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LETTER

Proportional processing of a visual mate choice signal in the green swordtail, *Xiphophorus hellerii*

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Abstract

During mate choice, receivers often assess the magnitude (duration, size, etc.) of signals that vary along a continuum and reflect variation in signaller quality. It is generally assumed that receivers assess this variation linearly, meaning each difference in signalling trait between signallers results in a commensurate change in receiver response. However, increasing evidence shows receivers can respond to signals non-linearly, for example through Weber's Law of proportional processing, where discrimination between stimuli is based on proportional, rather than absolute, differences in magnitude. We quantified mate preferences of female green swordtail fish, *Xiphophorus hellerii*, for pairs of males differing in body size. Preferences for larger males were better predicted by the proportional difference between males (proportional processing) than the absolute difference (linear processing). This demonstration of proportional processing of a visual signal implies that receiver perception may be an important mechanism selecting against the evolution of ever-larger signalling traits.

KEYWORDS

assessment signals, perception, Weber's Law

INTRODUCTION

During mate choice, the choosing sex must gather and process information about potential mates, often by evaluating visual traits, and much discussion has focused on why females prefer certain trait variants over others and how those preferences are exhibited (Moore & Moore, 1988; Real, 1990; Wittenberger, 1983). However, one key understudied aspect of preference is the perceptual processes that occur during mate choice, which can lend insight into what information choosers gather about potential mates, and how differences among potential mates are actually perceived, thus helping to explain why certain trait variants are preferred. For example, choosers often evaluate potential mates using traits that vary continuously across individuals, and it is generally assumed that receivers perceive this variation continuously, meaning each difference in signalling trait between signallers is detectable by the receiver and results in a commensurate change in receiver response (Searcy & Nowicki, 2005). However, increasing evidence suggests that receivers can perceive and respond to signals in a discontinuous manner (Baugh et al., 2008; Caves et al., 2018; Wyttenbach et al., 1996; Zuk et al., 1990), which has important implications for our understanding of signal evolution, in particular how the chooser's perceptual system exerts selective pressure on mate choice signals.

One mechanism by which a receiver's perceptual system discontinuously perceives continuous variation is proportional processing, which describes how perceptual systems adhere to Weber's Law, and which is thought to have arisen to help sensory systems reduce and efficiently process the large variation in magnitude that can occur within a sensory parameter. Weber's Law states that the ability of a perceptual system to

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discriminate between stimuli of magnitudes M_1 and M_2 is based on their proportional magnitude difference (i.e. (M_1-M_2/M_1, which is equivalent to $\Delta M/M$) rather than their absolute difference (ΔM). Under proportional processing, sensory systems discriminate between stimuli of different magnitudes based on their proportional (or relative), rather than absolute, difference (reviewed in Akre & Johnsen, 2014). Thus, an individual could more readily discriminate between two low-magnitude stimuli that differ by a given absolute amount than between two high-magnitude stimuli that differ by the same absolute amount, because the proportional difference between the two low-magnitude stimuli is greater (Figure 1a). In an assessment signalling context like mate choice, proportional processing predicts that receivers can more readily discriminate between low-magnitude (presumably low quality) signallers than between high-magnitude (presumably higher quality) signallers (Figure 1b). Thus, at a certain magnitude, the increase in benefits a sender can derive from investing in a higher magnitude signal will diminish – a critical assumption of honest signalling theory (Grafen, 1990; Johnstone, 1997; Searcy & Nowicki, 2005) – due to perceptual constraints in the receiver. Diverse taxa proportionally perceive variation in a range of stimuli, including amplitude and frequency in mammals, frogs and birds (Dooley & Moore, 1988; Forrest, 1994; Labarbera et al., 2020; Wyttenbach & Farris, 2004; Yost, 2006); chemical concentrations in bats, bees, ants and bacteria (Mesibov et al., 1973; Buckingham et al., 2007; Perna et al., 2012; Kojadinovic et al., 2013; Nachev et al. 2013); and electric field intensity in weakly electric fish (von der Emde, 2004). In the visual modality, humans, nonhuman primates, fish and birds proportionally perceive numerosity (Ditz & Nieder, 2016; Gómez-Laplaza & Gerlai, 2011; Merten & Nieder, 2008), and coyotes (Baker et al., 2011), humans (Lourenco et al., 2012), ants (Cammaerts & Cammaerts, 2020) and seals (Wartzok & Ray, 1976) proportionally perceive stimulus area. However, no studies have yet explored whether proportional processing holds during perception of visual assessment signals.

