# Carotenoids, Immunity, and Sexual Selection: Comparing Apples and Oranges?

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Endler (1980) suggested that in a carotenoid-poor environment, carotenoid-dependent sexual ornaments indicate foraging ability, and hence, they can be used by females to gauge male quality. This idea led researchers to view female mate choice from a fresh perspective, and it gained a fair level of acceptance (Kodric-Brown 1989; Milinski and Bakker 1990; Houde and Torio 1992; Frischknecht 1993); however, many years passed before the "carotenoid-poor-environment" assumption began to be questioned (Hudon 1994; Linville and Breitwisch 1997; Grether et al. 1999) or a viable alternative hypothesis was first conceived (Lozano 1994). Carotenoids stimulate the immune system, prevent cancer, and act as free radical scavengers (Ames 1983; Bendich and Olson 1989; Di Mascio et al. 1991; Diplock 1991). These physiological functions had not been considered in the ecological literature and led to the alternative hypothesis that carotenoid-dependent ornaments actually indicate the bearer's immune condition and health status (Lozano 1994). Lozano's hypothesis was recently expanded and generalized by Von Schantz et al. (1999), who proposed that sexual signals, carotenoid dependent or not, indicate resistance to oxidative stress. Hill (1999) recently outlined several alleged inconsistencies that "have been ignored or overlooked in the growing literature promoting the idea of carotenoids as signals of immunocompetence," but his arguments and supporting evidence require careful scrutiny.

First, Hill (1999) aptly titles a subsection "Comparing Apples and Oranges," fruits that contain carotenoids but of differing types and with different distributions (Burden and Bramlage 1994; Ben-Amotz and Fishler 1998; Reay et al. 1998; Mouly et al. 1999). Hill argues that differences in the "basic biology" of different taxa preclude us from generalizing across taxa, and whereas carotenoid-dependent sexual ornaments are more common in fish and birds, "virtually all data supporting an immunoenhancing role for carotenoids come from studies with mammals—primarily humans, other primates and rodents" (Hill 1999, p. 590). This is simply not so. Although most such work has indeed been done with humans and mice, there is ample evidence indicating that dietary carotenoids do have immunostimulant effects in many other taxa, including other mammals (e.g., Veksler et al. 1992; Michal et al. 1994; Chew 1996), birds (e.g., Sklan et al. 1989; Tengerdy et al. 1990; Haq et al. 1996*a*, 1996*b*), and fish (e.g., Christiansen et al. 1995; Torrissen and Christiansen 1995). This argument would be inadequate even in the absence of such evidence because the immunostimulant effects of carotenoids are primarily the result of their ability to neutralize free radicals (Bendich and Olson 1989; Di Mascio et al. 1991; Diplock 1991; Chew 1995, 1996; Burri 1997), a biochemical property of carotenoids that is not taxon dependent.

Second, Hill shows that circulating levels of carotenoids are higher in birds than they are in mammals and argues that, even if we could extrapolate across taxa, "if the immune systems of birds and fish have the same carotenoid needs as [those of] mammals, then the levels of circulating carotenoids seems far in excess of what is required for boosted immune response" (Hill 1999, p. 590). Hill further points out that carotenoids are a diverse group of compounds, and in some cases, those carotenoids that stimulate mammalian immune systems are not absorbed very efficiently from food by birds. These two arguments would be valid only if we were to assume that the "basic biology" of birds and mammals is similar, which is not so. Nonetheless, Hill's argument inadvertently leads to an ancillary point worth salvaging: dietary carotenoids act as immunostimulants in most vertebrate classes, but the types and levels of carotenoids used in experiments might be different than those found in nature; so if the hypothesis is

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to be properly tested, we must first obtain information regarding an animal's exact carotenoid requirements, immunological, ornamental, or otherwise.

Third, to advance his thesis, Hill uses results from three selected studies to support generalizations that in fact require further testing. Using as sole support a study of house finches (*Carpodacus mexicanus*; Hill 1995*b*), Hill argues that "the immune systems of birds" are unlikely to be carotenoid limited because, in species in which only males have carotenoid-dependent sexual ornaments, males have higher levels of plasma carotenoids than females; therefore, males probably have carotenoids far in excess of what would be required by the immune system. However, the study cited (Hill 1995*b*) showed that in house finches plasma carotenoids vary seasonally and similarly in both sexes, peaking at the time of molt, when the values of males were higher that those of females, but not significantly higher. Based on this study on a single species, Hill further concludes that "in many of these species" both sexes forage together and presumably have equal access to dietary carotenoids. Hill goes on to state that even among closely related species, carotenoid-dependent coloration is related to plasma carotenoid levels, citing as supportive evidence work on scarlet and white ibis (*Eudocimus ruber* and *Eudocimus albus*, respectively; Trams 1969), which supposedly shows that scarlet ibis have more plasma carotenoids than white ibis, and pink hybrids have accordingly intermediate levels. However, the study cited (Trams 1969), which was based on seven birds, actually showed that a single pink ibis had more plasma carotenoids than two white ibis but in the same range as the four scarlet ibis. Furthermore, in the body of the paper but not the abstract, Trams (1969) admits not knowing whether the pink bird was indeed a hybrid or a scarlet ibis albino. Finally, still referring to birds in general, Hill (1999, p. 592) states that "the amount of the integument that is pigmented with carotenoids predicts the concentration of circulating carotenoid pigments (Hill 1995*a*)." The study cited, however, was based on 14 species, 12 of which were passerines and eight of which were represented by three or fewer individuals. Among the six species represented by five or more individuals, the two redder species, house finches and Northern cardinals (*Cardinalis cardinalis*), had significantly redder plasma than the other four species (Hill 1995*a*).

Fourth, there is a growing body of recent work that is consistent with the idea that carotenoids are prevalent in sexual ornaments because of their immunostimulant properties. For example, Nolan et al. (1998) showed that in a house finch population, the redness of surviving males was higher after a single episode of a mycoplasm epidemic. Hill and Brawner (1998) demonstrated that combined coccidial and mycoplasm infections affect carotenoid-dependent plumage but not melanin-dependent plumage in house finches. Zahn and Rothstein (1999) showed that the decrease in redness of house finches over the last 40 yr has been correlated with, and presumably caused by, an increase in the incidence of avian pox. These studies did not directly test whether a trade-off exists in carotenoid use between sexual signaling and immune function (Lozano 1994) but are nonetheless consistent with the hypothesis.

Finally, in introducing the presumed troubling inconsistencies, Hill points out that "these problems will have to be addressed before we accept that animals pay a cost for carotenoid display in the form of reduced immune efficiency." In fact, the idea is only beginning to be tested and is far from being widely accepted, and although Hill's concerns may seem a little premature, a word of caution is probably always useful, as we would prefer not to repeat our past mistakes. Hill ends by restating his adherence to Endler's (1980) "foraging ability" hypothesis and reiterating the alleged inconsistencies with the hypothesis that carotenoids have dual and competing roles in sexual ornamentation and immunocompetence (Lozano 1994). Given that the foraging ability hypothesis has been the accepted dogma for nearly 15 yr, one would imagine most workers in the field would welcome an alternative hypothesis (Platt 1964), particularly one that merges seemingly disparate fields and in doing so opens up new areas of research. The eventual answer may even combine the two hypotheses; carotenoid-dependent sexual ornaments may have originated as signals of immune condition, but via sexual selection, they may have been exaggerated to the point of having lost their original meaning. Hill's most important message, and one with which everyone would agree, is that the hypothesis is indeed intriguing and compelling, and just like any other idea, it must be tested before it can be rejected or accepted.

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