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Original Article

Do prevailing environmental factors influence human preferences for facial morphology?

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Prevailing environmental factors influence preferences for attractive traits across many species. In humans, debate surrounds the role of environmental pathogens and economic development in determining facial attractiveness. We tested whether women and men's preferences for facial dimorphism, symmetry, skin tone, and adiposity differ among Melanesian participants from 3 islands (Espiritu Santo, Efate, and Tanna) in Vanuatu in the South West Pacific. These islands vary in their historical malarial pathogens respectively from pronounced to almost absent and are characterized by within and between island differences in economic development, ranging from urbanized market-based economies to remote rural horticultural communities. We found no support for the hypothesis that masculine male faces or feminine female faces are more attractive in environments with higher exposure to malarial pathogens or urban development. However, preferences for facial symmetry were highest in islands with higher malarial rates, possibly as symmetry indicates health and guides mate selection in disease rich environments. However, past evidence linking symmetry and health is weak, and we therefore interpret our findings cautiously. Women from peri-urban communities preferred male faces with lighter skin to rural and urban participants. Men from urban areas stated higher preferences for symmetry than peri-urban and rural male participants. All other effects were not statistically significant. While cross-cultural studies comparing preferences between disparate cultures provide evidence of associations between environmental effects and preferences for some facial traits, our results suggest these associations might not always persist at more fine-grain scales within small-scale societies.

Key words: **cross-cultural, evolution, facial attractiveness, human development, pathogens.**

INTRODUCTION

Preferences for attractive traits are posited to have been shaped by adaptation to the challenges faced by ancestral humans (Buss 2003). In particular, the widespread incidence of infectious disease throughout human ancestry is thought to have selected for many aspects of human sociality, including mate choice behaviour and preferences (Gangestad and Grebe 2014; Thornhill and Fincher 2014; Tybur and Gangestad 2011). Infectious disease may have shaped mating preferences in several ways. Notably, cognitive processes by which individuals avoid infection, what Schaller (2011) calls the "behavioral immune system", are expected to have favoured the detection and avoidance of infected individuals (Gangestad and Grebe 2014; Tybur and Gangestad 2011). Further, there is some support for the idea that preferences favour mates who show signs of having resisted infection themselves (Tybur and Gangestad 2011), or who have genotypes likely to confer resistance to infection (Gangestad and Grebe 2014).

Much of the evidence in support of these ideas comes from the observation that preferences vary among individuals, places and circumstances in ways that suggest preferences are phenotypically plastic in response to the chances of infection (Tybur and Gangestad 2011). Individual pathogen disgust, for example, is positively associated with women's preferences for men's facial masculinity (DeBruine et al. 2010c; Jones et al. 2013b) and men's preferences for women's facial femininity (Jones et al. 2013a; Lee et al. 2013). Priming with cues of contagion also heightens preferences in women and men for sexual dimorphism and symmetry in opposite-sex faces (Little et al. 2011). Women's preferences for facial masculinity were also highest in countries with poor health (DeBruine et al. 2010a) and high pathogen levels (DeBruine et al. 2012; Moore et al. 2013). However, men's preferences for facial

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femininity follow the opposite pattern, being highest in countries with better health (Marcinkowska et al. 2014). These studies suggest variation in the direction in which the behavioural immune system underpins women and men's mate preferences.

Importantly, the conclusions made from these studies are drawn from data primarily collected among participants living in WEIRD (Western, Educated, Industrialized, Rich, and Democratic) societies, who, when compared to small-scale indigenous societies, are sometimes outliers in psychological studies (Henrich et al. 2010). Owing to greater access to medical care and potentially lower exposure rates, infectious diseases impose fewer burdens in WEIRD societies than in traditional and developing societies. And yet participants from WEIRD societies show stronger preferences for sexually dimorphic faces (feminine female and masculine male faces) than those from small-scale societies with lower human development indices (Scott et al. 2014). This finding led Scott et al. (2014) to suggest that preferences for masculine male and feminine female faces may be a recent manifestation, formed within the evolutionarily novel ecological context of large, urban societies in which people encounter large numbers of faces, developing greater sensitivity to facial distinctiveness and to relatively minor sources of facial variation.

