



Cues to the sex ratio of the local population influence women's preferences for facial symmetry

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In nonhuman species, increasing the proportion of potential mates in the local population often increases preferences for high-quality mates, while increasing the proportion of potential competitors for mates intensifies within-sex competition. In two experiments, we tested for analogous effects in humans by manipulating pictorial cues to the sex ratio of the local population and assessing women's preferences for facial symmetry, a putative cue of mate quality in humans. In both experiments, viewing slideshows with varied sex ratios tended to increase preferences for symmetry in the sex that was depicted as being in the majority and tended to decrease preferences for symmetry in the sex that was depicted as being in the minority. In other words, increasing the apparent proportion of a given sex in the local population increased the salience of facial cues of quality in that sex, which may support adaptive appraisals of both potential mates' and competitors' quality. This effect of sex ratio was independent of (i.e. did not interact with) an effect of cues to the degree of variation in the attractiveness of individuals in the local population, whereby the degree of variation in men's, but not women's, attractiveness modulated symmetry preferences. These findings demonstrate that symmetry preferences in humans are influenced by cues to the sex ratio of the local population in ways that complement both the facultative responses that have been observed in many other species and theories of both intersexual and intrasexual selection.

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Sexual selection can result in traits that advertise aspects of mate quality in one sex and preferences for such traits in the other sex (Andersson 1994). Variation in the characteristics and demands of the local environment can cause systematic variation in preferences for cues of mate quality, however (Gangestad & Buss 1993; Jennions & Petrie 1997; Penton-Voak et al. 2004; Little et al. 2007a; DeBruine et al. 2010, 2011). One ecological constraint that may be particularly important for variation in mate preferences is the ratio of potential mates to potential competitors for mates within the local population (i.e. the operational sex ratio, Emlen & Oring 1977; Guttentag & Secord 1983). The potential costs of competing for high-quality mates are reduced considerably when potential mates are plentiful and competitors for mates are relatively scarce (Pedersen 1991; see also Noë & Hammerstein 1994; Kvarnemo & Ahnesjö 1996). In turn, this change in costs may allow individuals to increase their preferences for cues that are

associated with high quality in potential mates and require them to engage in less within-sex competition in order to secure mates (Pedersen 1991; see also Noë & Hammerstein 1994; Kvarnemo & Ahnesjö 1996).

Changing preferences as a result of experimentally manipulating the operational sex ratio of the local population have been reported for several different species. For example, female guppies, *Poecilia reticulata*, show stronger preferences for attractive male colour characteristics when the sex ratio is biased towards males than when it is biased towards females (Jirotkul 1999). In field crickets, *Gryllus pennsylvanicus*, female mate preferences also show greater selectivity when the sex ratio is biased towards males (Souroukis & Murray 1994). Additionally, greater selectivity in male mate preferences when the sex ratio is biased towards females has been observed in snapping shrimp, *Alpheus angulatus* (Mathews 2002), milkweed beetles, *Tetraopes tetraophthalmus* (Lawrence 1986) and pipefish, *Syngnathus typhle* (Berglund 1994). Other experiments have shown that the intensity of within-sex competition is also affected by altering the sex ratio. For example, biasing the sex ratio towards own-sex individuals causes more intense within-sex competition in Japanese medaka, *Oryzias latipes* (Clark &

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Grant 2010), guppies (Jirotkul 1999), red-spotted newts, *Notophthalmus viridescens* (Verrell 1983) and amphipods (Dick & Elwood 1996). Importantly, these effects of experimentally altered sex ratio complement findings from studies that investigated relationships between naturally occurring variation in sex ratios and indexes of either mate preferences or within-sex competition. This work includes studies of various fish species (e.g. Balshine-Earn 1996; Forsgren et al. 2004), ungulates (e.g. Clutton-Brock et al. 1997; Coltman et al. 1999), rodents (Michener & Locklear 1990), birds (e.g. Colwell & Oring 1988) and primates (Wang et al. 2009; see also Hohmann & Fruth 2003).

While the findings described above indicate that sex ratio can influence mate preferences and within-sex competition in many nonhuman species, correlational studies of naturally occurring variation in human sex ratios suggest that they may also be important determinants of human behaviour. For example, Pollet & Nettle (2008) reported that women in regions of the U.S. with male-biased sex ratios demonstrated stronger preferences for high socioeconomic status (i.e. attractive, Hume & Montgomerie 2001) men than did women in regions of the U.S. with female-biased sex ratios. Additionally, female–female competition appears to be more intense in societies with female-biased sex ratios than it is in those with male-biased sex ratios (Schuster 1983; Campbell 1995). Similarly, male–male competition appears to be more intense in societies with male-biased sex ratios than it is in those with female-biased sex ratios (e.g. Hudson & Den Boer 2002, 2004). These correlations raise the intriguing possibility that manipulating cues to the sex ratio of the local population may influence mate preferences and within-sex competition in humans. However, we know of no experimental studies examining this issue.

