests that red carotenoid-based colouration is more likely to persist through evolutionary history as a sexual signal than yellow colouration. Delhey et al. (2022) therefore also asked how the presence of the two types of pigments relates to sexual selection across the passerine tree of life. Previous studies have shown that carotenoid-based colours are often used as sexual signals for mate choice (e.g. Hill, 1990), and evolve in response to sexual selection

(Cooney et al., 2019). The study by Delhey et al. (2022) adds important nuance to this prior knowledge on carotenoid-based colour evolution by revealing that sexual dichromatism (a common proxy for the strength of sexual selection) increases the likelihood of male-specific red colouration (Figure 1b). In contrast, the origin of yellow carotenoid deposition is unlikely driven by sexual selection, and more typically shared between the sexes. The causes of this difference in evolutionary outcomes between carotenoid-based hues are currently unclear. Hence, this study opens new research avenues into the roles of sensory bias, favouring red as a sexual signal, or selection for crypsis, favouring yellow in both sexes against green backgrounds, as drivers of the distinct evolutionary patterns for red and yellow pigmentation.

Finally, Delhey et al. (2022) revisited a classical question (Endler, 1980) of whether carotenoid-based colouration is environmentally limited. If so, it is predicted that environments with higher primary plant productivity should harbour more lineages with carotenoid-based colours, by increasing the availability of dietary carotenoids, ultimately derived from plants. Delhey et al. (2022) found support for this hypothesis (Figure 1c), particularly for yellow carotenoids, which typically constitute larger patches of plumage colouration. Consistently, they also found that species with a higher content of carotenoids in their diet were more likely to have evolved both yellow and red carotenoid-based colours. Nonetheless, the results of this study suggest that the rate at which carotenoids can be consumed is perhaps even more important than environmental availability. Due to their higher metabolic rate, smaller birds ingest more food relative to their body mass, which may explain why smaller birds have higher levels of carotenoids circulating in their blood (Tella