Comparisons of WEIRD samples with smaller-scale societies reveal variation in preferences for several traits. Preferences for facial symmetry were stronger among Hadza hunter-gatherers (Little et al. 2007), and preferences for facial masculinity were higher among rural Jamaicans (Penton-Voak et al. 2004) compared to participants from more developed countries. While between-society comparisons suggest that plasticity in response to pathogenic challenges may drive variation in preferences, questions have been raised about the strength of the supporting evidence (Pollet et al. 2014; Scott et al. 2013), the paucity of tests from traditional societies (Scott et al. 2014), and the lack of consideration of alternative hypotheses (Brooks et al. 2011; Scott et al. 2013 2014). For example, reanalysis of one cross-national comparison suggested that income inequality was a stronger predictor of variation in women's preferences for masculine faces than health (Brooks et al. 2011). Cross-society studies comparing group-level aggregated data is inherently limited in the nature and strength of inferences that can be made regarding individual-level mating preferences (Pollet et al. 2014). Within-society comparisons among individuals with different experiences can offer new empirical tests (DeBruine et al. 2011; Scott et al. 2008). For example, within the same areas of Bangladesh, male and female participants who recollected more childhood diseases preferred more feminine female and masculine male faces respectively, possibly reflecting disease avoidance mechanisms in mate preferences (de Barra et al. 2013). Thus, within small-scale societies wherein regions vary in pathogen prevalence, disease control and income, mate preferences should not be expected to be homogenous.

Owing to their diversity and relative seclusion from outside influences, island settings provide an important ecological context to test how environmental variables influence mate preferences. Vanuatu comprises over 80 islands, with a total population of approximately 280 000 people, settled by Melanesians migrating from Papua New Guinea 3500–4000 years ago (Kaneko et al. 1998). Seventy-six percent of the population live in rural communities across 65 inhabited islands and practice forms of traditional subsistence, including swidden horticulture, small-scale animal husbandry and fishing (UNICEF 2013). The 24% of ni-Vanuatu people living in urban areas reside in the capital city of Port Villa on Efate island and the smaller town of Luganville on Espiritu Santo island (VNSO 2009). Outside of Port Vila, which has the densest urban population and is the hub for governance, trade and tourism, people throughout Efate island live in small rural communities and practice subsistence horticulture (VNSO 2009).

Vanuatu is situated at the cusp of the Asia-Pacific malarial band (Kaneko et al. 1998) and parasitic infection, including malarial infections, account for 27% of mortalities in infants under 5 years of age and 33–45% of mortalities in children aged 5–14 years (Carter et al. 2016). Communicable infectious diseases like yaws, which causes sores that develop into painful lesions, and trachoma, which causes blindness, occur at very similar rates among rural communities in the northern island of Espiritu Santo (21% and 22% respectively) and the southern island of Tanna (31% and 25%; Kazadi et al. 2014; Mathew et al. 2009; Taleo et al. 2017). However, malaria rates are higher in northern than in southern islands (Flint et al. 1985; Kaneko et al. 1998; 2014; Ubalee et al. 2005). The northern-most islands of Malo/Santo, Maewo, and Tongoa have malarial incidence rates of 182, 252, and 193 per 1000 respectively, while the Southern islands of Futuna, Aniwa and Aneityum have malarial rates of 13, 8, and 39 per 1000 respectively (Kaneko et al. 1998). Genetic resistance to malaria, as measured via glucose 6-phosphate dehydrogenase allele frequencies, is positively associated with malarial parasite incidences among these islands (R = 0.81, Spearman rank test; Kaneko et al. 1998), suggesting that malarial parasite rates and genetic resistance coevolved among founder populations (Flint et al. 1985; Kaneko et al. 1998 2014; Ubalee et al. 2005). Selection for genetic resistance to malarial parasite richness has been attributed to the human initiated movement and dispersal patterns of the malarial vector *An. farauti* within and between islands (Chan et al. 2015; Lum et al. 2007). Among the northern islands where malarial pathogens are richest, traditional trade networks are well documented (Huffman 2005) and studies of the genetic drift of *An. farauti* show that inter-island trading underpins the transmission of vectors carrying malaria (Chan et al. 2015). However, these trade networks did not extend to the southern most islands, so that any transmission of malarial pathogens is a recent phenomenon resulting from increased availability of air travel (Chan et al. 2015). Taken together, malarial prevalence appears to be higher in the northern than the southern most islands of Vanuatu.

