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Opening the "black box" of modeling animal color vision: a comment on Olsson et al.

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What do animals see? This question is central to all behavioral and ecological interactions involving the transfer of visual information. We cannot imagine what an animal sees; but we can attempt to model it. The most widely used mathematical model of animal color vision is the "Receptor Noise Limited" (RNL) model proposed by Vorobyev and Osorio 20 years ago (Vorobyev and Osorio 1998). It can be applied to any animal because it is based on a relatively small number of parameters and low-level visual physiology, making no assumptions about higher-level processing. But here lies the rub because, as highlighted by Olsson et al.'s (2018) review, many other factors influence how colors are ultimately perceived. The key take-home message of this review is that visual models generate hypotheses about color perception; but these hypotheses need to be validated with behavioral data because perception is often context-dependent.

The RNL model was originally formulated to describe detection thresholds—the smallest differences that can be perceived under ideal viewing conditions. The RNL model shows a good fit to the limited behavioral data on detection thresholds in a variety of taxa but other models may provide an equally good or better fit, depending on the species and conditions (Renoult et al. 2017). If receptor noise is the limiting factor determining detection thresholds, how good are our estimates of receptor noise? The estimates compiled by Olsson et al. (2018) show sometimes large variation within and between species. This suggests that other factors, such as the motivation of the animals and experimental conditions, are likely to influence estimates of receptor noise. Consequently, RNL model predictions, even based on the best available estimates of receptor noise, need to be treated as reasonable hypotheses at best.

Behavioral ecologists are generally not concerned with estimates of receptor noise. Instead, there are two relevant issues to behavioral ecologists, depending on the question being addressed. First, how well does the RNL model describe detection thresholds in nature? Detection thresholds are critical to many ecological and evolutionary questions, for example, regarding camouflage. Second, how well does the RNL model describe supra-threshold differences? Although formulated to describe detection thresholds, the RNL model is widely used to describe large perceptual distances in color space.

In terms of discriminating colors from a very similar background (camouflage), receptor noise is unlikely to be the limiting factor determining discrimination thresholds in many ecologically relevant conditions. Some of the factors influencing realized thresholds mentioned by Olsson et al. (2018) include the costs of making perceptual errors, phenotypic plasticity and learning in color discrimination, the illumination intensity of the background, and spatial frequency and noise within the visual scene.

In terms of supra-threshold differences, many questions in behavioral ecology concern highly conspicuous signals that are very different from the background to which the eyes are adapted. As Olsson et al. (2018) highlight, under these conditions, detection thresholds are likely to be larger than predicted by the Weber-Fechner law of proportional processing (Akre and Johnsen 2014). The empirical observation that variability of ornamental traits increases with increasing conspicuousness could be because detection thresholds increase with increasing conspicuousness—they are not fixed (Delhey et al. 2017).

Olsson et al.'s (2018) review compiles estimates of receptor noise from the vision science literature, which is not easily accessible to behavioral ecologists. It also opens the "black box" of modeling animal color vision by clearly explaining assumptions and limitations. Both will pave the way for a more judicious use of the RNL model by behavioral ecologists. Ultimately though, behavioral ecologists will be the ones testing hypotheses regarding color perception in ecologically relevant conditions.

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Receptor noise models: time to consider alternatives?: a comment on Olsson et al.

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Behavioral experiments are crucial to understand animal vision. A common experiment is to assess the just noticeable difference