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Synthesis

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abstract: The world in color presents a dazzling dimension of phenotypic variation. Biological interest in this variation has burgeoned, due to both increased means for quantifying spectral information and heightened appreciation for how animals view the world differently than humans. Effective study of color traits is challenged by how to best quantify visual perception in nonhuman species. This requires consideration of at least visual physiology but ultimately also the neural processes underlying perception. Our knowledge of color perception is founded largely on the principles gained from human psychophysics that have proven generalizable based on comparative studies in select animal models. Appreciation of these principles, their empirical foundation, and the reasonable limits to their applicability is crucial to reaching informed conclusions in color research. In this article, we seek a common intellectual basis for the study of color in nature. We first discuss the key perceptual principles, namely, retinal photoreception, sensory channels, opponent processing, color constancy, and receptor noise. We then draw on this basis to inform an analytical framework driven by the research question in relation to identifiable viewers and visual tasks of interest. Consideration of the limits to perceptual inference guides two primary decisions: first, whether a sensory-based approach is necessary and justified and, second, whether the visual task refers to perceptual distance or discriminability. We outline informed approaches in each situation and discuss key challenges for future progress, focusing particularly on how animals perceive color. Given that animal behavior serves as both the basic unit of psychophysics and the ultimate driver of color ecology/evolution, behavioral data are critical to reconciling knowledge across the schools of color research.

Keywords: biophysics, neural processing, perception, optics, sensory ecology, vision, color signaling.

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Introduction

Color is an exquisite natural phenomenon and an enduring source of inspiration for poets, artists, philosophers, and scientists. This allure has not escaped biologists, who have long sought to study color in many ecological and evolutionary contexts (Johnsen 2012). In recent times, growing appreciation that most animals perceive color differently to humans (Endler 1990; Bennett 1994) has created a new surge of interest. This has motivated widespread effort to quantify both color traits and their visual environments. Increased affordability and portability of spectroradiometers has assisted by placing the basic technology for color measurement within the reach of most researchers. Simultaneously, efforts to elucidate perception in nonhuman species have generated a range of analytical approaches (e.g., Vorobyev and Osorio 1998; Endler and Mielke 2005; Pike 2012*a*). These efforts draw variously on principles derived from human psychophysics that are known to operate similarly in limited animal models (e.g., honeybees; de Ibarra et al. 2014). Effective studies of color in nature require not only appreciation of these principles and how they have been derived but also how they factor in to the available color analyses and what assumptions apply. The need for an accessible intellectual basis at all levels of inquiry presents a fundamental challenge for the field.

Color traits are studied for many different objectives, such as understanding morphological adaptation (e.g., Stoddard and Prum 2008), visual orientation (e.g., Kelber 1999), communication (e.g., Arnold et al. 2002), and deception (e.g., Chiao et al. 2009), as well as for exploring processes such as speciation (e.g., Chamberlain et al. 2009) and mimicry (e.g., Jiggins et al. 2001). Precisely because these traits are assessed