In the current study, we use a sample of three islands in Vanuatu as quasi-experimental treatments of historic malarial parasitic exposure and current economic development, to test how ecological and economic factors influence women's and men's mate preferences. We collected data on women and men's preferences for facial shape, symmetry, skin tone, and adiposity in opposite sex stimuli from the islands of Espiritu Santo, Efate, and Tanna. Facial masculinity in men is associated with androgenic development and some aspects of long-term health (Scott et al. 2013). Similarly, facial femininity in women is associated with higher levels of reproductive hormones, maternal investment traits and health (Law Smith et al. 2006, 2012). Facial symmetry is also associated with some aspects long-term and developmental health in both sexes (Van Dongen and Gangestad 2011) and temporal variation in facial adiposity and skin complexion may also occur in response to disease contraction (Coetzee et al. 2009; Scott et al. 2010). Malarial infection causes acute periods of nausea, vomiting, and weight loss (Anstey et al. 2009; Breman 2001). Thus, we predicted that preferences for sex typical facial shape (i.e. male preferences for femininity in female faces and female preferences for masculinity in male

faces) and facial symmetry would be stronger in islands with higher than lower pathogens as an indication of long-term disease resistance (Thornhill and Gangestad 2006; Van Dongen and Gangestad 2011). We predicted that preferences for sex typical facial skin complexion (i.e. male preferences for lighter skin in female faces and female preferences for darker skin in male faces; Aoki 2002) and greater adiposity in both sexes would be greater in islands with higher than lower malarial parasitic exposure as a reflection of current health status (Coetzee et al. 2009; Scott et al. 2010).

While historical differences in malarial prevalence could contribute to inter-island variation in mate preferences, contemporary developmental and economic changes are rapidly shaping the ecology on some of the islands of Vanuatu from rural traditional small-scale horticulture towards more urban dwellings with market based economies (Olszowy et al. 2015). Our study sites varied in urban development from the urban centre of Port Vila and its surrounding peri-urban communities on Efate island, to the remote rural communities on Espiritu Santo and Tanna island. Recent findings suggest that preferences for sex-typical facial shape are stronger in more urbanized market based economic settings than among people from small-scale subsistence cultures (Scott et al. 2014). The degree of urbanization and Western media exposure may also underpin variation in face preferences within small-scale societies. For example, among the Yali of Papua preferences for lighter skin were stronger among men who lived nearer to towns with more developed trade and tourism (Sorokowski et al. 2013). In developing areas of El Salvador, women with access to the Internet preferred more masculine looking men than women without access to the internet, while men without access to the internet preferred female faces with higher adiposity (Batres and Perrett 2014). Thus, we also explored whether preferences for sex typical facial shape and skin tone, as well as greater adiposity and symmetry in both sexes would be greater in more developed market economies than in remote rural horticultural settings.

MATERIAL AND METHODS

Facial photographs

Photographs of 31 men and 27 women of Melanesian descent were taken in open-air conditions during fieldwork in the highland regions of Papua New Guinea as part of a previous set of studies on human mate preferences conducted in the region (Dixson et al. 2010b). Only photographs where the individual was posing a neutral expression looking directly at the camera with minimal head tilt were used.

Six male and six female base faces (composite average faces) were constructed by combining pairs of male or female images drawn randomly from the stimulus sets (Benson and Perrett 1993; Tiddeman et al. 2001). Base faces have the advantage of removing small idiosyncratic differences among sets of faces and allow for cleaner tests of experimental manipulations on preferences. Base faces were made symmetrical prior to being transformed on dimensions of sexual dimorphism, symmetry, skin tone, and facial adiposity as described below. The interpupillary distance was held constant across all images (Coetzee et al. 2011; Re et al. 2011). As we were testing the effects of male facial traits on female preferences and female facial traits on male preferences, transforms were performed on male base faces and female base faces separately. All images were masked on the outline of the face so that hair and clothing cues were not visible (Figure 1), which removes extraneous cues that can be altered in transforms (DeBruine et al. 2010d). While masking is unusual and may alter some perceptions, we note that this does not affect the relative difference between the faces (i.e. the masculine face should be equally affected by masking as the feminine face).

Facial masculinity and femininity

Sexual dimorphism was manipulated using the shape linear difference between a composite of 50 men and an equivalent composite of 50 young adult women of European descent (Perrett et al. 1998). The composite base faces were made symmetrical prior to being transformed to represent 50% ± the difference between a composite, resulting in 6 pairs of faces wherein one image was +50% masculinized and another was -50% masculinized (Figure 1a).

