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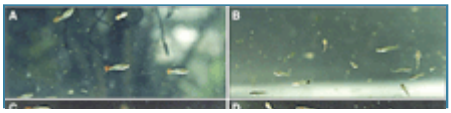
LETTERS

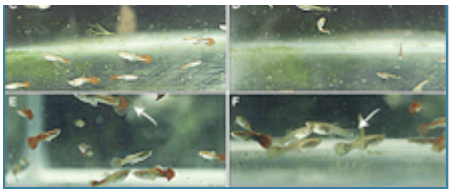
Attraction to Orange: Sexiness, Not Gluttony

In her article "Guppy sex and gluttony guided by orange glow" (News of the Week, 8 March, p. 1816), Virginia Morell reviews recent evidence published by Rodd *et al.* suggesting that the sexual preference of female guppies (*Poecilia reticulata*) for males with orange spots is explained by the notion that orange resembles food (1). Of course, it is difficult to separate females' attraction to food from the attraction to males that are stronger and faster and, thus, able to consume more orange-colored cabrehash fruit, which is limited in supply. Indeed, our observations suggest that, for female guppies, orange spots signal sexiness and, moreover, the virility of a potential mate.

One week after birth, a group of guppy fry, including both males and females, were separated into two cohorts and fed diets with or without the addition of testosterone (250 mg/kg of diet). Within 3 weeks, those fish consuming testosterone developed bright orange spots (panel A of figure), which continued to develop with maturation (panel C) and remained, throughout their lives (even in female guppies, panel E). However, those raised without testosterone did not express orange spots early in life (panels B and D), and females that were not exposed to testosterone did not express orange spots at any stage in life (panel F).

Coloration of fish skin is determined by deposition of pigments within the skin (2). As fish cannot synthesize carotenoids, the coloration of (male) *Poecilia reticulata* is indicative of their ability to forage within carotenoid-limited environments and thus is a measure of health and vigor. In addition, the orange spots of male guppies contain another pigment called red pteridine, which, unlike carotenoids, can be synthesized de novo (3).





(A) Four-week-old testosterone-treated fry. (B) Four-week-old nontreated fry. (C) Six-week-old testosterone-treated fry. (D) Six-week-old nontreated fry. (E) Three-month-old testosterone-treated adults (one female is indicated by an arrow). (F) Three-month-old nontreated adults (one female is indicated by an arrow).

The rapid appearance of orange spots in testosterone-treated guppy fry but not in untreated fish is curious, given that both groups consumed the same diet. One possibility is that testosterone is a key regulator of pteridine biosynthesis and influences the production and distribution of pigment within the skin, leading to the appearance of orange spots in males and females.

We favor sexiness, rather than gluttony, as the key determinant of female guppies' sexual preference for the orange spots of a male guppy, indicating testosterone (masculinity and vigor) and, by extension, the viability of the potential mate.

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References and Notes

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4. We thank A. S. Perera for daily maintenance of the aquaria used in this study.

Response

Charles Darwin (1) proposed the theory of sexual selection to explain the evolution of secondary sexual characters, such as gaudy coloration and weaponry. Put simply, he argued that these traits evolved because they increased the ability of their bearer to compete for or attract mates. In a classic conflation of proximate and ultimate causation, Nobel laureate T. H. Morgan (2, 3) argued against Darwin's theory on the grounds that sex hormones, such as testosterone, cause secondary sexual characters to develop. Darwin was trying to explain why such traits have evolved, not how they are produced developmentally. The relationship between Morgan's theory and Darwin's is that sex hormones are part of the developmental mechanisms that, over evolutionary time, may have been shaped by sexual selection.

Our recent paper (4), on which Virginia Morell reports, was concerned with the evolutionary origin of a mate preference. Female guppies are known to prefer males with orange spots, but the origins of this preference are unknown. We reported that wild guppies in Trinidad voraciously consume orange-colored fruits (*Sloanea* and *Clusia* spp.), which occasionally fall into streams from the rainforest canopy. By placing painted disks in the streams, we found that guppies of both sexes are especially attracted to the color orange. When

guppies were raised from birth in the laboratory (in the absence of fruit), attraction to orange disks persisted, and the degree of attraction to orange correlated with the strength of the female preference for orange (carotenoid) coloration in males (at the population level). These results suggest that the preference for orange coloration in males may be a "sensory trap" (5) that initially evolved for detecting rare but rich food sources.

The results presented by Jayasooriya *et al.* on the effects of testosterone on color expression in guppies are fascinating from a developmental perspective (6), but they bear the same relationship to our hypothesis as Morgan's results bore to Darwin's theory. That is not to say that the developmental basis of male coloration is irrelevant for female mate preference evolution. If females benefit from mating with high-testosterone males, this could select for exaggeration of the female preference for orange coloration. But simply showing that testosterone is involved in the regulation of color production does not illuminate the ultimate questions about why mate preferences, or the secondary sexual characters they favor, have evolved.

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