Symmetry is an important cue of mate quality in many species, including humans (reviewed in Gangestad & Simpson 2000). For example, in humans, facial symmetry is positively correlated with indexes of long-term, medical health (e.g. Thornhill & Gangestad 2006; Lie et al. 2008), other putative health cues (e.g. Gangestad & Thornhill 2003; Jones et al. 2004; Little et al. 2008) and attractiveness (Grammer & Thornhill 1994; Penton-Voak et al. 2001; Jones et al. 2001, 2004), and is negatively correlated with exposure to developmental stressors (Özener 2010; Özener & Fink 2010). Moreover, experimentally increasing the symmetry of digital face images tends to increase their attractiveness (e.g. Perrett et al. 1999; Little & Jones 2003, 2006). Collectively, these findings suggest that symmetry is a cue to the quality of both potential mates and potential competitors for mates. If manipulating cues to the sex ratio of the local population alters both behaviours that might function to promote successful within-sex competition and the selectivity of mate preferences (see earlier discussion), one might expect altering cues to the sex ratio of the local population to influence responses to symmetric individuals of both sexes.

Many researchers have suggested that preferences for symmetric mates may reflect adaptive responses that function, at least in part, to increase reproductive fitness by encouraging mating with high-quality individuals (e.g. Grammer & Thornhill 1994; Penton-Voak et al. 2001; Gangestad & Thornhill 2003). Other researchers have also emphasized that, because of the significant threat attractive women pose as competitors, cues to women's mate quality may be highly salient to other women and play a critical role in within-sex competition for mates (e.g. Buss & Dedden 1990; Maner et al. 2003; Fisher & Cox 2009; Puts et al. 2011). For example, perceptions of potential competitors' mate quality may be important both to gauge one's own market value and to identify competitors for mates with whom one could or could not successfully compete (e.g. Buss & Dedden 1990; Maner et al. 2003; Fisher & Cox 2009; Puts et al. 2011). These observations raise the possibility that preferences for symmetry in the faces

of a given sex may be stronger when there is a greater proportion of that sex in the local population than when there is a lower proportion of that sex in the local population. Such facultative responses to cues to the sex ratio of the local population would be adaptive if increased attraction to high-quality mates when there is a high proportion of potential mates supported efficient allocation of mating effort. They would also be adaptive if increased salience of quality cues in potential competitors when there is a high proportion of potential competitors supported successful within-sex competition for mates.

In light of the above, in experiment 1, we examined women's preferences for symmetry in faces of potential mates and competitors after pictorial cues to the sex ratio of the local population were experimentally manipulated. To do this, we first assessed women's preferences for facial symmetry in men and women in an initial (i.e. baseline) test. Immediately after this initial test, women watched one of two slideshows, both of which consisted of images of men's and women's faces. In one of these slideshows, the majority of images depicted men (i.e. potential mates) and in the other, the majority depicted women (i.e. potential competitors). After watching the slideshow, women repeated the initial symmetry preference test. We predicted that if attractiveness judgements of symmetric versus asymmetric faces are sensitive to cues to the sex ratio of the local population, preferences for symmetry in the faces of a given sex may be stronger when there is a greater proportion of that sex in the local population than when there is a lower proportion of that sex in the local population.

Some researchers have suggested that the effects of sex ratio on mating-related behaviours may be more closely linked to the degree of variation in the mate quality of individuals in the local population than to the sex ratio, per se (e.g. Owens & Thompson 1994; Kvarnemo & Simmons 1999). Thus, in experiment 2, we adapted the procedure from experiment 1 to investigate whether cues to the sex ratio of the local population and cues to the degree of variation in attractiveness in the local population have independent or interacting effects on women's symmetry preferences. To do this, we added an additional factor (attractiveness variation) to our experimental design. Thus, we assessed women's symmetry preferences before and after viewing slideshows of either male faces that varied greatly in attractiveness, male faces that varied little in attractiveness, female faces that varied greatly in attractiveness, or female faces that varied little in attractiveness. Importantly, all slideshows had the same mean facial attractiveness. If cues to the sex ratio of the local population influence behaviour independently of cues to the attractiveness variation in the local population, then we should see independent effects of the sex ratio depicted in the slideshows and of variation in attractiveness.

EXPERIMENT 1

In experiment 1, we tested whether preferences for symmetry in the faces of a given sex are stronger when there is a greater proportion of that sex in the local population than when there is a lower proportion of that sex in the local population.

Methods

Participants

One hundred heterosexual women (mean age \pm SD = 22.94 \pm 6.76 years) participated in experiment 1. Participants were recruited for an online study of face preferences by following links from social bookmarking websites (e.g. stumbleupon). Prior research has established that lab-based and online studies of women's face preferences produce very similar patterns of results (e.g. Jones et al. 2005; Conway et al. 2008).

