



Review

Carotenoid-based coloration in cichlid fishes

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ABSTRACT

Animal colors play important roles in communication, ecological interactions and speciation. Carotenoid pigments are responsible for many yellow, orange and red hues in animals. Whereas extensive knowledge on the proximate mechanisms underlying carotenoid coloration in birds has led to testable hypotheses on avian color evolution and signaling, much less is known about the expression of carotenoid coloration in fishes. Here, we promote cichlid fishes (Perciformes: Cichlidae) as a system in which to study the physiological and evolutionary significance of carotenoids. Cichlids include some of the best examples of adaptive radiation and color pattern diversification in vertebrates. In this paper, we examine fitness correlates of carotenoid pigmentation in cichlids and review hypotheses regarding the signal content of carotenoid-based ornaments. Carotenoid-based coloration is influenced by diet and body condition and is positively related to mating success and social dominance. Gaps in our knowledge are discussed in the last part of this review, particularly in the understanding of carotenoid metabolism pathways and the genetics of carotenoid coloration. We suggest that carotenoid metabolism and transport are important proximate mechanisms responsible for individual and population-differences in cichlid coloration that may ultimately contribute to diversification and speciation.

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1. Introduction

Carotenoids are an important class of pigments in animals. Vertebrates cannot synthesize carotenoids endogenously, but dietary carotenoids derived from photosynthetic organisms are responsible for red,

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orange and yellow hues of many species, including teleost fishes (Fox and Vevers, 1960; Goodwin, 1984; Kodric-Brown, 1998). In the integument, carotenoid pigments are stored in xanthophores and erythrophores (yellow and red pigment cells, respectively). In fishes and other poikilothermic vertebrates, these types of chromatophores can also synthesize yellow to red pteridine pigments (Braasch et al., 2007). In addition to their role in body coloration, carotenoids have important roles in vision, as precursors of transcription regulators, as antioxidants, and in the immune system (Bendich and Olson, 1989; von Schantz et al., 1999; McGraw and Ardia, 2003; Hill and Johnson, 2012). The size and hue of pigmented tissues are often subject to natural and sexual selection (Grether et al., 2004), and can be important traits in speciation (Boughman, 2002; Maan et al., 2006a). The role of body color in speciation is especially important in animals with acute color vision, such as birds and fishes.

Cichlid fishes (Perciformes: Cichlidae), a group of teleosts endemic to both the Old and New World, provide an excellent system in which to test hypotheses regarding coloration and speciation. Among the Old World cichlids of East Africa, which represent some of the most explosive adaptive radiations among vertebrates (Meyer, 1993; Kocher, 2004), body coloration is inextricably linked with diversification. Color patterns of cichlids diverge in sympatry as well as in allopatry, in response to both natural and sexual selection. In many species, mate choice and dominance interactions are profoundly affected by coloration (Maan and Sefc, 2013), and individuals use dynamic color patterns to communicate motivation and status in social and sexual contexts (Nelissen, 1976; Baerends et al., 1986). Some of these color patterns are carotenoid-based, and in other cases the pigments have yet to be identified. In this review we will (i) briefly introduce the hypotheses that address the signaling function of carotenoid ornaments, (ii) summarize our current understanding of the fitness benefits as well as the biochemical and genetic basis of carotenoid-based coloration in cichlids, and (iii) describe future avenues of research with respect to the role of carotenoids in cichlid coloration and evolution.

2. Carotenoid coloration in signaling

The display of carotenoid-based body coloration is costly. It requires the intake of sufficient amounts of carotenoids from the diet, diverts ingested carotenoids away from vital physiological processes to ornamentation, and makes its bearer conspicuous to predators (Ender, 1980; Lozano, 1994). Consequently, carotenoid-based coloration is believed to constitute an honest, condition-dependent signal with functions in both sexual and social contexts (Olson and Owens, 1998; Svensson and Wong, 2011).

Carotenoids are part of the antioxidant arsenal of animals. Antioxidants quench the potentially harmful pro-oxidant molecules generated during normal metabolism. Oxidative stress arises when the balance between antioxidants and pro-oxidants is disturbed, which can be due to a deficiency of antioxidants or to a surplus of pro-oxidants produced by processes such as somatic growth or an immune response. Animals employ a variety of endogenously produced and food-derived antioxidant compounds, including pigments, vitamins, enzymes and other proteins, and the different compounds can interact with and compensate for each other. Apart from their role as antioxidants, carotenoids may also enhance the immune system through increased T-cell activation, macrophage capacity and lymphocyte proliferation (Bendich and Olson, 1989; Pérez-Rodríguez, 2009).