Fish in the family *Poeciliidae* are a model system for mate choice and visual signalling. In many Poeciliids, females choose mates by assessing the size of traits, like the body (e.g (MacLaren et al., 2004; MacLaren & Rowland, 2006; Ptacek & Travis, 1997; Rosenthal & Evans, 1998) or signalling structures (e.g. (Basolo, 1990, 1995; MacLaren et al., 2004; MacLaren & Rowland, 2006)), preferences which may have arises as a result of sensory biases, given that larger stimuli provide greater stimulation to the viewer's retina (Ryan & Keddy-Hector, 1992). Green swordtail *Xiphophorus hellerii* females prefer larger males (i.e. those whose combined body and tail fin project a larger area (MacLaren, 2017; MacLaren & Daniska, 2008; Rosenthal & Evans, 1998); body size is heritable in green swordtails (Campton, 1992) and is likely linked to mating success (and thus fitness) through female preference for larger males that are more competitively successful, and that may also restrict access of smaller males to gravid females (Benson & Basolo, 2006). Furthermore, responses to animated stimuli can be used as a proxy for female preferences

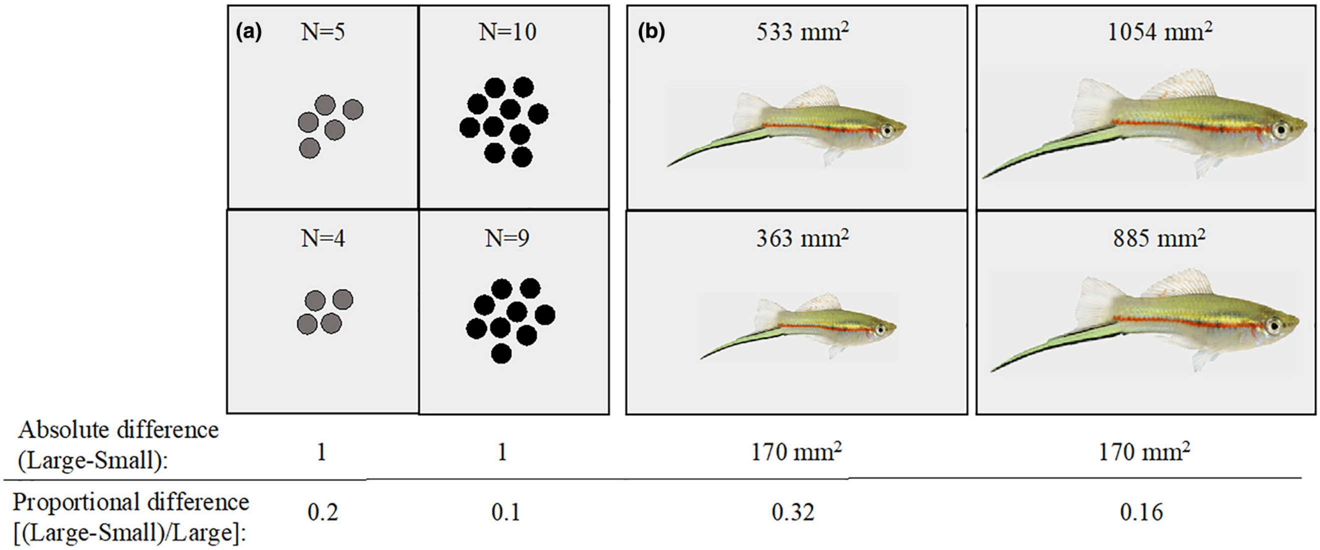

FIGURE 1 Proportional processing predicts it is easier to discriminate between two low-magnitude stimuli than between two high-magnitude stimuli, even if both pairs differ by the same absolute amount. (a) The absolute difference in number of objects between the top and bottom panels in each column is the same. However, the proportional difference on the left (grey dots) is greater than on the right (black dots), and thus easier to detect. (b) It is easier to discriminate between two smaller male swordtails (left-hand column) than two larger (right-hand column), even when the two males in each pair (top and bottom) differ by the same absolute amount, because the proportional difference is greater in the low-magnitude pair than the high-magnitude pair. The area measurements in (b) are based upon the size these stimuli are when displayed in our experimental setup.

while providing control over signalling traits and signaller behaviour: association time in two-choice tests predicts mating behaviour (Walling et al., 2010), and female preferences for video stimuli versus real males are qualitatively similar (Rosenthal & Evans, 1998; Trainor & Basolo, 2000).

We performed a series of two-choice assays in which female green swordtails were given a choice between two animations of courting males that differed only in lateral projection area (in mm^2, hereafter 'size'). Female preferences were tested twice each for 11 pairs of males, in which proportional size difference between males within a pair ranged from 0.16 to 0.66, and absolute size difference ranged from 169 mm^2 to 691 mm^2, to roughly parallel the range of variation in male size in our population (Table S1). We tested whether preference was based on either the proportional or absolute difference in size between two males. We also examined whether preference was based on the total size presented by a pair of males, represented by the mean size, the rationale being that greater overall stimulation of a female's visual system might weaken preferences for the larger male.