Stimuli

To assess symmetry preferences in the initial (i.e. baseline), preslideshow test and the final, postslideshow test, we manufactured 20 pairs of faces (10 male pairs and 10 female pairs), each pair consisting of a symmetrized and original (i.e. relatively asymmetric) version of an individual (see Fig. 1 for examples). First, full-colour digital face photographs were taken of 10 white young adult men and 10 white young adult women with neutral expressions and direct gaze. Photographs were taken against a constant background and photographic conditions were standardized. Next, using procedures first described by Perrett et al. (1999), we used computer graphic methods to warp each image into a more symmetric shape. This method for manipulating symmetry of face shape in digital images does not affect other aspects of facial appearance (e.g. identity, skin colour and texture, aspects of face shape other than symmetry, Perrett et al. 1999) and has been used to assess symmetry preferences in many previous studies (e.g. Jones et al. 2001; Little & Jones 2003; Little et al. 2007b).

We used full-colour images of 25 white, young adult men and 25 white, young adult women for the slideshows. Each individual was photographed with a neutral expression and direct gaze against a constant background and under standardized lighting conditions. None of the individuals whose photographs were used for the slideshow were used to manufacture the symmetry preference stimuli. To provide descriptive statistics for the attractiveness of these images, all 50 images were rated for attractiveness by 23 women using a 1 (very unattractive) to 7 (very attractive) scale. Interrater agreement for these attractiveness ratings was high for both men's faces (Cronbach's alpha = 0.96) and women's faces (Cronbach's alpha = 0.94). The mean rating for men's faces was 2.36 (variance = 0.24) and for women's faces 2.69 (variance = 0.36).

Procedure

In the first part of the experiment (the baseline, preslideshow test), the participants were shown the 20 pairs of face images



Figure 1. Symmetrized (left) and original versions (right) of men's and women's faces used in our experiment.

(10 pairs of men's faces and 10 pairs of women's faces), each pair consisting of a symmetrized and relatively asymmetric (i.e. original) version of an individual, and were instructed to indicate which face in each pair they thought was more attractive. Trial order and the side of the screen on which any given image was presented were both fully randomized. The inclusion of this baseline test is potentially important; it allows us to control for possible pre-existing individual differences in women's preferences for symmetric faces, such as those related to women's own attractiveness (Little et al. 2001), sociosexuality (Sacco et al. 2009; Quist et al. 2011), menstrual cycle phase (Little et al. 2007b), perceived vulnerability to disease (Young et al. 2011) or recent exposure to pathogen cues (Little et al. 2011).

Immediately after completing the pre-slideshow test, the participants completed the second part of the experiment (the slideshow). In this second part, participants were randomly allocated to one of two conditions in which they were instructed to watch a slideshow of 30 face images (none of which were seen in the pre-slideshow test), where each face image was shown for 2000 ms. In one condition, participants watched a slideshow in which 83% (i.e. 25/30) of the images depicted men and 17% (i.e. 5/30) were of women. In the other condition, participants watched a slideshow in which 83% (i.e. 25/30) of the images depicted women and 17% (i.e. 5/30) were of men. In common with other research employing similar observation phases (e.g. Jones et al. 2007), participants were simply instructed to watch the images closely. Other studies have established that priming participants with pictorial cues to the nature of the local environment (e.g. images associated with high or low pathogen loads, Little et al. 2011) can affect face preferences in ways that are consistent with findings from correlational studies of natural variation in ecological conditions (e.g. DeBruine et al. 2010, 2011).

In the third and final part of the experiment (the post-slideshow test), the participants repeated the initial, pre-slideshow test. This post-slideshow test was completed immediately after the slideshow.

Analysis, Results and Discussion

For each participant, we first calculated (separately) the proportion of trials on which she chose the symmetrized face as the more attractive when judging men's faces in the pre-slideshow test, men's faces in the post-slideshow test, women's faces in the pre-slideshow test and women's faces in the post-slideshow test. Two-tailed *P* values are reported for all analyses. Consistent with previous work (e.g. Perrett et al. 1999; Little et al. 2003, 2006), symmetry preferences at pretest (i.e. baseline) were significantly greater than chance for both women's faces ($t_{99} = 6.16$, $P < 0.001$, mean \pm SEM = 0.61 ± 0.02 , $d = 0.62$) and men's faces ($t_{99} = 3.00$, $P = 0.003$, mean \pm SEM = 0.55 ± 0.02 , $d = 0.31$). Summary statistics for each individual condition are shown in Table 1.

We then calculated the change in preference for symmetric women between the pre-slideshow test and the post-slideshow test for each participant. To do this, we subtracted the proportion of trials on which symmetric female faces were chosen in the pre-slideshow test from the corresponding score in the post-slideshow test. Positive scores indicate preferences increased after the slideshow, while negative scores indicate preferences decreased after the slideshow. Similarly, we calculated the corresponding change in each participant's preference for symmetric men between the pre-slideshow test and the post-slideshow test.

