

Animal allure and health linked by plant pigments

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Summary

Darwin⁽¹⁾ introduced the idea that ornamental secondary sexual traits have evolved in response to female preferences for showy males. Among such traits, yellow and red carotenoid-based ornaments have been considered as particularly good candidates for explaining why and how females would benefit from mating with showy partners. Because carotenoids can be used for promotion of both health and appearance, colourful male ornaments should honestly reveal the vigour of the bearers. Two recent experiments with birds^(2,3) now show how allocation of bodily carotenoids to sexual signalling is traded off against the use of carotenoids for boosting immune function. *BioEssays* 25:1–2, 2003.

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Sexual selection, honest signals and parasites

To explain the evolution of extravagant male ornaments, Darwin⁽¹⁾ proposed the theory of sexual selection, which he separated from the general theory of natural selection. Darwin suggested that elaborate secondary sexual traits, such as ornamental plumes of many bird species, could evolve if females would prefer ornamented males as mates. The question about why females should prefer such showy males, however, remained largely unanswered until the advancement of Zahavi's handicap principle in 1975.⁽⁴⁾ According to this, females' preference for elaborate male ornaments could evolve if these ornaments serve as indicators revealing the quality of the male. The honesty of the indicator traits would be ensured by the high cost (developmental, maintenance, behavioural etc.) of such signals, so that individuals of inferior quality could not afford to cheat. In 1982, Hamilton and Zuk⁽⁵⁾ proposed an explicit mechanism of how Zahavi's handicap principle could work. Their concept of parasite-mediated sexual selection suggested that an individual's ornamentation reveals its ability to resist currently prevailing parasites. Under this scenario, males that are more resistant to parasites and

in better health are able to invest more resources in sexual display. Such healthy males would be able to make higher paternal investment and/or transmit less parasites during physical contact.⁽⁶⁾ Furthermore, if resistance is heritable, females would also benefit by obtaining resistance genes for their offspring.⁽⁵⁾

Carotenoids—plant pigments used by animals

Carotenoids are a group of more than 600 different terpenic pigments produced by plants, algae and fungi.⁽⁷⁾ Although animals cannot synthesise carotenoids de novo, carotenoids are extraordinarily common components of the colour of animal signals such as those used in sexual communication, signaling between offspring and their parents and in warning colours. Examples range from the bright yellow, orange and red feathers, beaks and gapes to the elaborate coloration of the skin and various body parts of fish, reptiles, birds and mammals.^(7,8) Since animals have to acquire carotenoids from food, allocation of carotenoids to signals may simply reflect the foraging ability of individuals.^(9,10) However, carotenoids also participate in functioning of the endocrine and nervous system and play important roles in immunoregulation and immunostimulation, lymphocyte proliferation, free radical scavenging and detoxification.^(8,11,12) Hence, one might expect a trade-off between investment of carotenoids in maintenance and ornamentation because individuals that are forced to fight infections during formation of carotenoid-based ornaments have less carotenoids available for developing signal traits. This connection was first recognised by Lozano in 1994,⁽¹¹⁾ who proposed that, by choosing mates on the basis of carotenoid-dependent traits, females might be increasing the likelihood of obtaining healthy partners and deriving direct and/or genetic benefits from such a choice.

Flaunting health

What is the evidence for carotenoid-based signalling of superior health? Involvement of carotenoids in maintenance and sexual signalling functions has been well documented in separate model systems.^(7,8,11) However, the direct experimental evidence that these two functions are traded-off against each other by reallocation of carotenoids has been lacking until the recent reports of Blount et al.⁽³⁾ and Faivre et al.⁽⁴⁾ The study of Blount and his colleagues showed that supplementing the drinking water of captive male zebra

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finches with extra carotenoids caused them to develop significantly redder bills compared with their brothers maintained on control diet. Carotenoid supplementation also resulted in more than two times higher plasma carotenoid concentrations and, most interestingly, in significantly stronger cell-mediated immune responses against novel antigen. Thus, males who had more bodily carotenoids at their disposal, appeared potentially more capable of fighting off parasites and also became more ornamented. Evidently, this did not slip the notice of females who preferred to associate more with carotenoid-supplemented males than with their pale-beaked brothers disclosing low bodily carotenoid levels.

Complementary evidence for the carotenoid-based health signalling was provided by Faivre and his colleagues, who were able to demonstrate the reallocation of carotenoids from signalling function to immune response. Having first shown that the bright yellow and orange colours of the beaks of male European blackbirds are based on carotenoid pigments, they challenged the health state of birds by inducing an immune response against novel antigen (sheep red blood cells). This resulted in fading of the beak colour of immune-challenged birds compared to sham-injected control individuals. Since beak colour of blackbirds has a signalling function both in contests between males⁽¹³⁾ and presumably in mate choice,⁽¹⁴⁾ this study provides an important evidence about how such signals can honestly advertise bearers health.

What is noteworthy about both studies is that they used different types of antigen for inducing the immune response. Magnitude of the swelling response to plant lectin phytohaemagglutinin (injected to zebra finches) is an index of the efficiency of cell-mediated immunity.⁽¹⁵⁾ Sheep red blood cells injected into blackbirds induce antibody-based humoral response. Yet the associations with carotenoids were present in both cases, which suggests the general link between

immune function and carotenoids. If individuals who are able to mount strong immune responses against novel antigens are also superior in resisting infections (as might be expected), then carotenoid-based signalling may indeed appear the plausible pathway for parasite-mediated sexual selection to work.

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