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▶ To cite this version:

Hugo Gruson. Digest: Disentangling plumage and behavior contributions to iridescent signals. Evolution - International Journal of Organic Evolution, 2019, 73 (3), pp.623-625. 10.1111/evo.13685. hal-01987390

HAL Id: hal-01987390

https://hal.science/hal-01987390

Submitted on 21 Jan 2019

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Digest: Disentangling plumage and behavior contributions to iridescent signals

This article is a digest of Simpson, R. K., and K. J. McGraw. 2018. Experimental trait mis-matches uncover specificity of evolutionary links between multiple signaling traits and their interactions in hummingbirds. Evolution, doi: 10.1111/evo.13662.

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Abstract

To what extent do plumage properties and behavior interact to produce visual signals? Simpson and McGraw (2018) propose an elegant and novel experimental set-up to dissociate behavior and color and assess their relative effects in the resulting iridescent signal. They find that modification of either component leads to a modification of the resulting signal as seen by the receiver, suggesting that sexual selection acts simultaneously on both signal components.

Main text

Hummingbirds are famous for their bright colors that change rapidly with the angle of observation or illumination, a phenomenon known as iridescence (Doucet and Meadows 2009). This angle-dependency of color may produce flashes that are particularly conspicuous on feather patches such as the throat or the crown (Osorio and Ham 2002). Color as seen by the receiver (e.g. by a female during a male's courtship display) therefore results from both the intrinsic properties of the feather, and the orientation of the male during display. However, studying iridescent signals by taking into account both the feather properties and behavioral displays, and looking at how those two components might interact, has proven incredibly difficult. It requires a detailed knowledge of the courtship display behavior and a precise quantification of the iridescent color angle-dependency as seen in the receiver's visual system – birds, for example, can see ultraviolet colors.

In this study, Simpson and McGraw (2018) used data from their previous works at the intraspecific level to investigate how behavior and iridescent plumage interact in five hummingbird species from the "bee" clade (tribe: Mellisugini). These five bee hummingbird species recently diverged (McGuire et al. 2014) and have the same kind of courtship behavior (called a "shuttle display"), in which males fly back and forth in front of the female, while at the same time erecting their shiny throat feathers (Clark 2011).

Simpson and McGraw (2018) proposed an elegant and novel experimental set-up: they used plucked throat feathers and camera recordings of the display behavior, which allowed them to experimentally re-create the iridescent signal of a species during a display (top row of Fig. 1, also referred to as "species-specific color display" in the original article). To disentangle the relative effects of the plumage properties and courtship behavior on the resulting iridescent signal, they then created **mis-matches**¹, where the plucked throat feathers and the display behavior came from different species (bottom row of Fig. 1).

The researchers measured two iridescent signal variables: **average color appearance** (i.e. color characteristics averaged for all positions during the display) and **percent change in color appearance** (i.e. the sum of differences in color characteristics between each position during the display; also called "flashiness"). Those two variables were features of what the authors refer to as **color appearance during display** (Fig. 1).

They found that mis-matches between plumage and display behavior (i.e. when feathers and display behavior did not come from the same species) led to a different **average color appearance** and a different **flashiness**

 $^{^{1}\}mathrm{See}$ Simpson and McGraw (2018) Table 1 for a full list of definitions of bolded words.

Color appearance during a display

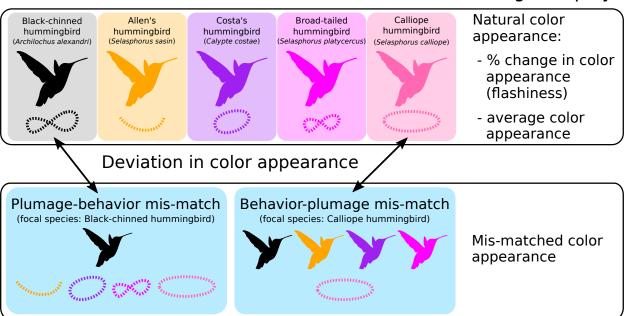


Figure 1: Summary of the protocol used in Simpson and McGraw (2018). Dashed paths represent shuttle display behavior of each species. The authors looked at deviations in color appearance during display (average color appearance and flashiness) between natural color appearance (feather and shuttle display from the same species, top block in this figure) and mis-matched color appearance (feather and shuttle display from different species, bottom block in this figure). Colors for each species match those used in the original paper (Fig. 4)

for the receiver. For example, throat feathers from all species changed more during display (higher **flashiness** value) when used in the shuttle display from the black-chinned hummingbird than when they were used in shuttle displays by other species (even their own). This suggests that sexual selection acts simultaneously on intrinsic plumage characteristics and courtship behavior, and that both components play an important role in the resulting iridescent signal within each species.

The authors also investigated the relative contributions of both plumage and shuttle behavior to the resulting iridescent signal. They found that the overall color appearance and changes in hue during a display were mainly influenced by behavior rather than plumage characteristics. On the contrary, changes in luminance during a display were correlated to throat patch size.

This article provides the first attempt to study a signal by evaluating and manipulating multiple signal components at the same time (behavior and feather properties) and by working at the interspecific level. In doing so, this study provides an interesting and reproducible experimental set-up that may be used to study other parts of courtship displays in bee hummingbirds (e.g. dives; Tamm et al. 1989) or in different species with complex colors and/or displays (e.g. birds of paradise; Stavenga et al. 2011). Future studies should also investigate the ecological and evolutionary drivers of the interspecific divergence in color and courtship behavior in bee hummingbirds. In particular, it remains unclear which specific signal features female prefer and use to select their mates.

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