Next, we coded these difference scores to reflect (1) the increase in symmetry preference for the sex of face that was in the majority during the slideshow that was viewed (i.e. men's faces when the sex ratio of the slideshow was male biased and women's faces when it was female biased) and (2) the increase in symmetry

Table 1

Summary statistics for each individual condition in experiment 1

Slideshow type	Sex of face judged	Test phase	Mean proportion of symmetrized faces chosen (SEM)	t_{49}	d
Female-biased	Male	Pre-slideshow	0.56 (0.02)	2.46*	0.35
Female-biased	Male	Post-slideshow	0.54 (0.02)	1.69†	0.24
Female-biased	Female	Pre-slideshow	0.56 (0.03)	2.40*	0.33
Female-biased	Female	Post-slideshow	0.62 (0.03)	4.34***	0.63
Male-biased	Male	Pre-slideshow	0.54 (0.02)	1.73†	0.25
Male-biased	Male	Post-slideshow	0.56 (0.02)	2.69**	0.39
Male-biased	Female	Pre-slideshow	0.66 (0.02)	6.84***	0.94
Male-biased	Female	Post-slideshow	0.59 (0.03)	3.72***	0.51

t, *P* and *d* statistics are for one-sample *t* tests comparing scores with the chance value of 0.5.

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

preference for sex of face that was in the minority during the slideshow that was viewed (i.e. men's faces when the sex ratio of the slideshow was female biased and women's faces when it was male biased), respectively. Because all participants judged both men's and women's faces in the symmetry preference test, this factor was represented in our experimental design by the within-subjects factor face type, which had two levels (sex in majority during slideshow and sex in minority during slideshow). Note that whether male face scores were coded as the majority condition and female face scores were coded as the minority condition (or vice versa) depended entirely on whether that participant had been shown the male-biased or female-biased slideshow in the slideshow phase of the experiment (see below).

The other critical factor in our design reflected whether participants saw a male-biased or female-biased slideshow in the slideshow phase of the experiment. Because each individual participant saw either a male-biased or female-biased slideshow (but not both), this variable was represented by the between-subjects factor slideshow type, which also had two levels (male biased versus female biased).

Coding the data in this way is important, as it is the only way that allows us to compare directly the effects of viewing cues to a male-biased sex ratio on evaluations of men's attractiveness and the effects of viewing cues to a female-biased sex ratio on evaluations of women's attractiveness. This comparison may be critical, since some studies have reported equivalent effects of sex ratio on mate preferences and competition-related behaviours (e.g. Jirotkul 1999), while other researchers have suggested that the effects of sex ratio on mate preferences may be generally weaker than those that have been observed for competition-related behaviours (e.g. Kvarnemo & Ahnesjo 1996).

We analysed the difference scores using a mixed-design ANOVA that had the within-subjects factor face type (sex in majority during slideshow versus sex in minority during slideshow) and the between-subjects factor slideshow type (male biased versus female biased). This analysis revealed the predicted main effect of face type ($F_{1,98} = 6.52$, $P = 0.012$, partial $\eta^2 = 0.06$; Fig. 2), whereby women showed a greater increase in symmetry preference when judging the sex that was in the majority during the slideshow than they did when judging the sex that was in the minority during the slideshow. One-sample *t* tests comparing the change in symmetry preference in each condition with baseline (i.e. the chance value of zero) showed that, although symmetry preferences tended to be increased from baseline when judging the sex that was in the majority during the slideshow ($t_{99} = 1.56$, $P = 0.12$) and tended to be decreased from baseline when judging the sex that was in the minority during the slideshow ($t_{99} = -1.83$, $P = 0.07$), these changes were not significantly different from baseline in either case. None the less, note that the significant main effect of face type

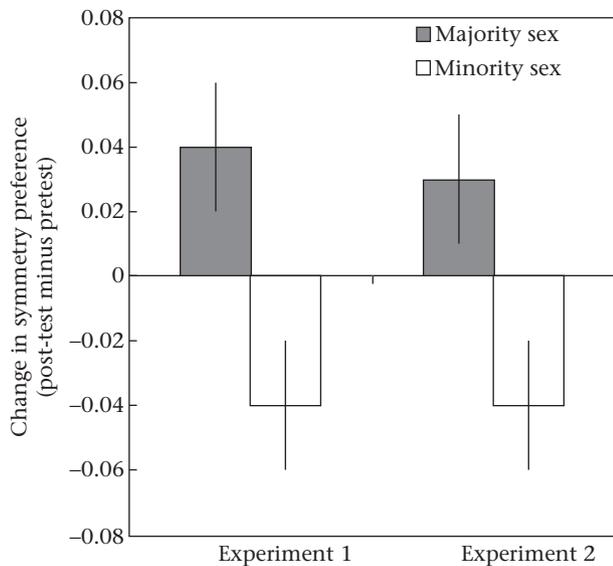


Figure 2. Change in symmetry preferences for the majority sex and minority sex conditions in experiments 1 and 2. Bars show means and SEMs.

reported above showed that these scores were significantly different from one another. There was no higher-order interaction between face type and slideshow type ($F_{1,98} = 0.05$, $P = 0.83$, partial $\eta^2 < 0.001$), indicating that the significant main effect of face type described above was not qualified by an interaction with slideshow type. This null finding is potentially important. It shows that the magnitude of the effect of viewing a male-biased slideshow on judgements of men's faces was not significantly different from the magnitude of the effect of viewing a female-biased slideshow on judgements of women's faces. This, in turn, suggests that cues to the nature of the sex ratio of the local population can have equivalent effects on mating-related and competition-related perceptions. The main effect of slideshow type was not significant ($F_{1,98} = 1.31$, $P = 0.26$, partial $\eta^2 = 0.013$).

