Is There an Immunological Cost to Carotenoid-Based Ornamental Coloration?

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Originally it was proposed that dietary access alone might explain variation in expression of carotenoid pigmentation (Endler 1980; Kodric-Brown 1985; Hill 1990). By this idea, carotenoids are scarce in the environment, and only those individuals in the best condition gain access to sufficient carotenoids for maximum ornament display. To this idea of limited access was added the idea that parasites might negatively impact expression of carotenoid pigmentation (Milinski and Bakker 1990; Houde and Torio 1992; Zuk 1992). Indeed, from studies with poultry it is well established that coccidia (protozoan gut parasites) directly inhibit carotenoid absorption (Ruff et al. 1974; Augustine and Ruff 1983; Allen 1987, 1992; Tyczkowski et al. 1991). In several studies with species that have carotenoid-based ornamental display, it has been shown that parasites, including particularly coccidia, inhibit expression of carotenoid pigmentation (Milinski and Bakker 1990; Houde and Torio 1992; Brawner 1997; Thompson et al. 1997). It seems likely that parasite load and limited access to dietary carotenoids combine to determine color expression in many species of animals (Hill 1999).

Carotenoids are used for more than integumentary colorants in animals. Some carotenoids, particularly beta-carotene and related molecules, function as vitamin A precursors (Bauernfeind 1972). In addition, a variety of carotenoids, including both carotenoids that serve as vitamin A precursors and carotenoids that do not serve as vitamin A precursors, have been found to reduce the risk of infection in mammals (Bendich 1989, 1993, 1996; Chew 1993) and help prevent the onset of cancer (Peto et al. 1981; Krinsky 1989; Ziegler 1989). Both of these immu-

noenhancing roles of carotenoids are apparently related to their function as free radical scavengers (Machlin and Bendich 1987; Burton 1989). By removing free radicals from the body, carotenoids reduce the chance of tumor development. Carotenoids also enhance the abilities of macrophages, killer T cells, and cytotoxic T cells to kill tumor cells (Bendich 1989; Chew 1993). During the initial response to an infection, free radicals are also produced and used by some white blood cells to kill and to inactivate foreign organisms in the body (Bendich 1989). While this is an effective means to combat infection, overproduction of free radicals can also damage white blood cells and surrounding tissue. Carotenoids apparently mop up the excess free radicals, thus increasing (perhaps performing a vital role in) the effectiveness of the immune system (Bendich 1989).

As is evident from the small sampling of references cited above, the role of carotenoids in both cancer suppression and immune promotion has become a prominent topic in the medical and nutrition literature. Lozano (1994) realized the potential importance of these carotenoid functions to the understanding of carotenoids as ornamental displays. He proposed that, rather than simply signaling dietary access to carotenoids or parasite infection, integumentary carotenoid displays might signal immunocompetence. The logic of the argument is compelling. Carotenoids are a finite resource and are needed both for immune function and for ornamental display. To produce a bright integumentary display, an individual would have to direct carotenoids away from vital immunological functions to the integument. Presumably, only the healthiest individuals with access to the largest quantities of carotenoids and with the most efficient immune systems would be able to sacrifice large quantities of carotenoid pigments and produce maximum ornament displays. The appeal of this immunological cost of carotenoid displays is that it potentially explains the interplay of parasites and dietary access to carotenoids.

The idea that expression of ornamental traits might be linked to immune competence and ability to deal with free radicals represents a growing literature in behavioral and evolutionary ecology. Folstad and Karter (1992) originally proposed a testosterone-mediated trade-off between in-

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vestment in production of ornamental traits and investment in maintenance of the immune system. More recently, Von Schantz et al. (1999) suggested that a major component of the condition of an individual is oxidative stress, which is the level of free radical buildup in the body. The ability to detoxify the body is critical to health state, and according to Von Schantz et al. (1999), the use of carotenoid pigments for ornamental displays rather than for bolstered free radical suppression and immune defense is one of many factors that might influence the oxidative stress that an individual experiences. Thus, Lozano's (1994) hypothesis that animals sacrifice potential immunological benefits of carotenoids by using them in ornamental displays is a carotenoid-specific version of a more general theory proposing that animals must trade-off between investment in reproduction (including ornament display) and investment in general body maintenance (including disease resistance and suppression of free radicals).

