

Courtship and genetic quality: asymmetric males show their best side

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Fluctuating asymmetry (FA), the small random deviations from perfect morphological symmetry that result during development, is ubiquitous throughout the animal kingdom. In many species, FA seems to play a role in mate choice, perhaps because it signals an individual's genetic quality and health. However, the relationship between an individual's FA and behaviour is generally unknown: what do more asymmetric individuals do about their own asymmetry? We now show for the first time that individuals respond behaviourally to their own morphological FA in what appears to be an adaptive manner. During courtship, male guppies exhibiting high FA in ornamental colour, bias their displays towards their more colourful body side, thus potentially increasing their attractiveness by exaggerating the quantity of their orange signal. This appears to be a strictly behavioural male response to cues provided by females, as it does not occur when males court a non-reactive model female. Whether inferior males realize any mating advantage remains uncertain, but our study clearly demonstrates a behavioural response to random morphological asymmetries that appears to be adaptive. We propose that the tendency to show or otherwise use a 'best side' is common in nature, with implications for sexual signalling and the evolution of more pronounced asymmetries.

Keywords: genetic quality; fluctuating asymmetry; mate choice; sexual signalling; behavioural lateralization; guppy (*Poecilia reticulata*)

1. INTRODUCTION

The role of symmetry in courtship behaviour and sexual signalling is far from understood (Tomkins & Simmons 2003; Dongen 2006). Most research to date has focused on fluctuating asymmetry (FA): the small random deviations from bilateral symmetry that result from developmental 'noise' in the morphological traits of individuals (Palmer & Strobeck 1986). It is thought that FA can provide an honest signal of an individual's genetic quality or condition during courtship (Møller & Pomiankowski 1993; Watson & Thornhill 1994; Roulin *et al.* 2003; Brown *et al.* 2005). This idea remains somewhat controversial, however, since many organisms exhibit no preference for symmetry in mate choice and/or no relationship between symmetry and apparent overall fitness (Lens *et al.* 2002; Polak & Stillabower 2004).

Surprisingly little is known about the capacity of individuals to respond behaviourally to their own FA. By focusing on the benefits of symmetry, behavioural ecology has largely ignored the potential for compensatory or exploitative behaviours that capitalize upon the subtle asymmetries resulting from developmental instability. This is surprising for two reasons. First, there is the simple observation that many otherwise bilaterally symmetrical organisms exhibit pronounced morphological asymmetries (Neville 1976), and adaptive behavioural responses to initially slight random deviations from symmetry (i.e. FA) have been postulated as a potential mechanism for the

evolution of these conspicuously asymmetric structures (Palmer *et al.* 1993; Palmer 1996). Second, recent research has shown that behavioural lateralization (i.e. the favouring of one body side over another), long thought to be a uniquely human trait (Corballis 1991), is actually exhibited by a variety of vertebrate taxa in a range of tasks (Rogers 2002). As in the case of conspicuous morphological asymmetries, current hypotheses for the evolution of behavioural lateralization are predicated upon an adaptive link between morphological and behavioural deviations from symmetry (Vallortigara & Rogers 2005). However, behavioural asymmetries in response to subtle individual FA have not been demonstrated (Vallortigara & Rogers 2005).

Behavioural responses to FA might be particularly apparent in mate choice and sexual signalling, since: (i) FA in ornamental characters is generally greater than that found in functional characters (Møller & Pomiankowski 1993; Palmer 1996), (ii) courtship behaviours are often elaborate and diverse, and (iii) sexual selection upon both morphology and behaviour is often intense. In female mate choice, male behaviours that 'cheat' sexual signals are expected, since the interests of the female (accurately assessing male quality) and the male (successfully attracting the female) are directly opposed (van Doorn & Weissing 2006). In other words, a so-called 'honest' signal (as FA is proposed to be) is somewhat of a misnomer (Dawkins & Guilford 1991): more accurately, there exists a coevolutionary struggle in which deceptive males that can successfully undermine the association between signalling and genetic quality may be favoured (van Doorn & Weissing 2006). In organisms where symmetry

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is not a trait targeted by females, we might anticipate that, where possible, males will attempt to take advantage of FA through deceptive asymmetric behaviour. Put more simply, when courting females, males might be expected to show their 'best side'.

Here we test this best-side hypothesis in the courtship behaviour of the guppy (*Poecilia reticulata*). The guppy is a popular model system for the study of sexual selection (Houde 1997; Magurran 2005). Males are highly colourful and court multiple females, while females are bland and give birth to live young. Female mate preference is well documented and linked to both ornamental (e.g. carotenoid and melanin pigmentation) and non-ornamental (e.g. body size) traits (Reynolds & Gross 1992; Brooks & Endler 2001). Ornamental orange pigmentation is highly variable among males and determined by both genes (Hughes *et al.* 2004) and the male's ability to obtain a carotenoid-rich diet (Grether 2000). Consequently, the quantity of orange pigment exhibited by the male may provide the female with information about its genetic quality and current condition (van Oosterhout *et al.* 2003; Evans *et al.* 2004). Males vary not only in pigment quantity, but also in lateral pigment symmetry (Sheridan & Pomiankowski 1997b). While female guppies are known to favour gross symmetry in ornamental colour spots (Sheridan & Pomiankowski 1997a), no correlation between FA and female preference has been found (Brooks & Caithness 1995). Male guppies present their ornaments to females in sigmoidal mating displays and frequently alternate the side exhibited. Since both sides of the male cannot be viewed concurrently, the ability of females to detect and respond to colour symmetry is questionable (Brooks & Caithness 1995; Sheridan & Pomiankowski 1997a; but see Merry & Morris 2001): in order to calculate symmetry, a female must not only assess information for each side of the male's body, but also combine this information across sides. This creates the potential for males to exploit ornamental FA by biasing their displays in favour of the body side with more orange pigment.