EXPERIMENT 2

In experiment 1, women's preferences for symmetrized faces tended to be increased when judging the attractiveness of the sex that was depicted as being in the majority during the slideshow phase of the experiment, but to be decreased when judging the attractiveness of the sex that was depicted as being in the minority. These findings suggest that experimentally manipulating pictorial cues to the sex ratio of the local population can alter symmetry preferences. However, it has previously been suggested that effects of sex ratio on mating-related behaviours in some nonhuman species depend on the degree of variation in the mate quality of individuals in the local population, rather than (or in addition to) cues to the sex ratio of the local population (e.g. Owens & Thompson 1994; Kvarnemo & Simmons 1999). To investigate this possibility, in experiment 2, we adapted the paradigm that we had used in experiment 1 to test whether the observed effect of viewing cues to the sex ratio of the local population is independent of or interacts with the possible effects of the degree of variation in the attractiveness of the images shown in the slideshows.

Methods

Participants

One hundred heterosexual women (mean age \pm SD = 24.97 \pm 8.74 years) participated in experiment 2. As in experiment 1,

participants were recruited for an online study of face preferences by following links from social bookmarking websites (e.g. stumbleupon).

Stimuli

The same stimuli that we used to assess preferences for symmetrized versus original (i.e. relatively asymmetric) versions of men's and women's faces in experiment 1 were used again here. To select the faces to show in the slideshows, a separate group of 50 male and 50 female face images were first rated for attractiveness by 100 men and 100 women using a 1 (very unattractive) to 7 (very attractive) scale. Trial order was fully randomized and none of these raters took part in either of the main experiments. Interrater agreement was extremely high (Cronbach's alphas: ratings of men's faces = 0.97, ratings of women's faces = 0.96) and ratings made by men and women were highly correlated for both face sexes (correlation between men's and women's ratings of men's faces: $r = 0.97$, $P < 0.001$; correlation between men's and women's ratings of women's faces: $r = 0.96$, $P < 0.001$). Consequently, we calculated a single attractiveness score for each face by averaging ratings across raters. These ratings were used to select four sets of face images (15 images per set) with the following properties: male images that varied greatly in attractiveness (variance = 0.42), male images that varied little in attractiveness (variance = 0.04), female images that varied greatly in attractiveness (variance = 0.40) and female images that varied little in attractiveness (variance = 0.05). These images were used in the male high variance, male low variance, female high variance and female low variance slideshows, respectively. The mean attractiveness rating for each set was 2.65. In each set, the attractiveness ratings of the seven least attractive images were below this mean value and the attractiveness ratings of the seven most attractive images were above this mean value. The remaining image in each set was the middle-ranked image and was within 0.08 of the mean attractiveness of the sample. All face images were full colour and were shown with neutral expressions and direct gaze.

Procedure

The procedure was identical to that in experiment 1, except that participants were randomly allocated to one of the male high variance, male low variance, female high variance or female low variance slideshow conditions and that each image was shown only once (for 4000 ms) in the slideshow.

Analysis, Results and Discussion

Responses were coded in precisely the same way as in experiment 1. Two-tailed P values are reported for all analyses. As in experiment 1, and consistent with previous work (e.g. Perrett et al. 1999; Little & Jones 2003, 2006), symmetry preferences at pretest (i.e. baseline) were significantly greater than chance for both women's faces ($t_{99} = 5.39$, $P < 0.001$, mean \pm SEM = 0.59 ± 0.02 , $d = 0.54$) and men's faces ($t_{99} = 2.08$, $P = 0.040$, mean \pm SEM = 0.53 ± 0.02 , $d = 0.21$). Summary statistics for each individual condition are shown in Table 2.

To keep terminology consistent between experiment 1 and experiment 2, the 'sex in majority' and 'sex in minority' conditions reflect the sex seen or not seen in the slideshow, respectively. As in experiment 1, difference scores were first analysed using a mixed-design ANOVA with the within-subjects factor face type (sex in majority during slideshow versus sex in minority during slideshow), the between-subjects factor slideshow type (male biased versus female biased), and the additional between-subjects factor attractiveness variation (high versus low). As in experiment 1, this analysis revealed the predicted main effect of face type