RESULTS AND DISCUSSION

We built four linear mixed-effects models where the response variable in each was preference for the larger male in a pair (total time with the larger male—total time with the smaller male). Each of three models had a single fixed effect: the proportional size difference between males (proportional model), the absolute size difference between males (absolute model) or the mean size of the two males (mean model). A fourth model was a 'null' model with no fixed effects. In all models, fish ID was included as a random effect. To determine which aspects of size best described female responses, we compared model fits using Akaike's information criterion (AIC; Akaike, 1974; Burnham & Anderson, 2002). We also built linear mixed-effects models in which both absolute difference and proportional difference were fixed effects (see Materials and Methods). However, absolute difference and proportional difference are significantly correlated (Pearson correlation coefficient, r_9 =0.87, $p = 0.001$), and so including them both in the same model can be problematic (Zuur et al., 2010). Therefore, in the main text, we present only the model comparison analysis which avoids problems with collinearity. Results from other modelling analyses are in Table S2, although conclusions derived from the two modelling approaches were similar.

Females (n = 23) displayed stronger preferences for the larger male in a pair as the proportional difference between the two males increased (Figure 2). Consistent with proportional processing of body size, the 'proportional' model was a much better fit to the data than the mean (ΔAIC = 10.01), absolute (ΔAIC = 11.63) or null (ΔAIC = 27.16) models (Table S3). This was driven by females spending both more time with the larger male as well as less time with the smaller male in a pair as proportional size difference increased (Figure S1 and Table S3).

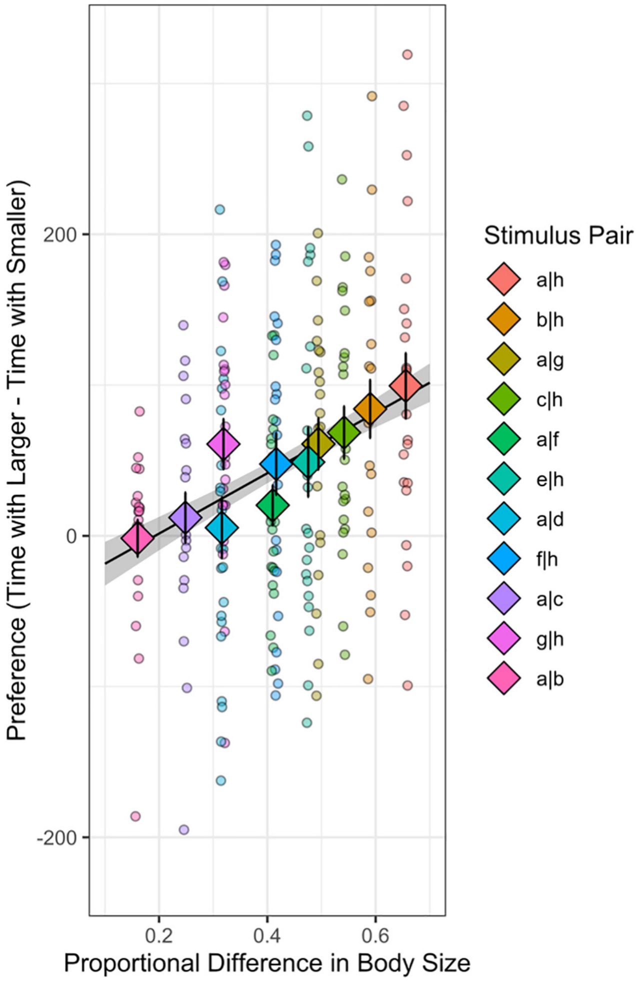

FIGURE 2 Females show a stronger preference for larger males when there is a greater proportional difference between the larger and smaller males in a pair. Diamonds represent means, bars show standard error, points show raw data and trendline shows fitted model estimates for the proportional model with 95% confidence interval (shaded area). Stimulus pair names are 'male 1 | male 2', with 'a' being the largest male and 'h' being the smallest; thus, absolute difference between males in a pair decreases from legend top to bottom. See Table S4 for the size of each male in mm^2. Sample size for each comparison is $n = 23$, except for a|d ($n = 21$), f|h ($n = 22$), a|c ($n = 21$), g|h ($n = 22$) and a|b ($n = 21$).

For five stimulus pairs, the two stimuli differed by the same absolute area but had different proportional differences in area. Thus, the absolute difference was held constant, but the proportional difference varied. Females spent more time with the larger male in the pair with the larger proportional difference compared with the corresponding pair with the smaller proportional difference (mean±standard deviation = 47.9 ±12.8 s,