In this paper, we demonstrate that male guppies with more symmetric body colour display both sides equally to the female during courtship, while those with high FA in body colour preferentially display their most colourful side. Since ornamental FA correlates negatively with other measures of genetic quality in these males (i.e. body size and amount of orange colour), the asymmetric males using lateralized courtship displays to show their 'best sides' are probably genetically inferior males. We test various mechanisms by which these display biases might arise, and conclude that lateralized displays are a strictly behavioural response by males to courtship cues provided actively or passively by females. Our study provides the first evidence for an adaptive link between the FA resulting from biological noise and behavioural lateralization. Furthermore, it challenges our understanding of symmetry as an honest sexual signal and raises questions regarding the extent to which asymmetric individuals might manipulate their sexual attractiveness.

2. MATERIAL AND METHODS

(a) *Experimental fish*

Guppies used in this experiment descended from a 1988 collection from the Lower Quare River, Trinidad. These were

housed as a breeding population of approximately 500 adults in a 960 l stock tank on a 12 : 12 h light regime. The mating behaviour tests were conducted between 1993 and 1998. Pregnant females from the stock tank were allowed to give birth in individual 36 l tanks. Immature males and females were separated from each other at the first sign of gonopodial development and maintained in all-male 'bachelor' or all-female 150 l tanks to ensure that all test fish used were virginal, and of a similar age.

(b) *Female preference and male display behaviour (F_1)*

Test males and females from the 150 l tanks were placed into individual 8 l (30 cm × 12 cm) tanks. In each trial, the rectangular male tank was positioned with its 12 cm side facing the 12 cm side of the paired female tank. The body side facing the opposite sex (right or left) was recorded for 15 s at 5 min intervals for at least 100 min. Each male tank was then paired with a different female tank, and the observation procedure was repeated. In total, 53 males were used, each exposed individually to each of 20–30 females. Male display bias was calculated as the average ratio of presentation of the right side and left side across all trials. An 'attentive' female response towards a male was scored when both were within the preference zone (within 3 cm of the interface between tanks) and the female was oriented towards the male. This was recorded every 15 s for 10 min (a total of 40 observations for each pair). The female preference score for each male was calculated as the average of the female attentiveness scores for that male across all 20–30 pairings. This resulted in over 1300 behavioural scores of female preference across the 53 males. The behavioural data were collected blind (in the sense that the observers could not identify individual test males, nor did they know the FA of the males).

(c) *Display behaviour of offspring (F_2) males*

Some of the original test (F_1) males ($n=26$) were later allowed to breed with randomly selected females. The male offspring (F_2) were raised as mature virgins and any brothers were randomly divided across two groups. F_2 males in the first group ($n=31$) were assigned to mating trials identical to those used for their F_1 fathers (with new virgin females). Males in the second group ($n=55$) were assigned to a model female (a dead female mounted on a stick within the preference zone) rather than a live test female. After placing the model in the female tank and allowing the male to acclimatize (approx. 5 min), male display was observed continuously for 15 min. Males in both groups actively courted females (625 total displays, or an average 20.2 displays per male for the first group, and 1298 total displays, or 23.6 displays per male for the second group). The ratio of right-side to left-side displays was calculated for each male.

(d) *Trait measurements*

A week after the mating trials were finished, all test males were anaesthetized with MS-222 and photographed on both sides. Photographs were stored as digital images. In 2004, these images were imported into the public domain image processing and analysis program NIH IMAGE (<http://rsb.info.nih.gov/nih-image/>). We classified each ornamental pigment (orange or melanin) along three components of the HSB colour model (hue, saturation, brightness) using the program's Plugin-Colour-Threshold Colour function. In this

model, we used the hue filter to select a range encompassing all orange coloration, and removed background and visual noise in the image using the saturation and brightness filters. For melanin pigment, we used both hue and brightness filters to select the colour, and removed noise via the saturation filter. Each colour spot was circumscribed, and the quantity of each colour was estimated as the total number of pixels (1 pixel = 0.36 μm^2). Three independent measures were performed for each colour trait and each body side, and these were averaged to reduce observational error, but each measurement was performed at consistent HSB filter ranges for all individuals. The measurer was not aware of the results of the behavioural tests when producing these data. As melanin colour did not produce any significant results, the data are reported in the electronic supplementary material, note 1, table S1, figure S1.

(e) Statistical analyses

All statistics were performed using JMP v. 4.0.2 (SAS Institute, Inc., Cary, NC, USA) with two-tailed significance.

