



## 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 fe-

male 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).

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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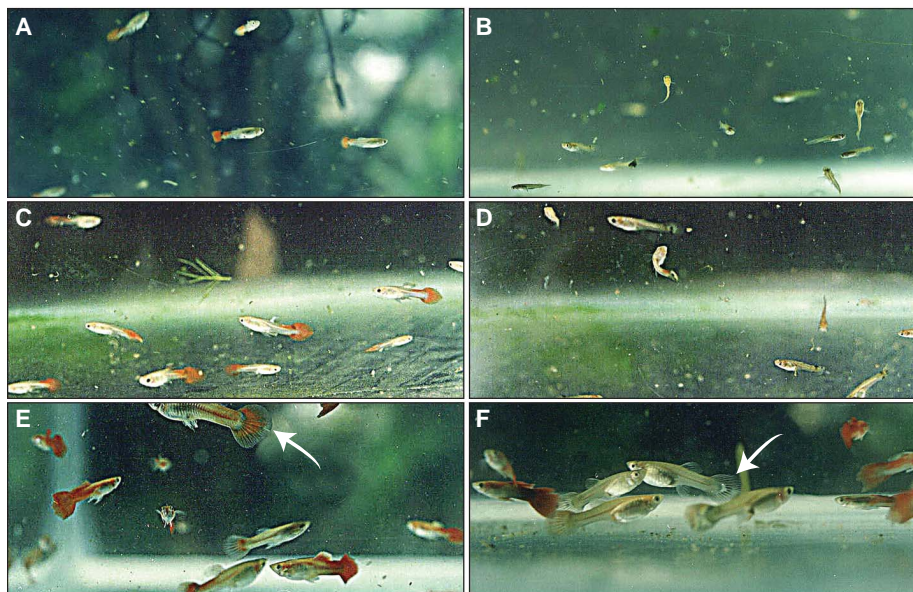
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### Response

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



(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).

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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## Tree-Ring Chronologies and Climate Variability

THE RECENT REPORT BY ESPER *ET AL.* ("Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability," 22 March, p. 2250) addresses important scientific questions on the spatial scale of past climate periods such as the so-called "Little Ice Age" and "Medieval Warm Period." It also presents a valuable set of data and demonstrates a novel use of a promising technique. As already indicated (1), the basis used by Esper *et al.* for comparison with previous studies of Northern Hemisphere (NH) temperature trends over

the past millennium (2-4) is flawed. For this and other important reasons, the previously established conclusion (5) that late 20th century warming appears to be unprecedented over at least the past millennium still stands.

Esper *et al.*, like previous studies (2-4), conclude that peak warmth about 1000 years ago was comparable to that of the mid-20th century. However, unlike these previous studies, they did not compare the peak medieval warmth against that of the past few decades, wherein hemispheric temperatures have risen several tenths of a degree Celsius further above mid-20th century levels. Their report is thus not a refutation of the basic finding (5) that late 20th century warmth is anomalous in the context of at least the past millennium.

The Esper *et al.* reconstruction exhibits greater century-scale variability than the hemispheric reconstruction of, e.g., Mann *et al.* (3), with the greatest differences seen in the level of cooling during the so-called Little Ice Age (17th to 19th centuries). As they indicate, some of these differences may have a geographic basis. Esper *et al.* estimate extratropical (and primarily, warm-season) temperature changes, using an entirely extratropical tree-ring data set. In contrast, the Mann *et al.* reconstruction estimates temperature trends over the full NH, using both extratropical (tree ring, ice core, and historical) and tropical (coral, tree ring, and high-elevation ice core) proxy data and targeting the full NH temperature. Half of the surface area of the NH temperature record estimated by Mann *et al.* lies at latitudes below 30°N, whereas the Esper *et al.* estimate is based entirely on latitudes above 30°N. Tropical surface temperatures are typically less variable than extratropical continental surface temperatures on almost all time scales. For example, Hendy *et al.* (6) have shown that there is little if any cooling in a substantial region of the tropical Pacific during the Little Ice Age, and they argue that the main signature of the Little Ice Age is an increase in the poleward temperature gradient. Such inferences are consistent with recently demonstrated dynamical mechanisms for enhanced extratropical continental cooling in the Little Ice Age (7). More moderate temperature variations at the scale of the full NH (2-4) are consistent with model (5) simulations.