Inconsistencies and Troubling Observations

Despite the intuitive appeal of the idea that the immune-enhancing properties of carotenoids play a critical role in the signal content of ornament display, there are a number of basic observations related to ornamental carotenoid display that make me question whether color display and immune function are really in direct competition over carotenoid resources. These problems have been ignored or overlooked in the growing literature promoting the idea of carotenoids as signals of immunocompetence. I think that each of these problems will have to be addressed before we accept the idea that animals pay a cost for carotenoid display in the form of reduced immune efficiency.

Comparing Apples and Oranges?

The first problem is that virtually all data supporting an immunoenhancing role for carotenoids come from studies with mammals—primarily humans, other primates, and rodents. In no species of animal with carotenoid-based color display has variation in circulating carotenoid pigments been linked to variation in immune function. Extrapolation from observations made in one group to what might be occurring in another group is the foundation of much of what behavioral and evolutionary biologists do. We do not, for example, want to understand mate choice in only the organism that we study; we want to understand the universal properties of mate choice. However, such extrapolation has to be consistent with the basic biology of the organisms to which a theory is being applied. On the basis of considerations of basic biology, the idea that there is a cost to the immune function of a bird or fish

due to the use of carotenoids in integumentary display may not be reasonable.

A Matter of Degree

Concentration of circulating carotenoid pigments, that is, carotenoid pigments that are suspended in blood either bound to carrier proteins, dissolved in lipid, or unattached, is the primary measure of the amount and types of carotenoids available to an individual. Circulating carotenoids are potentially available for competing uses such as immune enhancement, ornament display, or vitamin A production. In humans, and presumably in other animals, the concentrations of carotenoids in the plasma are also good predictors of the concentrations of carotenoids in other tissues of the body (Parker 1989).

The problem is that birds and fish with carotenoid-based ornamental display typically have levels of circulating carotenoid pigments that are one to two orders of magnitude higher than the levels of circulating carotenoids in humans, mice, rats, and other mammals (table 1). Studies have shown that, in humans, mice, and rats that start with normal (i.e. not artificially depressed), low-carotenoid diets, more dietary carotenoids lead to enhanced immune ability (Bendich 1989; Chew 1993). In contrast, birds and fish with carotenoid-based displays consume much greater quantities of carotenoids and have much higher levels of circulating carotenoid pigments (table 1). For instance, mice and rats increase their levels of circulating carotenoid pigments from 0 to 0.25 μg/mL and from 0 to 0.34 μg/mL, respectively, in response to carotenoid supplementation (Mathews-Roth et al. 1977; Ribaya-Mercado et al. 1989), and this increase seems to enhance immune function (Seifter et al. 1981; Bendich and Shapiro 1986). In contrast, American flamingos (*Phoenicopterus ruber*) on a natural diet have about 35 μg/mL of circulating carotenoid pigments (Fox et al. 1969) and roseate spoonbills (*Ajaia ajaja*) have about 10 μg/mL of circulating carotenoid pigments (Fox et al. 1965). During molt, male house finches, *Carpodacus mexicanus*, (a species with red plumage coloration) have such high quantities of circulating carotenoid pigments that their plasma is red (Hill et al. 1994; Hill 1995*a*, 1995*b*) and all the fatty tissues of the body are red (personal observation). If the immune systems of birds and fish have the same carotenoid needs as mammals, then the levels of circulating carotenoids seem far in excess of what is required for boosted immune response. The 0.25 μg/mL increase in circulating carotenoids that boosts a mouse's immune system represents only 0.7% of the circulating carotenoids found in a flamingo. Without knowing more about the role of carotenoids in avian immune systems, one would have to suppose that carotenoids are present in the body of animals with ornamental carotenoid