Table 2
Summary statistics for each individual condition in experiment 2

Slideshow type	Sex of face judged	Attractiveness variation	Test phase	Mean proportion of symmetrized faces chosen (SEM)	t_{24}	d
Female-biased	Male	High	Preslideshow	0.58 (0.03)	2.22*	0.45
Female-biased	Male	High	Postslideshow	0.52 (0.03)	0.74	0.15
Female-biased	Female	High	Preslideshow	0.60 (0.04)	2.49*	0.50
Female-biased	Female	High	Postslideshow	0.60 (0.04)	2.71*	0.54
Male-biased	Male	High	Preslideshow	0.48 (0.03)	-0.90	0.15
Male-biased	Male	High	Postslideshow	0.56 (0.03)	1.73†	0.35
Male-biased	Female	High	Preslideshow	0.60 (0.04)	2.45*	0.50
Male-biased	Female	High	Postslideshow	0.60 (0.04)	2.90**	0.58
Female-biased	Male	Low	Preslideshow	0.56 (0.03)	1.90†	0.38
Female-biased	Male	Low	Postslideshow	0.50 (0.04)	-0.11	0.02
Female-biased	Female	Low	Preslideshow	0.58 (0.03)	3.00**	0.60
Female-biased	Female	Low	Postslideshow	0.65 (0.03)	5.06***	1.01
Male-biased	Male	Low	Preslideshow	0.52 (0.03)	0.54	0.11
Male-biased	Male	Low	Postslideshow	0.48 (0.03)	-0.64	0.13
Male-biased	Female	Low	Preslideshow	0.58 (0.03)	3.06**	0.61
Male-biased	Female	Low	Postslideshow	0.54 (0.03)	1.24	0.25

t , P and d statistics are for one-sample t tests comparing scores with the chance value of 0.5.

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

($F_{1,96} = 4.42$, $P = 0.038$, partial $\eta^2 = 0.044$; Fig. 2), whereby women showed a greater increase in symmetry preference when judging the sex in the majority during the slideshow than they did when judging the sex in the minority. Symmetry preferences tended to be increased from baseline when judging the sex that was in the majority ($t_{99} = 1.53$, $P = 0.13$) and to be decreased from baseline when judging the sex that was in the minority ($t_{99} = -1.83$, $P = 0.07$), although these differences from baseline were not significant. As in experiment 1, note that the significant main effect of face type indicated that these difference scores were significantly different from one another. The main effect of face type was not qualified by any higher-order interactions (all $F < 1.31$, all $P > 0.25$, all partial $\eta^2 < 0.014$). These null findings suggest that (1) the magnitude of the effect of viewing a male-biased slideshow on judgements of men's faces was not significantly different from the magnitude of the effect of viewing a female-biased slideshow on judgements of women's faces and (2) the effect of sex ratio cues on symmetry preference is independent of the effects of attractiveness variation. The interaction between slideshow type and attractiveness variation was significant ($F_{1,96} = 4.82$, $P = 0.031$, partial $\eta^2 = 0.048$; Fig. 3). There were no other significant effects (all $F < 1.49$, all $P > 0.22$, all partial $\eta^2 < 0.016$).

We used one-way ANOVAs to interpret the significant interaction between slideshow type and attractiveness variation. Symmetry preferences were increased to a greater extent after viewing a slideshow of male images with high variation in attractiveness than after viewing a slideshow of male images with low variation in attractiveness ($F_{1,48} = 6.50$, $P = 0.014$, partial $\eta^2 = 0.12$). By contrast, symmetry preferences were not increased to a greater extent after viewing a slideshow of female images with high variation in attractiveness than after viewing a slideshow of female images with low variation in attractiveness ($F_{1,48} = 0.43$, $P = 0.51$, partial $\eta^2 = 0.009$).

ANALYSES OF COMBINED DATA SETS

We conducted an additional test for an effect of the sex ratio depicted in the slideshow in which we combined the data sets from both experiments and analysed the resultant data set using a mixed-design ANOVA with the within-subjects factor face type (sex in majority during slideshow versus sex in minority during slideshow) and the between-subjects factors slideshow type (male biased versus female biased) and experiment (experiment 1 versus

experiment 2). Attractiveness variation was not included in this analysis as it was not a factor in experiment 1 and did not interact with the effect of face type in experiment 2. The main effect of face type was significant ($F_{1,196} = 10.82$, $P < 0.001$, partial $\eta^2 = 0.052$) and did not interact with any other variables (all $F < 1.58$, all $P > 0.11$, all partial $\eta^2 = 0.008$). One-sample t tests showed that symmetry preferences were significantly increased from baseline when judging the sex that was in the majority during the slideshow ($t_{199} = 2.18$, $P = 0.03$) and significantly decreased from baseline when judging the sex that was in the minority ($t_{199} = -2.59$, $P = 0.01$).

GENERAL DISCUSSION

In both experiments, we assessed women's preferences for symmetry in men's and women's faces before and after viewing slideshows in which cues to the sex ratio of the local population had been manipulated. Consistent with previous studies of women's

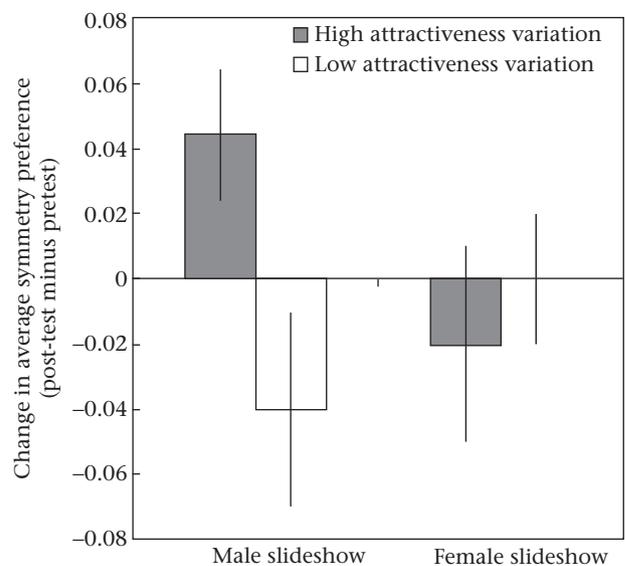


Figure 3. Change in symmetry preferences for the high and low attractiveness variance conditions after exposure to male or female slideshows in experiment 2. Bars show means and SEMs.

