



COMMENTARIES

Preference for symmetry in swordtail fish

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The study of fluctuating asymmetries has attracted a great deal of interest due to the hypothesis that females could use symmetry to detect high-quality mates (Watson & Thornhill 1994; Møller & Swaddle 1997). Nevertheless, problems with demonstrating that females prefer symmetrical male traits continue to surface. Two of the difficulties first identified were (1) not testing for symmetry of natural traits that function in mate choice (Swaddle 1999), and (2) separating preference for trait symmetry from preference for behaviours enhanced by symmetry (Balmford & Thomas 1992). Studies of female preference for symmetry in a vertical bar pigment pattern in sailfin mollies (*Poecilia latipinna*; Schlüter et al. 1998) and swordtails (*Xiphophorus cortezi*; Morris & Casey 1998) were successful at avoiding these problems. The vertical bar pigment pattern is a natural male trait that attracts females in some species (Morris et al. 1995). Choice tests in these studies were conducted using model males (Schlüter et al. 1998) or live males whose bars had been manipulated in a manner that would not influence the males' behaviour (Morris & Casey 1998), which controlled for the possibility of symmetry-enhanced behaviours biasing the results. In both species, females spent significantly more time with males that had an equal number of bars on both sides than with males that had an unequal number of bars, even though the total number of bars between males was held constant (Morris & Casey 1998; Schlüter et al. 1998). These results were interpreted as demonstrating female preference for symmetry in bar number.

In a recent commentary, Shettleworth (1999) proposed an alternative explanation for apparent preferences for symmetry. Shettleworth questioned whether the type of preferences demonstrated in the studies by Morris & Casey (1998) and Schlüter et al. (1998) could in fact be explained by a simpler perceptual process based on Weber's law, a logarithmic function common to many

sensory processes (Figure 1 in Shettleworth 1999). In this model, a female's response (r) is determined by the sum of the stimuli (n) from each side of the male. Therefore, the response to a male with equal numbers of bars on each side would be $r = k \log n + k \log n$ (in which k is an arbitrary constant). On the other hand, the response to a male with unequal numbers of bars would be $r = k \log(n-1) + k \log(n+1)$. Because the function is logarithmic, the difference in value between $k \log n$ and $k \log(n-1)$ would be greater than the difference between $k \log n$ and $k \log(n+1)$. Consequently, the value of r for a male with equal numbers of bars would be greater than that for a male with unequal numbers of bars if the total number of bars between the two males is held constant. Thus, females would prefer symmetric males to asymmetric males not due to a preference for symmetric males per se, but because of the nonlinear preference function for total bar number.

While this is an interesting and plausible explanation for the data acquired by Morris & Casey (1998) and Schlüter et al. (1998), a subsequent study on *X. cortezi* by Morris (1998) provides data that can be used to test Shettleworth's alternative model directly. In this study, females were presented with symmetric and asymmetric males as in Morris & Casey (1998). However, in contrast with the earlier study, the minimum number of bars on each fish within a pair was held constant. For example, while a symmetric male would have six bars on each side, an asymmetric male would have six bars on one side and eight bars on the other (Table 1 in Morris 1998). If female responses were based on the logarithmic model suggested by Shettleworth (1999), then the response of a female to a symmetric male would still be $r = k \log n + k \log n$. However, the response to the asymmetric male would be $r = k \log n + k \log(n+d)$, where d is the difference in bar number between the two sides. As the value of r will always be greater for an asymmetric male, it would be expected that, if females followed this model, they would strongly prefer asymmetric males in this experiment. This was not the case. Females spent significantly more time

associating with males that had equal numbers of bars on both sides but fewer total bars than they did with asymmetric males (test 1 and test 2 in Morris 1998). In addition, the same females in a subsequent test showed a strong preference for greater number of bars (test 3 in Morris 1998). Morris (1998) interpreted this data as evidence for two independent preferences: a preference for symmetry and a preference for greater total bar number. When the variables were at odds with one another, the preference for symmetry was stronger than the preference for bar number within the ranges of the variables tested. Consequently, female *X. cortezi* preferred symmetric males even though the asymmetric males had more bars.

Shettleworth (1999) suggested that the question of whether females are assessing symmetry can only be answered by measuring absolute preference functions (Wagner 1998). The experiment performed by Morris (1998) indicates that, in principle, one can demonstrate female preference for trait symmetry in addition to trait size without obtaining preference functions. Nevertheless, preference functions can yield great insight into the individual variation in female preferences within a population as well as avoid confounding factors such as variation in sampling behaviour, both of which can be undetectable in standard simultaneous mate choice tests (Wagner 1998). In addition, a simultaneous choice test that gives a female a choice between two states that lie near the asymptote of her logarithmic preference function for that trait might mistakenly assume no preference for variation in that trait. Therefore, preference functions based on either single-stimulus or simultaneous-stimulus data may be most valuable in cases in which population-level preferences are very weak and are undetectable using standard choice tests.

The demonstration of preference for symmetric traits that cannot be seen simultaneously has implications for the cognitive abilities of these animals. Shettleworth (1999) argued that assessment of body bar symmetry in poeciliid fishes would be a cognitively more demanding process than most other hypothesized examples of symmetry assessment. In examples such as the assessment of facial symmetry in humans or feather symmetry in birds, the right and left sides of the characters in question are visible from one vantage point, allowing simultaneous comparison. Shettleworth (1999) suggested that when assessing body bar symmetry, however, a female must first 'count' the number of bars on one side of a male, store that 'count' in memory, wait for a male to present his other side, recognize that the male is still the same male and not another individual, 'count' the number of bars on the other side, and then compare that image to the previous one to determine bar symmetry. We agree that assessment of symmetry when the right and left sides cannot be viewed simultaneously is different from, and perhaps more difficult than, assessment of symmetry patterns when both parts can be seen at once. Despite the potential difficulties, however, the strong preference for symmetry found in *X. cortezi* by Morris (1998) indicates that poeciliid fish are capable of assessing and responding to this type of symmetry.

Studies on insect visual pattern memory suggest a possible mechanism for assessment of symmetry when the two sides are not presented simultaneously. In *Drosophila melanogaster*, visual pattern memory appears to be based on a template-storage system, whereby an image is stored in memory and then compared to an image that is later received by the eyes. Dill & Heisenberg (1995) found that a graded similarity function based on the degree of overlap between an initial image and one presented later provided a significant correlation to the observed behaviour of the fruit flies. Comparisons made by fruit flies of geometric shapes from a fixed, tethered position is a considerably less complex process than the comparison of bars on two sides of a male involved in courtship displays. Nevertheless, a process by which a female swordtail records the bars on one side of a male as a visual template and then compares that template with input from the other side of the male could permit the symmetry assessment observed in swordtails. In *X. cortezi*, this comparison could be facilitated by male courtship behaviours, which involve displays in which a male presents a female with views of each of his sides in rapid succession (Morris & Casey 1998).

The assessment of symmetry is an important topic in the ongoing investigations of the complex decisions made by animals when selecting mates. Experiments attempting to demonstrate preferences for symmetry have often been faced with equally plausible alternative explanations to the data, a situation exemplified in Shettleworth's commentary on data of the type collected by Morris & Casey (1998) and Schlüter et al. (1998). Experiments such as those proposed by Shettleworth (1999) or employed by Morris (1998) are examples of the types of studies that can be used to discriminate among proposed mechanisms for female preferences.

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