3. RESULTS

(a) Male traits and genetic quality

Experimental males (F_1 ; $n=53$) had a mean body size (standard length) of 19.61 mm (range = 16.23–24.52 mm, s.d. = 2.06 mm) and a mean total orange colour area (both body sides) of 26.70 mm^2 (range = 8.93–55.36 mm^2 , s.d. = 10.64 mm^2). Symmetry in orange colour exhibited the statistics of a true FA character (Palmer 1996), with a normal distribution around zero (mean orange per side = 13.35 mm^2 , mean left-side – right-side = 0.19 mm^2 , s.d. = 1.37 mm^2) and fluctuating with no fixed directional effect (Shapiro–Wilk $W=0.96$, $p=0.21$). Absolute FA as a percentage of orange colour ($|\text{left-side} - \text{right-side}|/\text{mean orange per side}$) averaged 8.6% (arcsin transformed; range = 0.5–37.2%, s.d. = 1.3%), a non-zero value that is relatively high for an FA character, yet consistent with the higher and more variable FA values observed in ornamental traits (Palmer 1996).

We examined the correlations among these three potential indicators of male genetic quality (size, colour and symmetry). While male size and colour (two known female preference cues, each presumably indicative of male genetic quality) were uncorrelated, ornamental FA was negatively correlated with both body size and orange colour ($p < 0.01$; electronic supplementary material, table S2). This is consistent with FA theory and the hypothesis that ornamental FA is a reliable indicator of male quality.

(b) Female preference

Females preferred males with more total orange colour on their body (figure 1a) and, independently, males of larger size (figure 1b). However, female preference was not correlated with orange FA (figure 1c; electronic supplementary material, table S1). These relationships were confirmed with a three-way ANOVA (size, orange colour and orange asymmetry: $R^2=0.39$, $F_{3,49}=10.62$, $p < 0.001$; effect test: size, $F_{1,49}=9.16$, $p=0.004$; orange colour, $F_{3,49}=12.36$, $p=0.001$; orange FA, $F_{1,49}=0.07$, $p=0.79$).

(c) Male display behaviour

Asymmetric males (defined as males with $|\text{FA}| > \text{mean FA}$ of 8.6%; $n=27$) biased their courtship displays to females

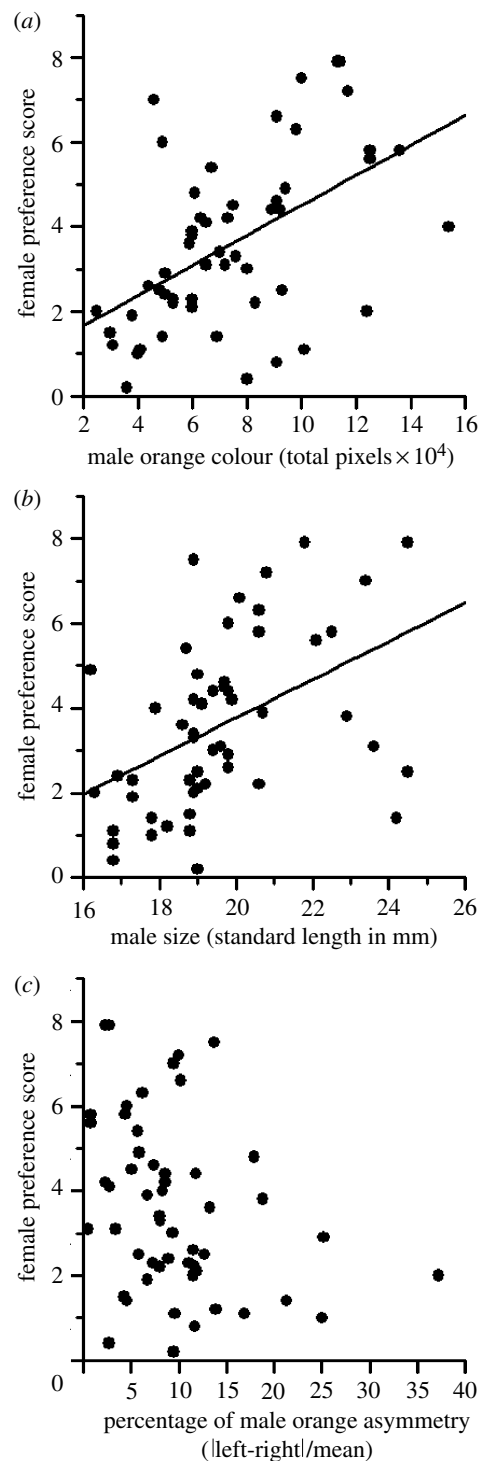


Figure 1. Female preference for orange colour, size and ornamental symmetry in males. (a) Females prefer males with greater quantity of orange colour (total pixel number for both body sides; $n=53$ males and 1330 trials; $y=0.35x+0.96$, $r^2=0.27$, $p < 0.001$). This relationship with female preference is significant regardless of how orange colour is measured: left side ($y=0.37x+2.36$, $r^2=0.24$, $p < 0.001$); right side ($y=0.38x+2.37$, $r^2=0.28$, $p < 0.001$); 'best' (most colourful) side ($y=0.37x+2.53$, $r^2=0.25$, $p < 0.001$); and 'worst' (least colourful) side ($y=0.38x+2.20$, $r^2=0.28$, $p < 0.001$). (b) Females prefer larger males (standard length; $n=53$ males and 1330 trials; $y=0.45x-5.23$, $r^2=0.21$, $p < 0.001$). (c) Females show no preference for bilateral symmetry in orange colour (calculated as $|\text{left-side orange} - \text{right-side orange}|/\text{mean orange per side}$; $n=53$ males and 1330 trials; $r^2=0.0003$, $p=0.68$; non-significant linear regression omitted for clarity).