preferences for symmetric faces (e.g. Perrett et al. 1999; Little & Jones 2003, 2006), preferences for symmetry in both men's and women's faces were significantly greater than chance in the pre-slideshow (i.e. baseline) tests. As we had predicted, however, symmetry preferences were sensitive to experimentally manipulated cues to the sex ratio of the local population; women's preferences for symmetrized faces tended to be increased when judging the attractiveness of the sex that was depicted as being in the majority during the slideshow phase of the experiments and tended to be decreased when judging the attractiveness of the sex that was depicted as being in the minority during the slideshow phase (see Fig. 2). More importantly, these changes in symmetry preferences differed significantly from one another in both experiments. Additionally, the effects of viewing female-biased slideshows on evaluations of women's attractiveness and of viewing male-biased slideshows on evaluations of men's attractiveness were equivalent (i.e. did not differ significantly from one another). Thus, our findings suggest that increasing the apparent proportion of a given sex in the local population increases the salience of facial cues of mate quality in that sex.

Preferences for symmetric mates are thought to reflect, at least in part, adaptive responses that evolved to encourage mating with high-quality individuals (e.g. Grammer & Thornhill 1994; Penton-Voak et al. 2001; Gangestad & Thornhill 2003). Additionally, and because particularly attractive women are likely to present particularly significant competition for mates, cues to women's mate quality, such as symmetry, may be highly salient to other women and perceptions of these cues may be important for effective within-sex competition for mates (e.g. Buss & Dedden 1990; Maner et al. 2003; Fisher & Cox 2009; Puts et al. 2011). Increasing the apparent proportion of a given sex in the local population appears to increase the salience of facial cues of mate quality in that sex. This finding is consistent with both increased preferences for high-quality mates when mates are relatively abundant and increased salience of cues of competitors' mate quality when competition for mates is likely to be relatively intense. Consequently, our findings complement those from experiments with nonhuman species that have demonstrated effects of sex ratio on both mate preferences and behaviours that might function to promote effective within-sex competition (e.g. Jirotkul 1999; Clark & Grant 2010) and studies that have reported correlations between natural variation in sex ratios and human behaviours that are related to mating and within-sex competition (Schuster 1983, 1985; Campbell 1995; Pollet & Nettle 2008). Additionally, our findings present new evidence that priming participants with pictorial cues to different ecological conditions can influence behaviour in ways that are consistent with previous findings from correlational studies of natural variation in ecological conditions, experimental studies exposing human participants to relevant pictorial cues and theories of sexual selection (e.g. DeBruine et al. 2010, 2011; Little et al. 2011).

In experiment 2, we also tested for effects of viewing cues to the degree of variation in attractiveness in the local population on women's symmetry preferences. We found that viewing a slideshow of male images that varied greatly in attractiveness increased women's symmetry preferences more than did viewing a slideshow of male images that varied little in attractiveness. Importantly, both slideshows possessed the same mean attractiveness and this effect of attractiveness variability was independent of the effects of viewing cues to the sex ratio of the local population that were observed in both experiments and that we have discussed above. By contrast with the observed effect of cues to the degree of variation in male attractiveness in the local population, there was no similar effect of cues to the degree of variation in female attractiveness. Collectively, these findings suggest that the effects of the sex ratio of the local population and of cues to the variability in

the attractiveness of available potential mates can indeed be dissociated. None the less, these results do support the proposal that cues to both the sex ratio and degree of variation in the attractiveness of potential mates in the local population can be important for mating-related behaviours (e.g. Owens & Thompson 1994; Kvarnemo & Simmons 1999).

The sex ratio depicted in our slideshows (5:1) may appear somewhat extreme, at least when compared with the sex ratios that are typically observed for relatively large geographical regions (e.g. countries), which are generally around 1:1 (Barber 2011). However, sex ratios that are similar to those in our experiment are often encountered in real life (e.g. at a social gathering at which there is a far greater proportion of women than men, or vice versa). Thus, it is important to note that sex ratios of the type presented in our slideshow are not necessarily unrealistic and, consequently, do not necessarily lack ecological validity. Indeed, in small-scale societies, violent between-group conflict may well have led to extremely biased sex ratios and, even in more recent times, the influence of war on sex ratios appears to have resulted in detectable changes in women's mate choices (Pawłowski et al. 2000). Moreover, our findings suggest that a minute's indirect visual experience can be sufficient for subtle recalibration of women's evaluations of facial attractiveness, suggesting that the sex ratios encountered in relatively brief social interactions may well have effects on appraisals of others' attractiveness. This rapid recalibration of women's evaluations of others' attractiveness may have played an important role in the evolution of mate preferences; if female dispersal was common in ancestral societies, as has been suggested (e.g. Seielstad et al. 1998), facultative responses that rapidly recalibrated assessments of potential mates and potential competitors for mates may have helped women compete for mates more successfully in unfamiliar groups. These facultative responses would also be potentially important in societies where primary partner choices were commonly determined by parental, rather than female, choice (e.g. arranged marriages), as they may have allowed women to evaluate better the quality of potential extrapair mates and potential competitors for extrapair mates.