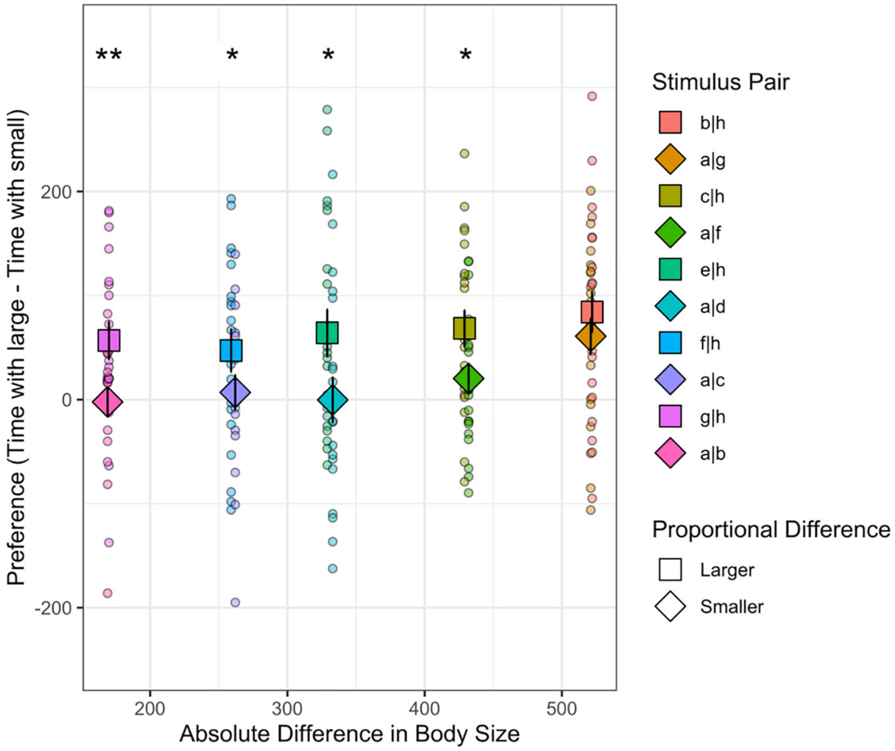

FIGURE 3 Female preference for the larger male was stronger when proportional difference was larger (squares) than when it was smaller (diamonds), even when absolute difference was held constant. Symbols represent means, bars show standard error and points show raw data. Significance levels ($0.01 < p < 0.05$ = *; $p < 0.01$ = **) are from paired t-tests (in one case where the paired differences were distributed non-normally, we used a paired two-samples Wilcoxon test). Stimulus pair names are 'male 1 | male 2', with 'a' being the largest male and 'h' being the smallest. See Table S4 for the size of each male in mm^2. Because the statistical tests are paired tests, we had to eliminate any fish that did not participate in trials for each comparison, resulting in the following sample sizes: b|h and a|g ($n = 23$), c|h and a|f ($n = 23$), e|h and a|d ($n = 21$), f|h and a|c ($n = 20$), g|h and a|b ($n = 20$).

range: 35.5–62.5 s; Figure 3). In four cases, preference for the larger male was significantly stronger in the pair with a higher proportional difference than the corresponding pair with a lower proportional difference (*t*-tests or Wilcoxon tests; g|h and a|b: V = 178, $p = 0.005$; f|h and a|c: $t_{19} = -2.12$, $p < 0.05$; e|h and a|d: $t_{20} = 2.35$, $p = 0.03$; c|h and a|f: $t_{22} = 2.54$, $p = 0.02$).

Interestingly, when proportional differences were small (Figure 3, pairs a|b, a|c and a|d), absolute differences could be quite large (as large as 330 mm^2) and females still displayed no significant preference for the larger male in a pair, despite displaying that preference when proportional differences were large (Figure 3, pairs g|h, f|h and e|h). Lastly, there was no significant difference in preference for the larger male between the two stimulus pairs with the largest absolute difference (b|h and a|g: $t_{22} = -1.46$, $p = 0.16$), suggesting that perhaps when absolute differences are very large, perceptual processing imposes little constraint on size discrimination.

Our results are the first demonstration of proportional processing of a visual mate choice signal. They are consistent with studies demonstrating proportional processing of acoustic mate choice signals in both túngara frogs *Physalaemus pustulosus* (Akre et al., 2011) and Cope's grey treefrog *Hyla chrysoscelis* (Labarbera et al., 2020). However, our results extend these findings about Weber's Law, a fundamental feature of perceptual psychophysics, to the visual modality, helping to establish the generality of proportional processing as a selective force on signals across modalities. Proportional processing, like we show here in green swordtails, also has implications for understanding how female perception could shape sexual signal evolution. Across many taxa, females prefer traits of greater magnitude (Ryan & Keddy-Hector, 1992). Selection for greater signal magnitude, however, is predicted to stop when the costs of further exaggeration outweigh the benefits. Proportional processing provides an additional mechanism by which the benefits of ever-exaggerated signals might diminish with increasing signal magnitude. In essence, proportional processing imposes a penalty upon signal exaggeration at larger magnitudes because females are less able to discriminate between potential signallers.

One way in which proportional processing could provide an even stronger brake on exaggerated signal evolution is through what is known as the 'opposite miss' (Labarbera et al., 2020; Nachev, Stich, & Winter, 2013) to Weber's Law. In the 'opposite miss', discrimination of high-magnitude stimuli is worse than predicted. Our finding that female preference for larger males nearly disappears when both males are large (and proportional size differences are small) motivated us to test for the 'opposite miss' using a series of statistical models (Materials and Methods; Figure S2). These models confirmed that, in our data, preference for the larger male conformed more closely to the 'opposite miss' than to 'pure' proportional processing, indicating that, as stimuli get larger overall, discrimination is even poorer than predicted by proportional processing.