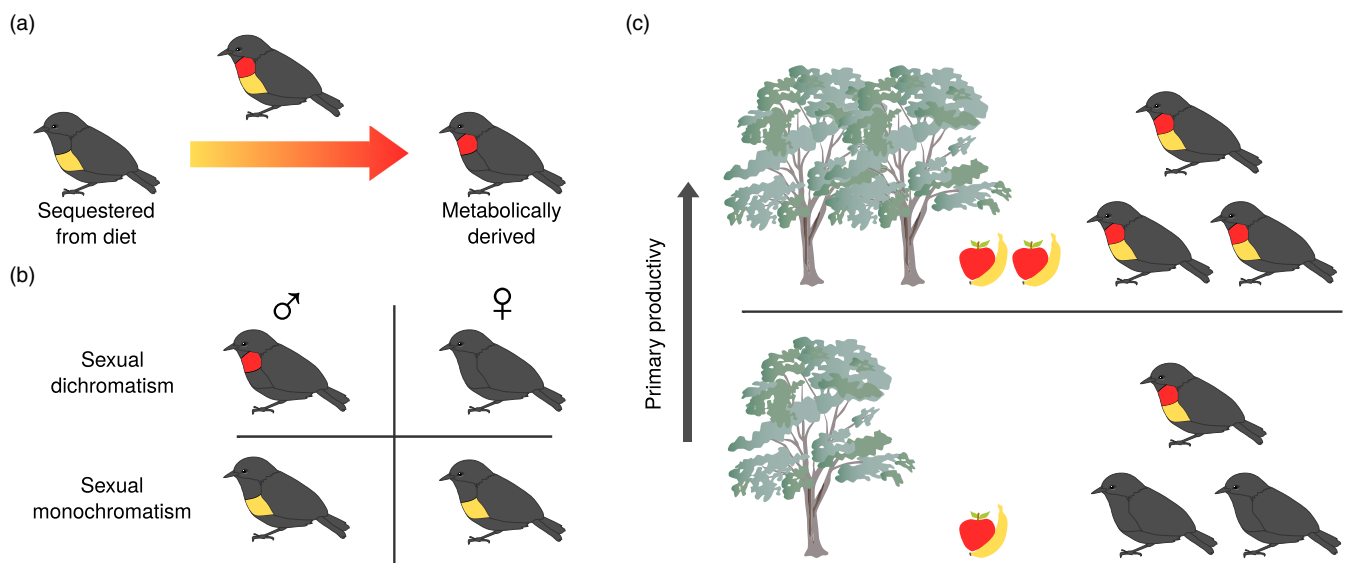


FIGURE 1 Schematic overview of some of the main results in Delhey et al. (2022). (a) Red carotenoid-based pigmentation in passerines is likely to originate after yellow carotenoid deposition has evolved, with the former colouration being more metabolically derived. (b) Sexually dichromatism is associated with the evolution red pigmentation in males and the absence of red pigmentation in females, while the evolution of yellow is not strongly linked with this proxy of the intensity of sexual selection. (c) Habitats with higher levels of primary productivity, and thus higher carotenoids availability, harbour more lineages with carotenoid-based colours. Species with carotenoid-rich diets and smaller body size (not shown) are also more likely to display carotenoid-based colours. The vector diagrams were obtained from the Integration and Application Network, Center for Environmental Science, University of Maryland (ian.umces.edu/media-library), under a CC BY-SA 4.0 licence.

et al., 2004). In Delhey et al. (2022), body size was negatively correlated with the evolution of carotenoid-based colouration. While evidence for environmental limitation does not necessarily imply that carotenoid-based colouration signals foraging ability, the work by Delhey et al. (2022) draws renewed attention to the roles of ecology and life history on the macroevolution of sexually selected signals.

Devising the causes of present-day phenotypic diversity and its distribution is a key aim in evolutionary ecology. Delhey et al. (2022) advance this field by reassessing classical hypotheses about the evolution of putative sexual signals in birds, at a greater phylogenetic scale than any previous effort. Their work supports the generality of some previous results based on smaller clades, but also argues for a refinement of working hypotheses for future studies. Specifically, this study suggests different roles for different hues of carotenoid-based colouration and calls for research at the same phylogenetic scale that looks beyond the presence or absence of colour patches and into continuous variation in the intensity of colour. This work will likely stimulate additional large-scale studies on other types of visual signals, such as iridescent colouration and UV reflectance (Fitzpatrick, 1998; Hausmann et al., 2003), as well as similar studies on carotenoid-based colour in other animals capable of sequestering these pigments (Ciccotto & Mendelson, 2016). Finally, an outstanding strength of Delhey et al. (2022) relies on its ability to synthesize scattered data sources to produce a comprehensive analysis. Thus, this study also highlights the fundamental role of those who contribute their efforts to produce and maintain publicly available resources and databases, enabling future synthesis.

AUTHOR CONTRIBUTIONS

Beatriz Willink wrote the first draft of the manuscript with input from Meng Y. Wu, who designed the figure. Both authors contributed to the final text.

ACKNOWLEDGEMENT

B.W. is funded by an International Postdoc Grant (2019-06444) from the Swedish Research Council (Vetenskapsrådet).

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article does not use data.