Although analyses of responses in the pre-slideshow symmetry preference tests suggested that the women in our experiments tended generally to prefer symmetrized versions of faces over relatively asymmetric versions (i.e. the original versions), the strength of these preferences was somewhat variable (see Tables 1, 2). This variability is consistent with previous work demonstrating individual differences in women's preferences for facial symmetry (reviewed in Quist et al. 2011) and underlines the potential importance of controlling for these individual differences as we have done in our experiments. Additionally, the current work identifies recent experience with potential cues to the sex ratio of the local population as an additional source of variation in symmetry preferences.

In both experiments, women's preferences for symmetrized faces tended to be increased when judging the attractiveness of the sex that was depicted as being in the majority during the slideshow phase and tended to be decreased when judging the attractiveness of the sex that was depicted as being in the minority. One interpretation of this pattern of results is that it implies that participants' default expectation about the sex ratio of the local population may well be approximately 1:1. However, it is also important to note that this pattern of results could equally be a consequence of averaging responses across individual participants, each of whom may have experienced different proportions of men and women immediately prior to participating in our experiment. Additionally, our findings could be due to varying cues to the absolute number of men or women in the local population, rather than the sex ratio, per se. While we acknowledge this

distinction could well prove to be an important one, we also note that cues to the absolute number of individuals of one sex in a local population and more direct cues to the sex ratio itself are both likely to have similar effects on women's perceptions of the size of the pool of potential mates and the size of the pool of potential competitors for mates in the local population. We suggest that these issues, together with experiments testing whether similar effects occur for perceptions of other putative cues of potential mates' and competitors' physical condition (e.g. sexually dimorphic shape characteristics and perceived health in faces) are potentially important topics for future research.

The cognitive and/or perceptual mechanisms that might underpin the sex ratio effects observed in our experiments remain unclear. It is unlikely that our findings reflect a simple priming effect whereby viewing potential mates' faces triggers a mating psychology under which cues of potential mates' qualities might become more relevant. For example, the women in our experiments showed corresponding effects for judgements of women's faces following female-biased slideshows, demonstrating that the observed effects are not specific to experience with opposite-sex faces. Similarly, it is unlikely that our findings simply reflect improved symmetry detection for a given sex of face after recent experience with a larger number of exemplars of that sex, which may have represented a wider range of facial asymmetries than a smaller number of faces would have. Given the correlation between symmetry and facial attractiveness, the variation in symmetry should have been greater in the high-variance than low-variance conditions in experiment 2. This issue is noteworthy since the effect of viewing cues to the sex ratio of the local population in experiment 2 was found to be wholly independent of the effect of attractiveness variation. Indeed, facial symmetry detection and facial symmetry preferences do not appear to be correlated in the way that a simple symmetry detection explanation for our findings would require (e.g. Little & Jones 2006; Oinonen & Mazmanian 2007). Finally, although our findings suggest that very little experience with cues to the sex ratio of the local population is needed to alter symmetry preferences, suggesting that our findings reveal a short-term, facultative response to the current environment, it is unclear whether similar cues can also have long-term effects on behaviour. For example, more prolonged exposure to cues to relatively stable (i.e. unchanging) sex ratios may have longer-term effects, as may experience with cues to the sex ratio of the local population during critical periods of development, such as childhood or adolescence. Our results do not speak directly to these issues and they require further investigation.

In summary, in two experiments, we found that manipulating pictorial cues to the sex ratio of the local population altered women's assessments of others' facial attractiveness. Increasing the apparent proportion of a given sex in the local population increased the salience of facial cues of quality in that sex. This effect of manipulating cues to the sex ratio of the local population on perceptions of symmetric versus relatively asymmetric faces is consistent with those observed in both previous experiments with nonhuman species (e.g. Jirotkul 1999; Clark & Grant 2010) and correlational studies of naturally occurring variation in human behaviour (e.g. Schuster 1983, 1985; Campbell 1995; Pollet & Nettle 2008). Moreover, the facultative responses observed in the current research may be adaptive; they suggest that women's evaluations of the attractiveness of both potential mates and potential competitors for mates are sensitive to cues of the sex ratio of the local population in ways that might function to promote efficient allocation of mating effort (i.e. increase preferences for high-quality mates when competition for mates is likely to be less intense) and successful within-sex competition (i.e. increased salience of cues to the quality of potential competitors for mates when competition

for mates is likely to be relatively intense), respectively. More fundamentally, our findings suggest that both intersexual and intrasexual selection have been important for shaping the effects of sex ratio on person perception.

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