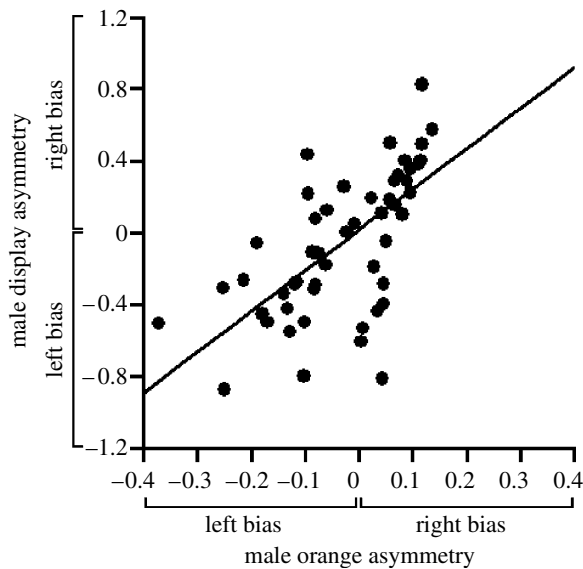


Figure 2. Asymmetry in orange colour and male display behaviour. Display asymmetry ((displaying left side – displaying right side)/mean number of displays) is correlated with orange colour asymmetry ((left – right)/average pixel number) ($n=53$ males, 2207 total displays; $r^2=0.20$, $p<0.001$).

in a manner that strongly correlated with their brighter (i.e. more orange) body side (figure 2). Out of 27, 25 asymmetric males preferentially displayed their best side, presenting the body side with greater orange colour in more than half of their displays. On average, asymmetric males presented their best side in 60% of their displays to females ($n=27$, range = 39.1–71.9%, s.d. = 3.2%; when $n=25$, bias is 61%). Conversely, symmetrically ornamented males ($|FA|<8.6\%$, $n=26$) exhibited no such correlation between orange asymmetry and display behaviour, but instead displayed both body sides with statistically equivalent frequency (mean best-side display frequency = 49%, range = 29.6–62.5%, s.d. = 4.7%). While there was no correlation between display lateralization and total orange ($p=0.20$), there was an independent negative correlation between display lateralization and male size ($p=0.03$), suggesting that smaller males may be more likely to bias their displays according to their ornamental FA.

The significant behavioural lateralization in the displays of the more asymmetric males suggests that they may be attempting to deceive females in mate choice through the behavioural exploitation of FA, presenting their body side with more colour more frequently in order to exhibit more colour, and thereby signal higher genetic quality than they may actually possess. However, we did not find a positive correlation between female preference and either ornamental FA (figure 1c) or display bias (percentage of best-side displays; $F_{1,50}=0.04$, $p=0.83$).

(d) Mechanisms for display biases

To determine the nature of the observed link between morphological and behavioural asymmetry, we considered four potential mechanisms that could provide males the ability to lateralize their display appropriately to the FA in their body colour. These mechanisms included: (i) an inherited genetic predisposition relating behavioural lateralization and ornamental FA, (ii) a developmental physiological coupling between display and body colour, (iii) a learned behaviour in which males identify their best

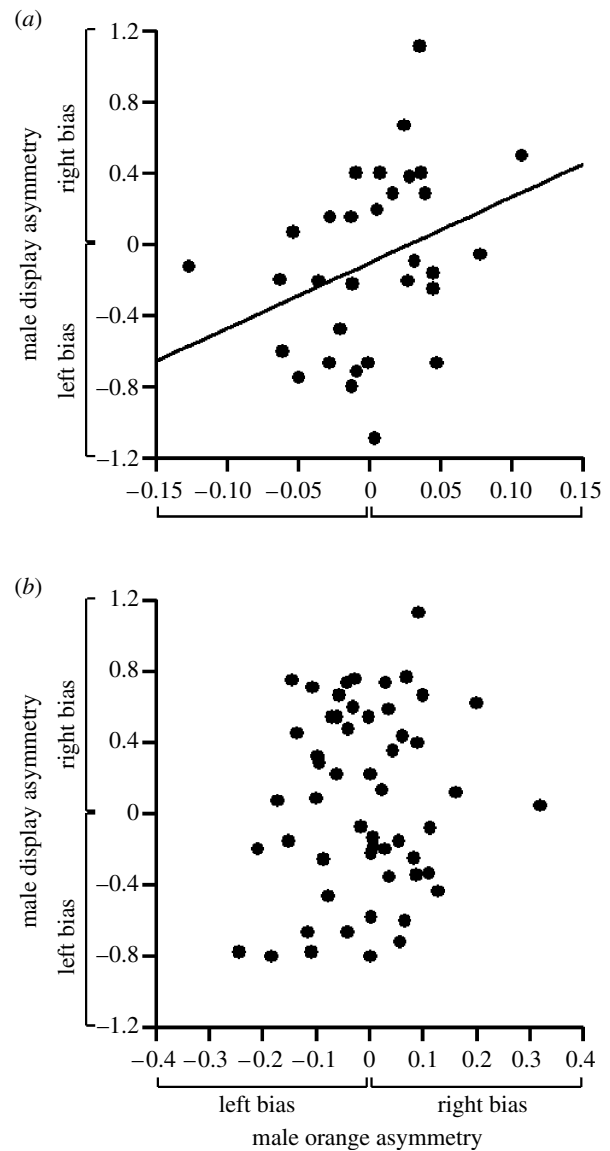


Figure 3. Asymmetry in orange colour and male display behaviour towards either live or model (dead) females. (a) Live female test: males biased their displays towards their 'best' (most colourful) sides ($n=31$ males and 625 total displays; $r^2=0.14$, $p=0.04$). (b) Model (dead) female test: males did not bias their displays ($n=55$ males and 1298 total displays; $r^2=0.008$, $p=0.51$; non-significant linear regression omitted for clarity).

side and retain this information, and (iv) a stimulus–response behaviour in which males respond to differential female interest in their body sides.