Therefore, our data suggest that receiver perception can impose an even stronger penalty on signal exaggeration than initially expected, perhaps contributing to limiting runaway selection (Fisher, 1930), and in the context of the handicap principle, contributing to mate choice signals remaining honest over evolutionary time. During mate choice, females should benefit from choosing higher-quality males, so males that signal they are high quality will secure more matings. What keeps low-quality males from dishonestly signalling that they are high quality? The handicap principle (Zahavi, 1975, 1977) provides a partial solution, stating that mating signals confer a 'handicap' on the signaller, such that only high-quality males can endure the costs of displaying high-magnitude signals. In population-genetic (Grafen, 1990) and graphical (Johnstone, 1997) models of the handicap principle, the marginal benefits of having larger signal magnitude are assumed to increase to an asymptote; proportional processing provides a possible mechanism underlying this asymptote.

Proportional processing could also favour the evolution of novel or multicomponent signalling traits (Akre & Johnsen, 2014). If increasingly exaggerating signalling traits has diminishing returns, the benefits of investing in a novel or additional signal component may outweigh the costs, and provide greater increases to mating success, than further elaborating the original signal. Body size in green swordtails is just one of several traits assessed during mate choice. Others include sword length (Basolo, 1990), colour patterns (Basolo & Trainor, 2002) and courtship behaviours (Rosenthal et al., 1996). These may have evolved, at least in part, as novel signals related to the constraints imposed by proportional processing of body size, but this is as yet unstudied.

Lastly, our results contribute to a growing body of literature suggesting that mate choice can be thought of as an information-processing problem, and often one that the choosing sex must solve quickly (Bateson & Healy, 2005). Such quick decision-making can be supported by the use of heuristics and perceptual mechanisms that involve direct comparisons between individuals, rather than absolute assessments of mate quality (reviewed in (Bateson & Healy, 2005)). Employing decision-making heuristics may not necessarily be costly. In swordtails, for example, when choosing between two larger males, the difference in real benefits of choosing one male over the other may be minimal (as both males may well be perfectly acceptable mates). By contrast, when faced with two smaller, low-quality males, the need to determine which of the available mates is actually better may be more important. Under proportional processing, the difference between the two smaller males should be apparent, so a perceptual constraint that results in females frequently choosing the smaller male may cost little. In addition, female swordtails may benefit from making mating decisions quickly, for example by minimising costly aggression or harassment (e.g. (Magurran & Seghers, 1994) or the chances of forced copulation (Morris et al., 2008; Ryan & Causey, 1989; Zimmerer & Kallman, 1989)). It is also possible that females had the ability to discriminate between larger males but were less motivated to do so, as our assays measured discrimination performance rather than actual discrimination ability. Overall, our results suggest that, although the classic view is that females choose mates with the most exaggerated traits because those males signal more benefits for their offspring (Andersson, 1994), cognitive and perceptual processes like proportional processing can lead to selection not always favouring larger, more exaggerated traits. We suggest that studies investigating preferences for visual signals that vary across individuals in magnitude (e.g. length, area), which exist in a wide range of taxa, need to consider proportional processing of stimuli, rather than linear processing as previously assumed.

MATERIALS AND METHODS

Animal care and ethics

All animals were treated in accordance with the ethical guidelines of the University of Exeter (ethics approval eCORN002243). Fish handling and experiments were carried out by EM Caves (Home Office Personal Licence I56658687) under Home Office Project Licence PF6E68517. All fish used in this experiment were sexually mature descendants of a wild-derived population originally collected in Belize in 2002. Fish were housed in single-sex groups of 3–7 individuals in 30-litre tanks and fed with a mixture of bloodworm, mysis shrimp, and artemia each morning and flake food (ZM Flake, Fish Food and Equipment, Hampshire UK) each evening. Water temperature was kept between 22 and 24°C and tanks were lit from above with AquaBeam LED lights (Tropical Marine Centre Ltd.) on a 12:12 light:dark cycle (although during portions of one COVID-19 lockdown, the light cycle was temporarily shifted to 15:9 light:dark cycle). All fish were tagged with an individually identifiable combination of elastomer tags (Northwest Marine Technology Inc.).

Behavioural experiments

We used a two-choice behavioural paradigm to assess the preferences of females (measured as difference in association time with the larger versus smaller male in a pair) when offered a choice between animations of two males that differed in size. Two-dimensional animations have been used successfully in a wide variety of previous studies to examine mate preferences in fish (Baldauf et al., 2009; Fischer et al., 2014; Levy et al., 2014), including in swordtails in the genus *Xiphophorus* (Morris et al., 2003).

Stimulus design

To prepare artificial stimuli, a digital image of a male swordtail in our experimental population (body length 44 mm, sword length 32 mm) was taken in RAW format using a Nikon D60 DSLR camera fitted with a Nikkor 18–55 mm lens. This particular male was chosen because both his body size and his sword length were relatively close to the mean in our population (mean ± standard deviation body size: 42.5 ±5.31 mm; sword length: 28.5 ±9.97 mm). The fish was briefly removed from his home tank and photographed with his sword fully extended alongside a size standard, and lit from overhead by a full spectrum arc lamp (Iwasaki EyeColor 6500 K, Iwasaki Electroc Co. Ltd.) fitted with a 70 W electronic ballast (Venture Lighting Europe Ltd.). The photo was then imported into ImageJ (Schneider et al., 2012) where we used the magic wand tool to separate the fish from the background and insert it into a blank, bright grey (RGB: 238, 238, 238) background (following (Baldauf et al., 2009)).

