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Carotenoids, parasites, and sexual selection

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In recent years carotenoids have become increasingly important in the study of sexual selection. Endler (1980) found that the colour pattern diversity and conspicuousness of males of a population of guppies (*Poecilia reticulata*) increased after a few generations without predation. He argued that males, emancipated from the constraints of predation, were able to respond better to sexual selection brought about by female preference for colourful males. He subsequently (Endler 1983) showed that in the early stages of courtship females prefer males with more red spots. Kodric-Brown (1985) and Houde (1987) later confirmed these results. Finally, Kodric-Brown (1989) showed that, as previously thought, dietary carotenoids affect male guppy coloration and, as a consequence, female preference.

Analogous results have been found in other taxa. Female house finches (*Carpodacus mexicanus*) prefer males with redder plumage (Hill 1990).Zuk et al. (1990a) found that red jungle fowl (*Gallus gallus*) females prefer males with redder combs. Milinski and Bakker (1990) found a positive correlation between the intensity of male coloration and female preference in the three-spined stickleback (*Gasterosteus aculeatus*). In these three species the expression of the traits being used by females to select males depends partially on dietary carotenoids (Brush and Power 1976, Rothschild 1973, Brush and Reisman 1965, respectively).

Endler's (1980) explanation has always been embraced when interpreting these results. Endler (1980) suggested that, by choosing mates based on a carotenoid-dependent trait, females choose superior mates. He argued that, because these males are able to obtain carotenoids from a carotenoid-poor environment, they are better foragers, and, because they are more conspicuous, they must also be better at avoiding predators.

In recent years carotenoids have also aroused the attention of nutritionists, immunologists and oncologists. Carotenoids are currently recognized not only as an essential part of a normal diet (e.g. Simpson and Chichester 1981, Goodwin 1986), but also as free radical scavengers (e.g. Burton 1989, Olson 1989, Sueki 1991), stimulants of the immune system (e.g. Alexander et al. 1985, Bendich and Shapiro 1986, Olson 1989, Prabhala et al. 1990, Jyonouchi et al. 1991, Sueki 1991, Watson et al. 1991; see reviews by Bendich 1989a, b), and even as potential prophylactics against cancer (e.g. Modan et al. 1981, Mathews-Roth 1982, Santamaria et al. 1983, Mathews-Roth and Krinsky 1985, Trechsel et al. 1985, Schoen and Watson 1988, Schwartz and Shkalr 1988, Olson 1989, Wang et al. 1989, El Attar and Lin 1991, Sueki 1991; see reviews by Ames 1983, Olson 1986, Ritenbaugh 1987, Temple and Basu 1988, Connett et al. 1989, Krinsky 1989, Ziegler 1989). This rise in the interest in carotenoids in nutritional and medical circles not only parallels, but might also be closely related to the study of sexual selection.

In terms of sexual selection an intricate picture emerges if these functions of carotenoids are considered. By choosing males based on carotenoid-dependent traits, females may not be merely choosing males who are good foragers and efficient at avoiding predators. Females might also be increasing the likelihood that their mates are not only healthy, but also better able to deal with any future health problems. The benefits to females would be a lower risk of getting pathogens from their mates, and a greater likelihood that males will be able to provide adequate paternal care if such care is required. Ties with Hamilton and Zuk's (1982) hypothesis on the role of parasites in sexual selection are immediately apparent.

For the purposes of this discussion, parasites are broadly and functionally defined as any organisms living in or on, as well as lowering the fitness of a heterospecific animal. Hamilton and Zuk (1982) proposed an explicit mechanism by which Zahavi's (1975) handicap principle could work: they suggested that male secondary sexual traits used by females to choose males indicate heritable variation in parasite resistance. If the immuno-stimulant effects of carotenoids are considered (see references above), then features dependent on dietary carotenoids might indicate parasite resistance, though not necessarily the genetically induced resistance required by Hamilton and Zuk's idea.

There have been a few studies linking carotenoid-dependent coloration to parasite loads. For example, infection with a monogenean parasite reduces the expression of carotenoid-dependent colours in guppies; females prefer colourful males and by doing so also avoid parasitized individuals (Houde and Torio 1992). Milinski and Bakker (1990) and Zuk et al. (1990b) have found similar results in, respectively, three-spined sticklebacks and red jungle fowl. These results are as predicted by the parasite-sexual selection hypothesis, a hypothesis that is based on the assumption of heritable variance in parasite resistance. However, in light of the effects of carotenoids on the immune system, an alternative explanation could be that females are indeed choosing the healthiest males, but their choice is based on environmentally induced, not genetic, differences among males.

Female mate choice based on carotenoid-dependent male traits implies that males are not necessarily always foraging to maximize their rate of nutrient or energy intake, but must also take time specifically to seek carotenoids. There has been a recent trend towards the recognition that animals might sometimes forage for specific items to deal with the risks of parasitism (Newton 1991, Clayton and Wolfe 1993). Carotenoids further complicate the picture: males, while foraging, would have to consider their usual nutritional requirements, the benefits from carotenoids both in terms of female preference and protection against parasites, the risks of longer foraging bouts, and the costs of parasitism. If carotenoids are limited in the environment Endler's (1980) original argument might still hold true under this scenario.

The type of carotenoid-dependent trait would affect whether it is current carotenoid levels or past ability to gather them that is being revealed. For example, plumage coloration would reflect the carotenoid levels at the time of moulting and would not necessarily convey information about the amount of a male's currently available carotenoids. Furthermore, these carotenoids would be lost at the next moulting. In contrast, carotenoids present in wattles, combs or skin could be mobilized if the necessity arises. Therefore, the ability to mobilize carotenoids away from these presumably epigamically selected traits would affect the type of information conveyed and, consequently, on the predictions that we can generate.

Several interesting predictions arise if the physiological effects of carotenoids are considered. (1) If females choose colourful males because carotenoid levels indicate current and not merely past quality, non-movable carotenoid levels (e.g. carotenoid-dependent plumage colour) should be correlated with movable carotenoid levels. (2) Intraspecifically, female selection for carotenoid-dependent traits should be stronger in conditions of higher parasitism. (3) Parasite load should be affected by pre-infection levels of carotenoid-dependent coloration. This is distinct from Hamilton and Zuk's prediction that parasite load affects post-infection differences in colour (4) Finally, upon parasitic infection, carotenoids present in secondary sexual traits would be mobilized (if possible) to deal with the infection. This prediction offers an alternative explanation as to why parasitic infection decreases carotenoid-dependent male coloration in sticklebacks (Milinski and Bakker 1990), guppies (Houde and Torio 1992), and red jungle fowl (Zuk et al. 1990b).

Carotenoids in the context of sexual selection have been studied only in a few species, but given the widespread instances of carotenoid-dependent coloration these animals, similar situations might occur in other taxa. There are many other epigamic traits that do not depend on carotenoids, so this is obviously not a general explanation for epigamically selected male traits. I am merely pointing out that, nutritionally and immunologically, carotenoids are known to have important functions that force us to view the role of carotenoids in sexual selection under a new light.

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