To examine genetic predisposition, we compared the courtship displays of F_2 male offspring with those of their F_1 fathers. We found that the F_2 males showed a very similar pattern of biasing their displays towards their best side ($n=31$, figure 3a). However, there was no correlation between F_1 fathers and F_2 offspring in either the side (i.e. left or right) with greater orange colour, the degree of asymmetry in colour, or the side favoured in courtship displays. Heritability values for these traits, estimated as twice the slope of the father–offspring regression, were 0.01, –0.19 and 0.16, respectively, none of which are significant (electronic supplementary material, table S3). These results suggest that asymmetries in orange colour and display behaviour are not linked by genetic predisposition.

To test whether FA in body colour was physiologically coupled with display behaviour, we conducted additional mating trials in which the live female was replaced with a model (non-living) female (i.e. one that could not provide any behavioural cues reflecting preference for either male body side). While F_2 males actively courted this model female, they did not show any lateral display bias (figure 3b), demonstrating an absence of physiological coupling between display-biasing behaviour and FA in body colour. In addition, we compared the results of the live- and model-female tests (figure 3a,b) via ANCOVA, with a factor dividing all samples into two groups (live and model tests). We then calculated the contribution of this factor and covariates to differences in male display. While group assignment did not contribute significantly to male display ($F_{1,1} = 2.119$, $p = 0.149$), covariates (slope effect) were significant ($F_{1,1} = 4.325$, $p = 0.0421$), confirming that male display bias became strong when responding to live females. We therefore conclude that the left–right bias in male colour does not appear to dictate the left–right bias in male behaviour, absent a live female.

To determine whether biasing courtship displays towards the more colourful side is a learned behaviour in males, we looked for an increase in best-side displays within and across the mating trials of virgin males. We found that the percentage of best-side displays did not increase with time (electronic supplementary material, figure S2), and thus there is no evidence that male guppies learn their more attractive side.

Since (i) laterality in courtship display behaviour did not occur without response from a live female and (ii) we found no evidence for genetic predisposition, physiological coupling or male learning, the most parsimonious explanation for lateralization of male courtship behaviour is that it is a direct response to cues from the female. The cues do not appear to be based on female orientation (left or right relative to the male), as female orientation was random towards both symmetric males (L : R = 51.7 : 48.3, $\chi^2 = 0.08$, $p = 0.81$) and asymmetric males (L : R = 54.7 : 46.3, $\chi^2 = 0.44$, $p = 0.51$; also electronic supplementary material, table S4). While separate tanks prevented olfactory cues, there are many visual cues that females might present, including both active (e.g. fin flicks, eye movements) and passive (e.g. time spent ‘looking’) behaviours. It is clear, however, that female response is an important component of biased display behaviour in males.

4. DISCUSSION

Sexual signalling theory predicts that, while females will attempt to accurately assess male genetic quality during mate choice, males will attempt to ‘game’ the system wherever possible (Johnstone 1998; Rowell *et al.* 2006). Our analysis conclusively demonstrates that male guppies bias their courtship displays in a manner consistent with our hypothesis that they will preferentially show their best side to the female: ‘asymmetric’ males (i.e. those with above-average FA in orange colour) displayed their more colourful side, on average, 50% more often than their less colourful side (i.e. 60%/40%, or 1.5 \times). But is this apparent ‘cheating’ profitable? We found no direct evidence of increased female preference resulting from male display lateralization, but a mating advantage for

cheating males cannot be ruled out. Based on the mean distribution of orange coloration across body sides, asymmetric males displaying according to their ornamental FA could hypothetically increase the total amount of orange presented to the female throughout the mating trial by approximately 7.2% if they displayed only their best side (i.e. best-side orange/mean orange per side). In actuality, the 25 asymmetric males appropriately biasing their display presented their best side in an average 61% of displays (range = 51.5–71.9%), increasing their apparent orange (i.e. (percentage of best-side displays \times best-side orange + percentage of ‘worst-side’ displays \times worst-side orange)/mean orange per side) by an average of only 1.8% (range = 0.3–5.5%). Translating total amount of orange presented to the female into female preference scores according to the regression equation in figure 1a, we can estimate that asymmetric males could potentially increase their preference score by 5.2% (relative to an unbiased display) if they fully biased their display. At observed display biases (61%), asymmetric males are estimated to have achieved a 1.3% increase (range = 0.2–3.2%) in their female preference scores relative to what they would have achieved with an unbiased display (50 : 50). This small increase in average preference, while potentially very meaningful in sexual selection and mating success, could be easily lost in experimental error and uncertainty. Detecting the advantages of display lateralization, if present, could be further confounded by the many interacting factors that are known to operate upon female preference in guppies (Endler 1987; Reynolds *et al.* 1993; Brooks & Caithness 1995).