The size of the original stimulus was measured using the magic wand tool to measure the lateral projection area (mm^2) of the fish, including both body and sword. Image size was calibrated such that the size of the stimulus equalled the size of the fish image when displayed on a Samsung Galaxy Table 10.1 Tablets (Samsung Corp; 22.3 × 14 cm screen, 1200 × 1920 pixel resolution, 60 Hz refresh rate), the display used during trials.

Male stimuli of different sizes were then created by scaling the entire original image either up or down, following MacLaren and Daniska (2008), who found that female *X. hellerii* preferences for males of larger area held when the fin: body size ratio matched that of a typical male in a population, rather than selectively increasing the size of either body or sword. The smallest stimulus had a body size comparable to the size of the smaller males used in other two-choice studies of mate preference in *X. hellerii* (e.g. (Basolo, 1990; MacLaren, 2017; Rosenthal & Evans, 1998; Walling et al., 2008, 2010)). The photo of the same male was used for all stimuli, to hold all features that might additionally be used to evaluate male quality constant, aside from body size. This resulted in a total of eight stimuli (Table S4) that, when presented in various combinations, differed from one another by specific absolute and proportional amounts. Absolute difference in area was calculated as:

$$A_1 - As$$

And proportional difference was calculated as:

$$\left(A_l - As\right) / A_l$$

where A_l is the area of the larger stimulus and A_s is the area of the smaller stimulus.

Pairs of stimuli (referred to throughout in the format of 'stimulus 1 | stimulus 2') from Table S4 were selected to cover a broad range of both proportional (range: 0.16–0.66) and absolute (169–691 mm^2) differences (Table S1). In addition, stimulus pairs were designed such that the difference in area between them is theoretically resolvable by a female swordtail in our experimental setup, given visual acuity of female green swordtails (3 cycles per degree; Caves et al., 2021) and the size of our experimental tanks. Lastly, stimuli were put into specific pairs such that we created five sets of stimulus pairs in which the absolute difference was the same, but the proportional difference was not. For example, we created two sets of stimulus pairs in which the absolute difference was roughly 170 mm^2, but in one of the pairs proportional difference was 0.32 (g|h) and in the other it was 0.16 (a|b) (Figure 1b). This allowed us to directly test the effects of proportional difference on preference while holding absolute difference constant.

To create animations, stimuli were imported into a blank Microsoft PowerPoint (version 16.57) slide with a matching grey background. We used PowerPoint 'animation paths' to animate the stimulus moving from one side of the screen to the other over the course of 15 s, after which it moved off the screen and then appeared to swim back in the opposite direction for another 15 s (following (Baldauf et al., 2009; Fischer et al., 2014; Thünken et al., 2014)). In addition, backward-swim manoeuvres, mimicking a courting behaviour performed by male green swordtails (Rosenthal et al., 1996), were added using animation paths, at a rate of 3 backward-swim manoeuvres every 60 s (per (Rosenthal et al., 1996), who found that female green swordtails responded most strongly to dynamic video stimuli, specifically those performing courting manoeuvres). Preliminary trials with all 23 females showed that females in our population spent a significantly greater proportion of their time associating with one of our courting animated males (mean ± standard deviation: 0.65 ± 0.17) than a plain grey slide (0.35 ± 0.17; Welch's two-sample *t*-test; $t_{44} = 5.87$, $p < 0.0001$). One slide show was created for each stimulus size, such that all aspects of the animation (stimulus and background colour, location of stimuli on the screen, and path and speed of stimulus) were identical, with only the size of the male varying.

Two-choice trials

Females ($n = 23$) were housed in groups of 4–7 females, and were physically and visually isolated from males for at least 1 month prior to testing (following (Rosenthal & Evans, 1998)). Immediately prior to a trial, we caught a pair of females using a dip-net and moved them to a tank in which groups of males (*n* = 7 total) were housed in tanks on either side, for 20 min. This placed the females in visual, but not physical, contact with males, priming females for a mate choice task. Pairs of females were used to minimize time fish spent in physical isolation, per animal ethics guidelines. The seven males to which females were exposed prior to trials remained the same throughout all trials for all females. We performed behavioural observations of females during this priming period in a subset of trials (*n* = 61), specifically monitoring for a set of behaviours that indicate females are sexually receptive, including backwards swimming towards males; parallel side to side or up and down swimming alongside males at the acrylic divider; a 'still-to' behaviour in which females remained motionless while oriented towards displaying males; and rapid approaches towards males (e.g. (Basolo, 1990; Rosenthal et al., 1996)). Out of 61 trials in which we monitored sexual receptivity, females exhibited three or more of these behaviours in 28 trials (46%), and at least two behaviours in all but three trials (95%), providing strong evidence that females were sexually receptive to males prior to two-choice trials.