ORCID

Beatriz Willink  <https://orcid.org/0000-0002-4579-6909>

Meng Y. Wu  <https://orcid.org/0000-0002-8562-7667>

REFERENCES

- Biard, C., Surai, P. F., & Møller, A. P. (2006). Carotenoid availability in diet and phenotype of blue and great tit nestlings. *Journal of Experimental Biology*, 209(6), 1004–1015.
- Ciccotto, P. J., & Mendelson, T. C. (2016). Phylogenetic correlation between male nuptial color and behavioral responses to color across a diverse and colorful genus of freshwater fish (*Etheostoma* spp., Teleostei: Percidae). *Ethology*, 122(3), 245–256.
- Cooney, C. R., Varley, Z. K., Nouri, L. O., Moody, C. J. A., Jardine, M. D., & Thomas, G. H. (2019). Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nature Communications*, 10(1), 1–9.
- Costantini, D., & Møller, A. P. (2008). Carotenoids are minor antioxidants for birds. *Functional Ecology*, 22(2), 367–370.
- Delhey, K., Valcu, M., Dale, J., & Kempenaers, B. (2022). The evolution of carotenoid-based plumage colours in passerine birds. *Journal of Animal Ecology*, <https://doi.org/10.1111/1365-2656.13791>
- Ender, J. A. (1980). Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, 34(1), 76–91.
- Fitzpatrick, S. (1998). Colour schemes for birds: Structural coloration and signals of quality in feathers. *Annales Zoologici Fennici*, 35(2), 67–77.
- Gray, D. A. (1996). Carotenoids and sexual dichromatism in north American passerine birds. *The American Naturalist*, 148(3), 453–480.
- Hausmann, F., Arnold, K. E., Marshall, N. J., & Owens, I. P. F. (2003). Ultraviolet signals in birds are special. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1510), 61–67.
- Hill, G. E. (1990). Female house finches prefer colourful males: Sexual selection for a condition-dependent trait. *Animal Behaviour*, 40(3), 563–572.
- Ligon, R. A., Simpson, R. K., Mason, N. A., Hill, G. E., & McGraw, K. J. (2016). Evolutionary innovation and diversification of carotenoid-based pigmentation in finches. *Evolution*, 70(12), 2839–2852.
- Mahler, B., Araujo, L. S., & Tubaro, P. L. (2003). Dietary and sexual correlates of carotenoid pigment expression in dove plumage. *The Condor*, 105(2), 258–267.
- McGraw, K. J., & Ardia, D. R. (2003). Carotenoids, immunocompetence, and the information content of sexual colors: An experimental test. *The American Naturalist*, 162(6), 704–712.
- Olson, V. A. (2006). Estimating nutrient intake in comparative studies of animals: An example using dietary carotenoid content in birds. *Oikos*, 112(3), 620–628.
- Olson, V. A., & Owens, I. P. F. (1998). Costly sexual signals: Are carotenoids rare, risky or required? *Trends in Ecology & Evolution*, 13(12), 510–514.
- Prum, R. O., LaFountain, A. M., Berro, J., Stoddard, M. C., & Frank, H. A. (2012). Molecular diversity, metabolic transformation, and evolution of carotenoid feather pigments in cotingas (Aves: Cotingidae). *Journal of Comparative Physiology B*, 182(8), 1095–1116.
- Read, A. F. (1987). Comparative evidence supports the Hamilton and Zuk hypothesis on parasites and sexual selection. *Nature*, 328(6125), 68–70.
- Tella, J. L., Figuerola, J., Negro, J. J., Blanco, G., Rodríguez-Estrella, R., Forero, M. G., Blazquez, M. C., Green, A. J., & Hiraldo, F. (2004). Ecological, morphological and phylogenetic correlates of interspecific variation in plasma carotenoid concentration in birds. *Journal of Evolutionary Biology*, 17(1), 156–164.
- Toews, D. P. L., Hofmeister, N. R., & Taylor, S. A. (2017). The evolution and genetics of carotenoid processing in animals. *Trends in Genetics*, 33(3), 171–182.
- von Schantz, T., Bensch, S., Grahm, M., Hasselquist, D., & Wittzell, H. (1999). Good genes, oxidative stress and condition-dependent sexual signals. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1414), 1–12.

How to cite this article: Willink, B., & Wu, M. Y. (2023). To colour a bird: The evolution of carotenoid-based colouration in passerines is shaped by sexual selection, ecology and life history. *Journal of Animal Ecology*, 92, 4–6. <https://doi.org/10.1111/1365-2656.13840>