It is also possible, however, that ‘biasing’ males are not gaining any cheating advantage from their behavioural lateralization. A signalling system open to cheating will inevitably be compromised, resulting either in the signal being discarded or in it being driven to escalated biological costs that guarantee its reliability (Rowell *et al.* 2006). Thus, signals that persist are likely to become honest, even if they were initially deceptive. For example, a recent study of six fish species in the Goodeinae family proposed that a reliable sexual signal, in the form of a yellow band on male tails, had evolved from what was originally a deceptive ‘sensory trap’ (Macias Garcia & Ramirez 2005). Similarly, the persistence of male ornamental orange colour as a sexual signal in guppies suggests that it is, for the most part, a reliable indicator of male quality, although some level of deception may be maintained by frequency-dependent selection if the cost of detecting cheats is high or if the cost of being deceived is low (Stuart-Fox 2005). Thus, female guppies may have evolved a resistance to dishonest signalling by males, perhaps by paying increased costs to detect deception by assessing the total amount of orange on both sides of the male, regardless of its display behaviour. Further support for the idea that ornamental orange colour remains an honest indicator of male quality despite the presence of deceptive behaviour comes from a related question: if males obtain significant mating advantages through biased displays, what prevents the evolution of male antisymmetry, in which most or all orange coloration is concentrated on a single body side? Female resistance to deception is one possible answer, although so is the potentially large biological cost to males in breaking the fundamental body plan for bilateral symmetry (Palmer 2004).

A final explanation for the observed link between male ornamental FA and behavioural lateralization in courtship displays is the possibility that male behaviour is mediated entirely by the female. We found that the presence of a live female was required to precipitate male display biases. This finding does not itself preclude male deception, as males in several species are known to tactically adjust their display intensity according to various factors (Dill *et al.* 1999), including female response (Patricelli *et al.* 2002). However, it is also plausible that females actively or passively cue males to display according to the relative amount of orange on each body side. This might, for example, assist the female in assessing the total amount of orange pigmentation across both sides of the male, consistent with our finding that while total amount of orange colour predicted female preference (figure 1a), FA in orange colour did not (figure 1c).

Note that each of the three alternative explanations we propose for the observed FA-related behavioural lateralization depends implicitly upon the ability of the female to detect and respond to ornamental FA in males. This capacity of female guppies to detect such subtle differences in the relative amount of orange colour across male body sides, while deemed unlikely in prior studies of guppy courtship (Brooks & Caithness 1995; Sheridan & Pomiankowski 1997a), is supported by both our finding of FA-related adjustments in male behaviour only in the presence of a live female, and studies of symmetry-related preferences in other fish species (e.g. Merry & Morris 2001). Furthermore, we estimate that the threshold for discrimination of colour asymmetry in guppies (i.e. the level of orange FA above which females appear to cue a bias in male display behaviour) lies between 8 (the mean FA) and 10%: above 10%, all males biased their displays in a manner appropriate to their ornamental FA (figure 2). This is consistent with a recent FA study, which found that starlings are capable of discriminating area-based asymmetries at a threshold of 5–10% (Swaddle & Johnson 2007). The fact that this threshold appears so close to the mean ornamental FA in guppies may not be accidental.

Behavioural lateralization was once thought to be an adaptation unique to humans, and any apparent laterality in other species was presumed to result from random environmental factors. The majority of research on lateralization has therefore been confined to experimental psychology and neuroscience, particularly in the areas of human handedness and hemispheric cognition (e.g. Stephan *et al.* 2003). Recent evidence for lateral biases in the everyday behaviour of many vertebrate species (Rogers 2002), including poeciliid fishes (Bisazza *et al.* 1997, 2000), has prompted the field's expansion into evolutionary biology in search of a broader evolutionary understanding of the phenomenon's prevalence (Vallortigara & Rogers 2005). The adaptive advantages of behavioural asymmetries, the relationship between population- and individual-level laterality and the roles of social communication and sexual selection are currently topics of considerable interest in the behavioural and brain sciences (Vallortigara & Rogers 2005). Current hypotheses for the evolution of advanced behavioural, cognitive and physiological (e.g. cerebral) lateralization propose that individual behavioural asymmetries may evolve to exploit sometimes subtle asymmetries in individual morphology (i.e. FA), which under certain

specific cognitive or social conditions can lead to more advanced laterality (Vallortigara & Rogers 2005). However, no link between FA in morphology and behavioural laterality has previously been shown (Bisazza *et al.* 1998; Vallortigara & Rogers 2005). This is perhaps unsurprising, since the vast majority of studies in lateralization have focused on population-level laterality (where most or all individuals of a population share the same cognitive or behavioural laterality), and comparatively few studies have examined individual-level lateralization (the hypothesized precursor to population-level lateralization). Where behavioural laterality has been observed solely at the individual level, its adaptive advantages have either been ambiguous (e.g. Marzona & Giacoma 2002) or, as in the case of the only other study of which we are aware to suggest an adaptive advantage to individual-level behavioural lateralization, not examined in relation to individual morphology (McGrew & Marchant 1999).

Our findings are the first demonstration in any animal, including humans, of a potential adaptive relationship between behavioural lateralization and morphological FA at the individual level. Even in situations where females could potentially see both sides of the male body at the same time, males may not always allow them to do so (e.g. human facial portraits). Lateral display biases in humans are often found in photographs and portraits (Nicholls *et al.* 1999), but even in humans any association between morphological asymmetry and adaptive behavioural laterality in courtship is unknown (Nicholls *et al.* 2005). We are unaware of any study showing that individuals are capable of preferentially displaying or using their best side in relation to their FA. The capacity shown here to respond to even slight morphological asymmetries, requiring only a simple behavioural response to preference cues provided during courtship, may offer a broad context for the initial evolutionary origins of more advanced behavioural laterality and more pronounced morphological asymmetries. We suggest that displaying or using one's best side may be an overlooked but widespread behavioural pattern in nature.

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REFERENCES

- Bisazza, A., Pignatti, R. & Vallortigara, G. 1997 Laterality in detour behaviour: interspecific variation in poeciliid fish. *Anim. Behav.* **54**, 1273–1281. (doi:10.1006/anbe.1997.0522)
- Bisazza, A., Rogers, L. J. & Vallortigara, G. 1998 The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neurosci. Biobehav. Rev.* **22**, 411–426. (doi:10.1016/S0149-7634(97)00050-X)
- Bisazza, A., Facchin, L. & Vallortigara, G. 2000 Heritability of lateralization in fish: concordance of right–left asymmetry between parents and offspring. *Neuropsychologia* **38**, 907–912. (doi:10.1016/S0028-3932(00)00018-X)
- Brooks, R. & Caithness, N. 1995 Female choice in a feral guppy population: are there multiple cues? *Anim. Behav.* **50**, 301–307. (doi:10.1006/anbe.1995.0246)

- Brooks, R. & Endler, J. A. 2001 Direct and indirect sexual selection and quantitative genetics of male traits in guppies (*Poecilia reticulata*). *Evolution* **55**, 1002–1015. (doi:10.1554/0014-3820(2001)055[1002:DAISSA]2.0.CO;2)
- Brown, W. M., Cronk, L., Grochow, K., Jacobson, A., Liu, C. K., Popovic, Z. & Trivers, R. 2005 Dance reveals symmetry especially in young men. *Nature* **438**, 1148–1150. (doi:10.1038/nature04344)
- Corballis, M. C. 1991 *The lop-sided ape*. New York, NY: Oxford University Press.
- Dawkins, M. S. & Guilford, T. 1991 The corruption of honest signalling. *Anim. Behav.* **41**, 865–873. (doi:10.1016/S0003-3472(05)80353-7)
- Dill, L. M., Hedrick, A. V. & Fraser, A. 1999 Male mating strategies under predation risk: do females call the shots? *Behav. Ecol.* **10**, 452–461. (doi:10.1093/beheco/10.4.452)
- Dongen, S. V. 2006 Fluctuating asymmetry and developmental instability in evolutionary biology: past, present and future. *J. Evol. Biol.* **19**, 1727–1743. (doi:10.1111/j.1420-9101.2006.01175.x)
- Endler, J. A. 1987 Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). *Anim. Behav.* **35**, 1376–1385. (doi:10.1016/S0003-3472(87)80010-6)
- Evans, J. P., Kelley, J. L., Bisazza, A., Finazzo, E. & Pilastro, A. 2004 Sire attractiveness influences offspring performance in guppies. *Proc. R. Soc. B* **271**, 2035–2042. (doi:10.1098/rspb.2004.2815)
- Grether, G. F. 2000 Carotenoid limitation and mate preference evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulata*). *Evolution* **54**, 1712–1724.
- Houde, A. E. 1997 *Sex, color and mate choice in guppies*. Princeton, NJ: Princeton University Press.
- Hughes, K. A., Rodd, F. H. & Reznick, D. M. 2004 Genetic and environmental effects on secondary sex traits in guppies (*Poecilia reticulata*). *J. Evol. Biol.* **18**, 35–45. (doi:10.1111/j.1420-9101.2004.00806.x)
- Johnstone, R. A. 1998 Game theory and communication. In *Game theory and animal behavior* (eds L. A. Dugatkin & H. K. Reeve), pp. 94–117. New York, NY: Oxford University Press.
- Lens, L., Van Dongen, S., Kark, S. & Matthysen, E. 2002 Fluctuating asymmetry as an indicator of fitness: can we bridge the gap between studies? *Biol. Rev.* **77**, 27–38. (doi:10.1017/S1464793101005796)
- Macias Garcia, C. & Ramirez, E. 2005 Evidence that sensory traps can evolve into honest signals. *Nature* **434**, 501–505. (doi:10.1038/nature03363)
- Magurran, A. E. 2005 *Evolutionary ecology: the Trinidadian guppy*. Oxford, UK: Oxford University Press.
- Marzona, E. & Giacoma, C. 2002 Display lateralisation in the courtship behaviour of the alpine newt (*Triturus alpestris*). *Laterality* **7**, 285–295. (doi:10.1080/13576500244000058)
- McGrew, W. C. & Marchant, L. F. 1999 Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates* **40**, 509–513. (doi:10.1007/BF02557586)
- Merry, J. W. & Morris, M. R. 2001 Preference for symmetry in swordtail fish. *Anim. Behav.* **61**, 477–479. (doi:10.1006/anbe.2000.1589)
- Møller, A. P. & Pomiankowski, A. 1993 Fluctuating asymmetry and sexual selection. *Genetica* **89**, 267–279. (doi:10.1007/BF02424520)
- Neville, A. C. 1976 *Animal asymmetry*. The Institute of Biology's Studies in Biology. London, UK: Edward Arnold.
- Nicholls, M. E., Clode, D., Wood, S. J. & Wood, A. G. 1999 Laterality of expression in portraiture: putting your best cheek forward. *Proc. R. Soc. B* **266**, 1517–1522. (doi:10.1098/rspb.1999.0809)