Each female was then moved to a two-choice test tank (dimensions 45.7 × 25.4 × 25.4 cm) that had been filled to a depth of 15 cm using water from the home tank system so that water parameters matched. Only one female was placed in each two-choice test tank; thus, although females were housed in pairs during the pre-trial acclimation period, they were tested singly to ensure there was no effect of mate choice copying on the preferences they displayed. Tanks were filmed from above using a Sunkwang C160 video camera with 6–60 mm manual focus lens suspended above the tank and connected to a computer running the Viewer tracking software (BiObserve). The Viewer software virtually divided the tank into three equally sized zones (centre, left and right) and tracked all movements made by the fish for the duration of a trial. A clump of java moss was provided in the centre compartment as shelter. Two-choice tanks were like from underneath (following, e.g., (Houslay et al., 2018; Prentice et al., 2020)) with a lightpad (UltraSlim LED LightPad, MiniSun Limited.), to improve the accuracy of the tracking software. A cardboard screen was placed around the tank prior to the trial to prevent external visual disturbance.

Females were placed inside of a clear acrylic cylinder (15 cm diameter) in the centre zone of the tank, and allowed 15 min to acclimate, during which time tablets were placed against each end of the tank, displaying only a plain grey background. During the acclimation, a small amount of water from a tank housing four males was added to the two-choice arena, to provide the female with olfactory cues from real males that spanned a range of body sizes, and further prime her for a mate choice task. Following the 15-min acclimation, trials began with each tablet displaying 1 min of plain grey followed by 1 min of a male stimulus, during which time the female was still constrained to the cylinder in the centre compartment. This helped to ensure that females viewed both male stimuli before making any choices about which end of the tank to approach. The cylinder was then removed, allowing the female free access to the entire tank. The male stimuli continued to play at each end of the tank for 3 min, during which time all movements by the female were tracked and recorded by the Viewer software. Following trials, we returned the female to her home tank and used Viewer to extract and record the amount of time (in seconds) a female spent in each zone, that is, spent with each male stimulus. After 48 h, the same procedure was followed with the same female and the same pair of male stimuli, but with each stimulus presented on the opposite side of the tank to the first trial to account for possible side biases. All females were shown the stimulus pairs in the same order, and presentation order had no effect on female preference for the larger male in a pair (Figure S3).

We feel confident that females were able to assess both males in each of our trials, for several reasons. First, females were given 1 min while constrained at the centre of the tank to view both males before the cylinder was removed and they were allowed to move about the tank, and from the centre of the tank the size differences between the two males are theoretically resolvable by a female green swordtail visual system (Caves et al., 2021). In addition, in 85% of trials, females made at least one visit to each end zone, that is, to each male. In the 15% of trials where females made a visit to only one male, they took an average of 76 s to visit any male, and informal behavioural observations during that time suggest that females were swimming around the centre zone before making a choice about which end zone to enter.

In total, 23 females were presented with 11 stimulus pairs, with two trials per stimulus pair (over two 3-min periods) for a total of 506 trials. If a female did not leave the centre zone during a trial, that trial was rerun at a later date, and if the female did not leave the centre zone during the second run of a given trial, that trial was excluded from further analysis. Following re-trials, we had data from only one, rather than two, 3-min trial periods in 30 instances, and only eight instances where a fish participated in no trials for a given comparison.

Statistical analyses

The effects of absolute and proportional difference on time spent with a given male

All analyses were run in R version 4.0.3 (R Core Development Team, 2022). For analyses, we combined the association time data from the two trials to result in a total number of seconds that a female spent associating with a given male across the two trials in which a given male was presented at opposing ends of the tank. The preference for the larger male was taken to be the total time with the larger male minus the total time with the smaller male.

We fit four separate linear mixed effects models using the *lmer* function of the package *lme4* (Bates et al., 2015) in which the response variable was preference for the larger male, but in which the fixed effect varied. Fixed effects were either the absolute (the 'absolute' model) or proportional difference (the 'proportional' model) between two males, or the mean size of the two males (the 'mean' model). We also fit a null model, in which neither absolute nor proportional difference was included as a fixed effect (the 'null' model). Fish ID was included as random effect in all models. We then ranked models based on the AIC (Akaike, 1974; Burnham & Anderson, 2002) and assigned ΔAIC values by calculating the difference between AIC value of a given model and the AIC value of the best-fit model (i.e. that with the lowest AIC value in that set). Following Burnham et al. (2011), ΔAIC values were used to calculate relative likelihoods for each model *i* within a set using the formula

$$l_i = \exp\left[-(1/2)\,\Delta_i\right].$$

We then calculated the probability that each model, w_i, within a set of models, is the best by dividing the likelihood of a given model l_i by the sum of the likelihoods of all models within that set (Burnham et al., 2011). To explore further whether differences in preference were driven by changes in association with the larger male, the smaller male, or both, we fit additional models with the same fixed and random effects, but in which the response variable was either (1) the total amount of time with the high-magnitude stimulus or (2) the total amount of time with the low-magnitude stimulus.