An influential hypothesis regarding carotenoids posits that trade-offs arise from the dual use of carotenoids for physiological functions and ornamentation (Lozano, 1994; von Schantz et al., 1999; Lozano, 2001). The “carotenoid trade-off hypothesis” suggests that competing physiological demands for carotenoid pigments for immunity and oxidative protection may increase the cost of carotenoid allocation to the skin (McGraw and Ardia, 2003; Clotfelter et al., 2007; Peters, 2007; Alonso-Alvarez et al., 2008; Vinkler and Albrecht, 2010; Svensson and

Wong, 2011). This scenario requires that carotenoids are in limited supply in the natural diet (Hill, 1992), an assumption that has not found unanimous approval (Hudon, 1994) and lacks empirical evidence (Hill and Johnson, 2012). However, there is considerable support for two predictions of the carotenoid trade-off hypothesis (reviewed in Blount and McGraw, 2008; Svensson and Wong, 2011). The first is that carotenoid supplementation increases coloration, immunity and/or antioxidant capacity (Hill et al., 2002; Blount et al., 2003; Clotfelter et al., 2007). The second is that immune challenges, which also cause oxidative stress, cause re-allocation of carotenoids and reduce coloration of carotenoid-pigmented structures (Pérez-Rodríguez et al., 2010; Toomey et al., 2010).

In the past decade, the importance of carotenoids as *in vivo* antioxidants has been questioned (Costantini and Møller, 2008; Pérez-Rodríguez, 2009). Hartley and Kennedy (2004) suggested that carotenoids themselves are particularly vulnerable to oxidative damage, and that carotenoid-based ornamentation is therefore an honest indicator of the antioxidant capacity of other, non-pigment molecules such as vitamin E, rather than itself being traded against antioxidant defense. This hypothesis has become known as the “protection hypothesis” (Pérez et al., 2008) because the non-pigment antioxidants protect the carotenoids from oxidation. A related hypothesis, termed the “sparing hypothesis” (Svensson and Wong, 2011), posits that non-pigment antioxidants may protect carotenoids from oxidation (similar to the protection hypothesis), but that carotenoids are still important components of the antioxidant arsenal. The presence of non-pigment carotenoids (again, such as vitamin E) allows the animal to “spare” carotenoids for re-allocation to other functions such as coloration.

While these hypotheses focus on the availability of, and competition for, antioxidant resources, Hill and Johnson (2012) concentrate on the efficiency of cellular processes, which simultaneously control carotenoid coloration, vitamin A homeostasis and redox balance (“shared pathways,” Hill, 2011). In their view, carotenoid coloration signals body condition by reflecting how well such cellular processes are functioning. Physiological models of shared pathways were developed from bird data (Hill and Johnson, 2012; Johnson and Hill, 2013), and although some metabolic pathways and the tissues in which they occur are different in fish (Katsuyama and Matsuno, 1988), the concept may in principle apply to cichlids and other fishes as well.

Another potential clue to the signal value of carotenoid coloration is its connection to glucocorticoid hormones, which are released during the stress response. Glucocorticoids can increase oxidative stress (Costantini et al., 2008) and cause the reallocation of resources to self-maintenance (Bonier et al., 2009). In spite of this, however, positive correlations between glucocorticoids and redness have been reported in lizards (Fitze et al., 2009), fish (Backström et al., 2014) and birds (McGraw et al., 2011; Fairhurst et al., 2014; Lendvai et al., 2013). However, the relationship between stress hormone levels and carotenoid coloration appears to be condition-dependent, constraining the positive correlation to individuals in good condition (Loiseau et al., 2008; Cote et al., 2010). It is possible that only high-quality animals can tolerate high glucocorticoid levels, and thus advertise this ability through their carotenoid coloration. Additionally, the relationship between glucocorticoids and coloration may depend on the net effect of ornament expression on fitness (Candolin, 2000; Cote et al., 2010). Fairhurst et al. (2014) predict that a correlation between coloration and glucocorticoids will exist only when color signals are key to reproductive success, with its direction dependent on the individual's ability to cope with the energetic demands of ornament production.

The alternatives to the carotenoid trade-off hypothesis are based on the assumption that carotenoids are not the currency in which signaling costs are paid. Experimentally discriminating among the different hypotheses is not easily accomplished. The frequently reported effects of immune challenges and antioxidant supplementation on pigmentation are compatible with the traditional trade-off hypothesis as well as with its more recent alternatives (Svensson and Wong, 2011; Hill and

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