Facial skin tone

Photographs of 113 young adult European men, taken under standard lighting conditions and with a neutral expression, were rated for skin-darkness on a 7-point scale (1 = very light, 7 = very dark) by 2 Caucasian raters (N = 113, r = 0.69, P < 0.001). The skin-darkness of base faces was transformed using units of brightness quantified from a mean score calculated from 2 raters and used

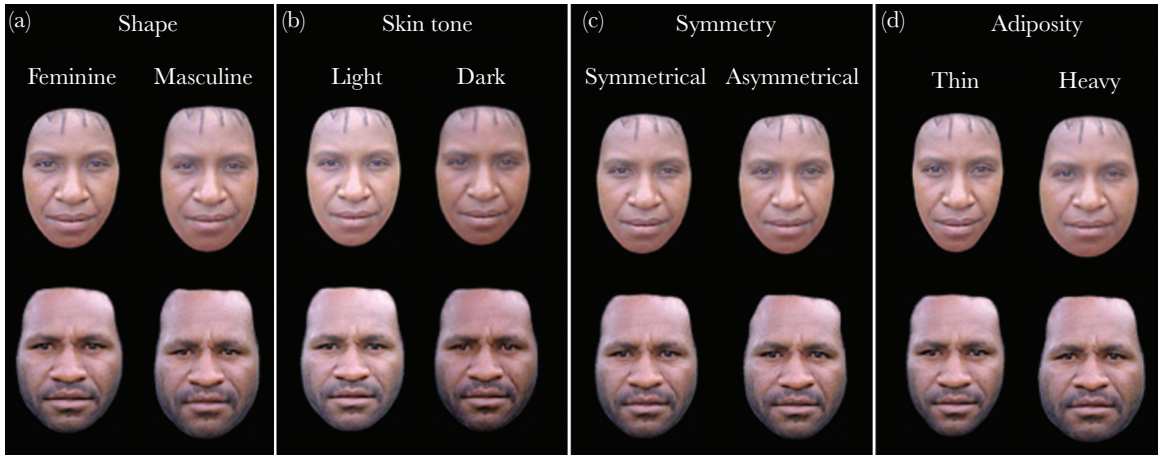

Figure 1
An example of the stimuli used in this study. Images show composites of female (upper row) and male (lower row) faces manipulated to vary in shape (feminine, masculine, a), skin tone (light, dark, b), symmetry (symmetrical, asymmetrical, c), and adiposity (thin, heavy, d).

to create two composite images by combining images for the top 25 (mean rating = 6.0) and bottom 25 (mean rating = 1.8) scoring faces for skin-darkness. The composite base faces were made symmetrical prior to being transformed on the colour difference between the light and dark skinned composites (Benson and Perrett 1993; Tiddeman et al. 2001) to represent −50% and +50% of the difference between the 2 composites (Figure 1b).

Facial symmetry

The transform applied was different for each image, representing 100% of the difference between an original image and its symmetric counterpart. Transforms were based on randomly selected Caucasian faces from a set unrelated to the transformed faces. The transforms were applied to the symmetric base face creating images that had 100% asymmetry from an unrelated face. The transform then created 2 images, one symmetric and one asymmetric, for each base face. Final images were 6 pairs of female and 6 pairs of male symmetric/asymmetric faces (Figure 1c).

Facial adiposity

Photographs of 150 young adult European men and 213 women, taken under standard lighting conditions and with a neutral expression, were rated for facial adiposity on a 7-point scale (1 = very thin, 7 = very fat) by 3 Caucasian raters ($r = 0.66$, $r = 0.65$, $r = 0.56$; all $N = 363$, all $P < 0.001$). The adiposity of base faces were made symmetrical prior to being transformed using these ratings of perceived weight. Using the mean ratings, images for the top 30 (15 women, 15 men, mean rating = 5.8) and bottom 30 (15 women, 15 men, mean rating = 2.4) scoring faces were combined to create composites of male and female faces. Each composite base face was transformed to simulate changes in weight by transforming +50% and −50% of the difference between the high and low composite. We created 6 pairs of faces with one thin (low weight) and one heavy (high weight) face (Figure 1d).

Procedure

Approximately 113 different Austronesian languages are spoken across the islands of Vanuatu (Dixson et al. 2017a). However, almost the entire population of Vanuatu speak the lingua franca, Bislama, a creole that incorporates English, French, and indigenous vocabulary with Melanesian grammar (Vanuatu Cultural Centre 2008). