

Warbler coloration shaped by evolution via distinct paths

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According to a new study, the evolution of two color related genes helps explain the striking diversity in colors and patterns among wood warblers, like the blackburnian warbler pictured here. Credit: Darrell Cochran

Two genes that are important for the diverse colors and patterns of

warbler plumage have evolved through two very different processes, according to a new study led by Penn State researchers. These evolutionary processes could help explain the rapid evolution of these songbirds into so many unique species.

"Wood warblers are an incredibly colorful and diverse group of birds, with more than a hundred species in total," said Marcella Baiz, postdoctoral researcher at Penn State and first author of the paper.

"These species arose very quickly in evolutionary time in what biologists call a species radiation. To better understand this radiation, we studied genetic regions related to plumage coloration within a particularly colorful subset of warblers."

The research team sequenced the genomes of all 34 species within the Setophaga genus of wood warblers and created a phylogenetic tree that clarifies how each species is related to one another. Then, they focused on nine closely related pairs of "sister species." Each pair is the result of one species diverging into two. Seeing if similar [evolutionary processes](#) are at play in each of the pairs allowed the researchers to gain a better understanding of the overall radiation.

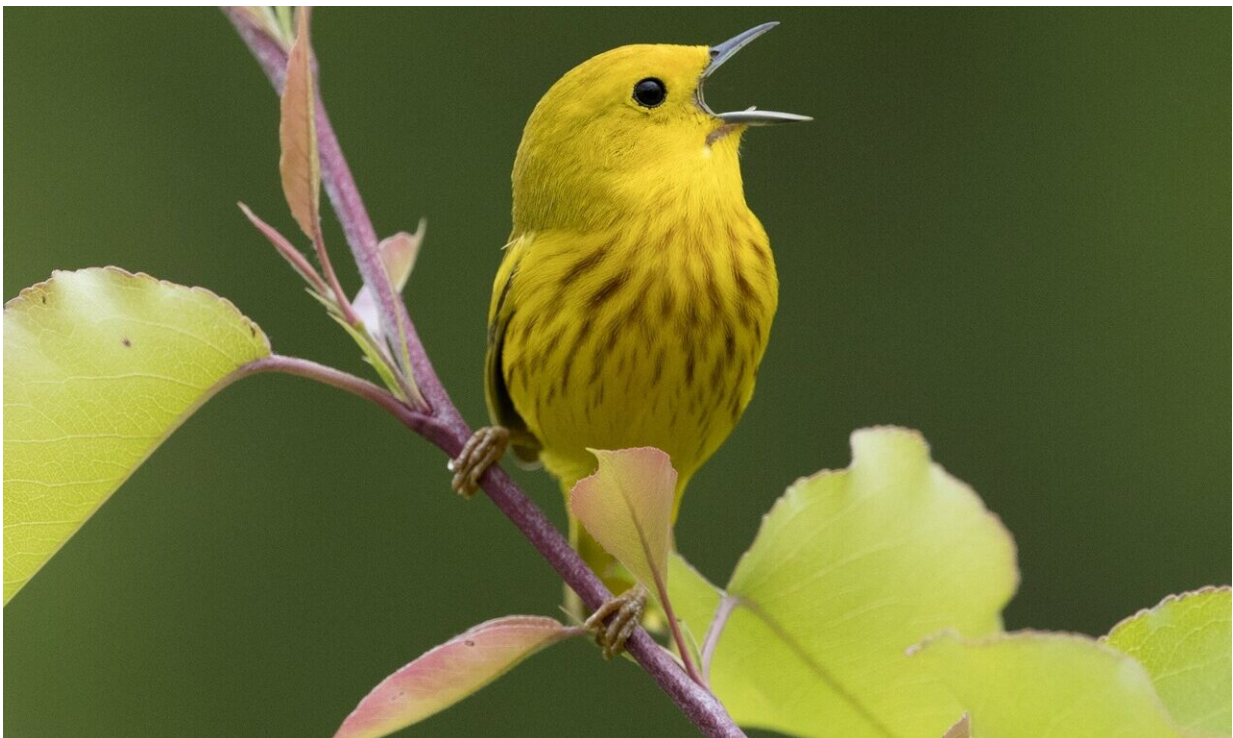
A paper describing their results appears today (Nov 30.) in the journal *Current Biology*.