Table 1: Levels of circulating carotenoids in various species of vertebrates

Common name	Latin name	Class	Status[a]	Type of supplement[b]	Carotenoid display[c]	Total plasma carotenoids (μg/mL)	Reference
Human	*Homo sapiens*	Mammalia	Wild	…	No	.46	Snodderly et al. 1990
Squirrel monkey	*Saimiri sciureus*	Mammalia	Captive, NS	…	No	.24	Snodderly et al. 1990
Macaque	*Macaca fascicularis*	Mammalia	Captive, NS	…	No	.29	Snodderly et al. 1990
House mouse	*Mus musculus*	Mammalia	Captive, NS	…	No	.0	Mathews-Roth et al. 1977
House mouse	*M. musculus*	Mammalia	Captive, S	B	No	.23	Mathews-Roth et al. 1977
Guinea pig	*Cavia porcellus*	Mammalia	Captive, NS	…	No	.0	Mathews-Roth et al. 1977
Guinea pig	*C. porcellus*	Mammalia	Captive, S	B	No	.0	Mathews-Roth et al. 1977
Rat	*Rattus rattus*	Mammalia	Captive, NS	…	No	.0	Ribaya-Mercado et al. 1989
Rat	*R. rattus*	Mammalia	Captive, S	B	No	.005	Ribaya-Mercado et al. 1989
Rat	*R. rattus*	Mammalia	Captive, S	B	No	.34	Bendich and Shapiro 1986
Rat	*R. rattus*	Mammalia	Captive, S	C	No	.68	Bendich and Shapiro 1986
Ferret	*Mustela putorius*	Mammalia	Captive, NS	…	No	.006	Ribaya-Mercado et al. 1989
Ferret	*M. putorius*	Mammalia	Captive, S	B	No	.42	Ribaya-Mercado et al. 1989
Cow	*Bos taurus*	Mammalia	Wild	…	No	2.25	Yang et al. 1992
Goat	*Capra* sp.	Mammalia	Wild	…	No	.004	Yang et al. 1992
Sheep	*Ovis aries*	Mammalia	Wild	…	No	.006	Yang et al. 1992
American flamingo	*Phoenicopterus ruber*	Aves	Wild	…	Yes	35.0	Fox et al. 1969
Roseate spoonbill	*Ajaia ajaja*	Aves	Wild	…	Yes	8.0–14.0	Fox et al. 1965
White stork[d]	*Ciconia ciconia*	Aves	Wild, S	A	Yes	12.7	Negro et al., in press
White stork[d]	*C. ciconia*	Aves	Wild	…	Yes	2.1	Negro et al., in press
Red-legged partridge	*Alectoris rufa*	Aves	Captive, NS	…	Yes	4.0–6.5	J. J. Negro, personal communication
American kestrel	*Falco sparverius*	Aves	Captive, NS	…	Yes	14–25	Bortolotti et al. 1996
Loggerhead shrike	*Lanius ludovicianus*	Aves	Captive, NS	…	No	10–20	Bortolotti et al. 1996
Rainbow trout	*Salmo gairdnerii*	Osteichthyes	Captive, S	A	Yes	3.6–4.5	March et al. 1990
Atlantic salmon	*Salmo salar*	Osteichthyes	Captive, S	A	Yes	2.8	Storebakken and Gosvami 1996
Arctic char[e]	*Salvelinus alpinus*	Osteichthyes	Captive, S	A	Yes	.6–7.7	Hatlen et al. 1995

[a] "Wild" versus "captive" is used in a general sense to distinguish caged laboratory animals from free-ranging animals. Hence, goats and sheep on open pasture are wild, as are humans. S = carotenoid supplement added to diet; NS = no carotenoid supplement added to diet.

[b] Type of carotenoid supplement used: B = beta-carotene; C = canthaxanthin; A = astaxanthin.

[c] Carotenoid-based coloration of feathers, bill, legs, or skin.

[d] A wild colony of storks was "supplemented" with astaxanthin when human introduced crayfish rich in astaxanthin and the crayfish became a major component of diet. The nonsupplemented storks had a diet of fish.

[e] One year old.

display in such abundance that the immune systems of these animals are not carotenoid limited.

As a matter of fact, the very high levels of circulating carotenoids observed in birds and fish may have serious detrimental health effect if they occur in mammals. For instance, in the 1980s canthaxanthin tablets (a red carot-enoid that is used by some species of birds and fish for ornamental coloration) were sold as tanning pills (Roueche 1991). The concentrated dose of canthaxanthin caused various maladies in humans who took them, including aplastic anemia (Bluhm et al. 1990). High carotenoid doses are also known to cause crystal-like deposits in the retina

of humans and other primates (Leyon et al. 1990; Goralcyzk et al. 1997). In contrast, I fed male house finches very high doses of canthaxanthin over 4 yr and the birds suffered no apparent ill effects—they simply grew red plumage (Hill 1992, 1993). How birds and fish maintain very high levels of circulating carotenoid pigments with no ill effects is unknown. The point is that the differences in levels of circulating carotenoid pigments affect birds and mammals differently and indicate that extrapolating between organisms that are so different in their use of carotenoids may lead to over simplifications.