- Nicholls, M. E., Wolfgang, B. J., Clode, D. & Lindell, A. K. 2005 The effect of left and right poses on the expression of facial emotion. *Neuropsychologia* **40**, 1662–1665. (doi:10.1016/S0028-3932(02)00024-6)
- Palmer, A. R. 1996 Waltzing with asymmetry. *Bioscience* **46**, 518–532. (doi:10.2307/1312930)
- Palmer, A. R. 2004 Symmetry breaking and the evolution of development. *Science* **306**, 828–833. (doi:10.1126/science.1103707)
- Palmer, A. R. & Strobeck, C. 1986 Fluctuating asymmetry: measurement, analysis, patterns. *Annu. Rev. Ecol. Syst.* **17**, 391–421. (doi:10.1146/annurev.es.17.110186.002135)
- Palmer, A. R., Strobeck, C. & Chippindale, A. K. 1993 Bilateral variations and the evolutionary origin of macroscopic asymmetries. *Genetica* **89**, 201–218. (doi:10.1007/BF02424514)
- Patricelli, G. L., Uy, J. A. C., Walsh, G. & Borgia, G. 2002 Sexual selection: male displays adjusted to female's response. *Nature* **415**, 279–280. (doi:10.1038/415279a)
- Polak, M. & Stillabower, E. M. 2004 The relationship between genotype, developmental stability and mating performance: disentangling the epigenetic causes. *Proc. R. Soc. B* **271**, 1815–1821. (doi:10.1098/rspb.2004.2786)
- Reynolds, J. D. & Gross, M. R. 1992 Female mate choice enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. *Proc. R. Soc. B* **250**, 57–62. (doi:10.1098/rspb.1992.0130)
- Reynolds, J. D., Gross, M. R. & Coombs, M. J. 1993 Environmental conditions and male morphology determine alternative mating behaviour in Trinidadian guppies. *Anim. Behav.* **45**, 145–152. (doi:10.1006/anbe.1993.1013)
- Rogers, L. J. 2002 Lateralization in vertebrates: its early evolution, general pattern and development. In *Advances in the study of behavior*, vol. 31 (eds P. J. B. Slater, J. Rosenblatt, C. Snowdon & T. Roper), pp. 107–162. San Diego, CA: Academic Press.
- Roulin, A., Ducrest, A.-L., Balloux, F., Dijkstra, C. & Riols, C. 2003 A female melanin ornament signals offspring fluctuating asymmetry in the barn owl. *Proc. R. Soc. B* **270**, 167–171. (doi:10.1098/rspb.2002.2215)
- Rowell, J. T., Ellner, S. P. & Reeve, H. K. 2006 Why animals lie: how dishonesty and belief can coexist in a signaling system. *Am. Nat.* **168**, E180–E204. (doi:10.1086/508809)
- Sheridan, L. & Pomiankowski, A. 1997a Female choice for spot asymmetry in the Trinidadian guppy. *Anim. Behav.* **54**, 1523–1529. (doi:10.1006/anbe.1997.0562)
- Sheridan, L. & Pomiankowski, A. 1997b Fluctuating asymmetry, spot asymmetry and inbreeding depression in the sexual colouration of male guppy fish. *Heredity* **79**, 515–523. (doi:10.1038/sj.hdy.6882380)
- Stephan, K. E., Marshall, J. C., Friston, K. J., Rowe, J. B., Ritzl, A., Zilles, K. & Fink, G. R. 2003 Lateralized cognitive processes and lateralized task control in the human brain. *Science* **301**, 384–386. (doi:10.1126/science.1086025)
- Stuart-Fox, D. 2005 Deception and the origin of honest signals. *Trends Ecol. Evol.* **20**, 521–523. (doi:10.1016/j.tree.2005.08.004)
- Swaddle, J. P. & Johnson, C. W. 2007 European starlings are capable of discriminating subtle size asymmetries in paired stimuli. *J. Exp. Anal. Behav.* **87**, 39–49. (doi:10.1901/jeab.2007.103-05)
- Tomkins, J. L. & Simmons, L. W. 2003 Fluctuating asymmetry and sexual selection: paradigm shifts, publication bias, and observer expectation. In *Developmental instability: causes and consequences* (ed. M. Polak), pp. 231–261. New York, NY: Oxford University Press.

- Vallortigara, G. & Rogers, L. J. 2005 Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav. Brain Sci.* **28**, 575–633. (doi:10.1017/S0140525X05000105)
- van Doorn, G. S. & Weissing, F. J. 2006 Sexual conflict and the evolution of female preferences for indicators of male quality. *Am. Nat.* **168**, 742–757. (doi:10.1086/508634)
- van Oosterhout, C., Trigg, R. E., Crarvalho, G. R., Magurran, A. E., Hauser, L. & Shaw, P. W. 2003 Inbreeding depression and genetic load of sexually selected traits: how the guppy lost its spots. *J. Evol. Biol.* **16**, 273–281. (doi:10.1046/j.1420-9101.2003.00511.x)
- Watson, P. J. & Thornhill, R. 1994 Fluctuating asymmetry and sexual selection. *Trends Ecol. Evol.* **9**, 21–25. (doi:10.1016/0169-5347(94)90227-5)