"In most cases it is difficult to get at the genes underlying the diversification process because it can be hard to link [specific genes](#) to specific traits, like colors," said David Toews, assistant professor of biology at Penn State and leader of the research team. "But many species of warblers readily interbreed, producing hybrid offspring with a mix of the parent species' traits, so we were [previously able to link](#) certain color patterns with their underlying genetic regions. In this study, we focused on two coloration genes, but were able to study them across all the species in this large genus, to give us a window into the rest of the

radiation."

The first gene, the Agouti-signaling protein (ASIP), is involved in producing the pigment melanin, which underlies brown and black plumage in these warblers. Within each pair of sister species where there were differences in the amount or location of the black or brown in their plumage, the team predictably found genetic differences near ASIP.

"We created an [evolutionary tree](#) based solely on the ASIP gene region, which more clearly shows how the gene has changed across the genus," said Baiz. "The patterns in this gene tree mirror patterns in the [phylogenetic tree](#) based on what we see across the whole genome. This implies that the differences we see in ASIP resulted from mutations that arose independently in different species. However, the gene tree from the second gene, BCO2, showed a very different pattern that did not match up with the whole genome tree, which suggests different processes are at play."



The research team found that one color-related gene has undergone a standard mode of evolution, with mutations arising in separate species. By contrast, portions of the second gene in some cases have been transferred between species through a process known as introgression, where hybrid birds mate with a parent species and, over generations, transfer genetic material. Credit: Todd Fellenbaum

The second gene, beta-carotene oxygenate 2 (BCO2), is involved in producing carotenoid pigments, which result in bright yellow, red, and orange plumage. The researchers suggest that a process called introgression—the exchange of genes between species that have evolved separately—may explain why the pattern of genetic changes in BCO2 didn't align with the overall radiation of the group.

"Introgression can occur when two separate species hybridize, and the hybrid offspring go on to mate with one of the original species," said Baiz. "After several generations, genetic material from one species can be incorporated into the other. The signal of this kind of ancient introgression can be maintained in the genomes of living individuals—like how ancestry tests can reveal how many Neanderthal genes you have. In this instance, we unexpectedly found evidence for ancient introgression at BCO2 in two otherwise distantly related warblers in this genus."

The researchers found evidence of introgression involving the yellow warbler and magnolia warbler and involving the prairie warbler and vitelline warbler, all species with colorful carotenoid coloration in their feathers. However, they note that with the current data it is difficult to tell the directionality of the gene transfer.

"One possibility is that the magnolia warbler version of BCO2 introgressed into the yellow warbler, and this 'new to them' version produced a broader deposition of carotenoids in the feathers of the yellow warbler," said Toews. "It is fun to think that ancient introgression is what made the yellow [warbler](#) so yellow!"

This is one of the first examples of carotenoid gene transfer among vertebrates. Collectively, the results of this study suggest that both introgression and a more standard mode of evolution, where mutations occur and are passed from parent to offspring, have played a role in generating the diversity of colors in this genus and could have helped enable the extreme diversification of warblers.

In the future, the researchers hope to link specific mutations in these [genes](#) to changes in plumage coloration and to map out the molecular pathways involved in pigment production. They would also like to expand their study to all 110 [species](#) of warblers.

"There's a possibility that there may be introgression from another genus entirely," said Toews. "Expanding to other warblers would allow us to explore this possibility, and to more broadly understand the radiation of these fascinating birds."

More information: Marcella D. Baiz et al, Pigmentation Genes Show Evidence of Repeated Divergence and Multiple Bouts of Introgression in Setophaga Warblers, *Current Biology* (2020). [DOI: 10.1016/j.cub.2020.10.094](#)

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