As a second method to statistically analyse the effect of proportional and absolute difference on female preference, we fit models (the 'complete' models) in which the response variable was preference, and both absolute difference between two stimuli and proportional difference between two stimuli (standardised using the *scale* function in R) were included as fixed effects. Fish ID was included as a random effect. For each analysis, we assessed the significance of each fixed effect by comparing the likelihood ratio of a full model, which included both fixed effects and their interaction, to that of a model without the interaction term using the 'drop1' function in *lme4* (Bates et al., 2015). In cases where the interaction term was not significant, we removed non-significant interactions to test the main effects (Engqvist, 2005), but to avoid problems associated with stepwise model reduction we did not remove non-significant main effects (Forstmeier & Schielzeth, 2011; Mundry & Nunn, 2009; Whittingham et al., 2006). To confirm that the assumption of normality in the residuals was met, we examined model diagnostic plots. One potential issue, however, is that absolute difference and proportional difference are themselves highly correlated (Pearson correlation coefficient, $r_9 = 0.87$, $p = 0.001$), and thus perhaps should not be included in the same model (Zuur et al., 2010). Given these issues with collinearity between absolute and proportional difference, we present the results of the 'complete' models only in the supplement (Table S2), and the results of the 'absolute,' 'proportional,' 'mean' and 'null' model comparison analysis in the main text. However, it should be noted that in all cases, the results of the 'complete' models were in line with those of the model comparison analysis.

To further explore strength of female preference in sets of two stimulus pairs where absolute size was held constant, but proportional difference varied, we used paired t-tests (or paired two-sample Wilcoxon tests if paired differences were distributed non-normally) to statistically examine whether the preference for the larger male was stronger in one pair over the other. Note that to perform paired tests, we had to remove any individual that had not participated in (i.e. made visits to each male in a pair; see Two-Choice Trials above) any trials with one of the stimulus pairs, which occurred a total of seven times in our dataset.

The opposite miss and near miss to Weber's law

Some sensory systems adhere to the 'near-miss' (Augustin, 2009; Guilford, 1932; Nachev, Stich, & Winter, 2013; Osman et al., 1980) or 'opposite miss' (Forrest, 1994; Labarbera et al., 2020; Nachev, Stich, & Winter, 2013) to Weber's Law, in which discrimination of high-magnitude stimuli is better or worse, respectively, than predicted by Weber's Law. To test statistically for the near-miss to Weber's Law (in which receiver discrimination of high-magnitude stimuli is better than predicted by Weber's Law) and the opposite-miss to Weber's Law (in which receiver discrimination of high-magnitude stimuli is poorer than predicted by Weber's Law), we followed a method outlined in Dixit et al. (2022), which makes use of the fact that one formulation of Weber's Law can be written as:

$$\mathrm{R} \sim \frac{|\,a-b\,|}{b^k}$$

where *R* is the predicted response, *a* is the magnitude of the larger stimulus, *b* is the magnitude of the smaller stimulus and *k* is a constant often called the Weber fraction (Akre & Johnsen, 2014; Fechner, 1966; Labarbera et al., 2020). When $k = 0$, the above expression is equivalent to $|a\text{-}b|$, which is the absolute difference between two stimuli; when $k = 1$, the above expression equals $\frac{|a-b|}{b}$, which is the proportional difference between two stimuli. Both the near-miss and opposite-miss to Weber's Law can also be described by this expression: values of k between 0 and 1 describe the near miss (Augustin, 2009; Nachev, Stich, & Winter, 2013), while values of k greater than 1 describe the opposite miss.

Therefore, we created a series of models that followed the above expression, with the response variable (R) being preference for the larger male, a being the magnitude of the larger male in a pair, and b being the magnitude of the smaller male in a pair. Fish ID was included as a random effect, resulting in a model of the form: $[\text{Response} \sim \text{abs}(\text{high} - \text{low})/\text{high}^{k} + (1|\text{FishID})]$. We then calculated the AIC score for a set of models in which the value of k ranged from −1 to 4 at intervals of 0.5, and determined the value of k in the best-fit model. The magnitude of k in the best-fit model allowed us to assess whether our data most closely adhere to the near-miss ($0 < k < 1$), opposite-miss ($k > 1$) or Weber's Law/proportional processing ($k = 1$), or if the absolute difference was the best predictor ($k = 0$).

AUTHOR CONTRIBUTIONS

Conceptualisation: EMC, LAK; Methodology: EMC, LAK; Investigation: EMC; Visualisation: EMC; Writing – original draft: EMC; Writing – review and editing: EMC, LAK; Supervision: LAK; Project Administration: EMC, LAK; Funding Acquisition: EMC, LAK.

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Authors declare that they have no competing interests.

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OPEN RESEARCH BADGES

This article has earned the Open Data badge. Data are available at: https://doi.org/10.6084/m9.figshare.21701645

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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