Sexual Dimorphism and Interspecific Variation in Carotenoid Abundance

Another observation that is hard to reconcile with the idea that the immune systems of birds would benefit from more carotenoids is that, when males have carotenoid-based ornamental displays and females do not, males have substantially higher levels of circulating carotenoid pigments than females (Hill 1995*b*). In many of these species, males and females feed together and presumably have access to similar levels of carotenoids. Moreover, for most species of birds, molt and feather pigmentation occur when females are not breeding, so females are not diverting carotenoids into eggs or obviously by using them for other sex-specific reproductive functions. Why should one sex ingest, uptake, and transport more carotenoid than the other if both have immune systems that are carotenoid limited? The difference only makes sense if males are increasing circulating carotenoid levels above what is normally needed by the body for immune function. This being the case, variation in expression of ornamental carotenoid pigmentation among males in a population would have nothing to do with immune function—even the most poorly pigmented male would have circulating carotenoid pigments in excess of what would be needed by the immune system.

Still more observations that are difficult to reconcile with the idea that birds in general would experience immune benefits if they had access to more carotenoid pigments are that individuals of species with carotenoid-based display have greater concentrations of circulating carotenoid pigments than individuals of closely related species without such displays. For instance, scarlet ibises (*Eudocimus ruber*), which have scarlet colored feathers as well as red bills and legs, have three times more circulating carotenoid pigment than individuals of their sister taxon the white ibis (*Eudocimus albus*), which have much less carotenoid pigment in their integument—white plumage with red legs and bills (Trams 1969). Hybrids between white and scarlet ibis, which have pink plumage, are intermediate in circulating carotenoid pigments (Trams 1969). In general, the amount of the integument that is pigmented with carotenoids predicts the concentration of circulating carotenoid pigments (Hill 1995*a*). If one assumes that the immune systems of animals are carotenoid limited and that animals would experience enhanced immune function if they increased levels of circulating carotenoid pigments, it is hard to explain why red species would have more circulating carotenoids pigments than closely related white species. It seems likely that, to produce ornamental coloration, species with color displays have levels of circulating carotenoid pigments far above what is needed for maximum immune system function.

Carotenoid Specificity

Another observation that seems to contradict the idea that ornamental displays compete with the immune system for carotenoids is the specificity with which carotenoid pigments are absorbed, transported, and displayed by animals (Brush 1981; Goodwin 1984). More than 600 carotenoid molecules have been identified (Straub 1987). These molecules can be grouped into classes depending on the structure of their basic carotene backbone (beta-carotenes, alpha-carotenes, etc.) and they can be divided into those that are very nonpolar (carotenes) and those that contain oxygen (xanthophylls). In the middle of this century, physiologists noted that in many bird species, one type of carotenoid might be used very efficiently while another type might not be used at all. In general, it has been noted that birds absorb from food and accumulate in tissue xanthophylls almost to the exclusion of all other carotenoids (Brush 1981; Goodwin 1984). For example, in the African golden oriole (*Oriolus auratus*), the xanthophyll lutein, which is the primary pigment that makes plumage yellow, is absorbed efficiently from food, while beta-carotene, which serves as neither pigment nor pigment precursor, is not absorbed (Thommen 1971). Similarly, American flamingos are efficient in their absorption of the xanthophyll astaxanthin but do not absorb beta-carotene efficiently (Fox et al. 1969; Fox and McBeth 1970). Only astaxanthin is used as a feather pigment by flamingos. If, for whatever reason (see Hill 1996), beta-carotene was not used for ornamental display and not needed for other functions, then it makes sense that it would not be absorbed by the organism. However if carotenoids are limiting and valuable resources for immune system enhancement, then it is hard to explain why these carotenoids are "wasted." And, it is important to note that while enhanced immune function has been linked to xanthophylls in a few studies, beta-carotene (the carotenoid not absorbed by some birds with ornamental carotenoid displays) is the carotenoid most consistently linked to bolstered immune defense (Bendich 1989, 1993, 1996; Chew 1993). These

observations only make sense if organisms that accumulate large quantities of carotenoids from the environment for ornamental display have access to quantities of carotenoid pigments far in excess of what is needed for maximum immune function. Animals could then focus on accumulating carotenoids in a manner that maximizes ornament display rather than immune function, and the pattern of carotenoid accumulation in the above examples is consistent with this idea.

Conclusions

Ultimately, the question of whether or not the immune system competes with ornamental displays for carotenoid pigments will be resolved through experimental study. While this idea is intriguing, at present I see many inconsistencies between what is known about carotenoid physiology of birds, fish, and mammals and what is proposed by the hypothesis.

Acknowledgments

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