Esper *et al.* use the regional curve standardization (RCS) technique in their estimation of temperatures between 800 and 1100 A.D. in spite of the cautions of Cook *et al.* (8) and their own injunction that "Successful use of the RCS method generally requires a large number of ring-width series because the method of detrending is not based on any explicit curve-fitting to the individual series..." (p. 2251). Large numbers of samples were used in their study, but not for the period

around 1000 A.D. Their supplemental Web fig. 2 (9) shows that only 6 of the total of 14 sites cover this period and that the total number of samples used for any one year is between 50 and 70. Dendrochronologists usually take two samples per tree, so their estimate of extratropical NH temperature 1000 years ago is probably based on 25 to 35 trees spread across six locations. They rightly point to the need for more long, well-replicated tree-ring collections covering the period 900 to 1300 A.D.

Rather than refuting past temperature estimates, the Esper *et al.* record underscores the mounting evidence for substantial differences between tropical and extratropical temperature trends in past centuries and the need for more records of millennial length and for a better understanding of the situations under which multicentennial climatic information may be extracted from tree-ring data.

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## Response

MANN AND HUGHES BRING UP CERTAIN ISSUES about our report that require a reply. The purpose of our report was first to document how it is possible to preserve multicentennial climate variability in certain long tree-ring records if the proper methods of analysis are applied. This demonstration was in response to the claim that this was not possible (1). We then inferred that the presence of a coherent large-scale multicentennial signal in the mean tree-ring chronology from the 14 analyzed sites in the extratropical Northern Hemisphere (NH) was probably due to long-term changes in temperature. To demonstrate this, we compared our record (ECS) with the largely data-independent and widely cited Mann *et al.* (2) NH annual temperature reconstruction. In so doing, we carefully point-

ed out the differences between the spatial domains that each series represents. We feel that this point is unnecessarily emphasized by Mann and Hughes because our report clearly states what they regard as a critical difference between the two temperature reconstructions. Of greater significance is the fact that we produced a new history of extratropical NH temperature variability with significantly higher multicentennial variability than previously thought (3).

We differ with Mann and Hughes on two points. First, we do not agree that the scaling of the ECS series is necessarily "flawed." The scaling issue is complicated by the way in which the tree-ring data were aggregated

before doing any temperature modeling, and we show in Table 1 of our report that there is little useful NH temperature information in the series at periods shorter than about 20 years. This is why we scaled the ECS series to NH temperatures, as described in the paper. Even so, Briffa and Osborn (3) point out some ambiguity in the scaling of ECS, which we acknowledge here as well. However, they also show that, after their rescaling, our reconstruction (3) is compatible with gridded borehole temperature estimates back to 1500 A.D. So, although the scaling issue does deserve further attention, we think that it is a premature to call our temperature reconstruction "flawed."

We also disagree with the criticism of the usefulness of the regional curve standardization chronology in the Medieval Warm Period (MWP; about 900 to 1300 A.D.) interval. The replication in ECS is described in great detail in our report and in the accompanying supplementary materials (4). We also provide bootstrap confidence limits as direct information about the uncertainty of the reconstruction over its entire length. In doing so, we show (Fig. 2 in our report) that even with six sites before 1072 A.D., there were "significant" periods of above average growth (and inferred temperatures) during the MWP.

In terms of spatial representation and the use of confidence limits/error estimates, our results also compare well with other published (mostly extratropical) NH temperature reconstructions covering the past 1000 years [e.g., (5, 6)]. Our reconstruction expands on those previous results and contributes potentially important new insights into the nature of past NH temperature variability in the extratropics. Clearly, more millennia-long tree-ring records, with better replication and preservation of multicentennial variation, will improve our confidence in determining how warm the MWP was.

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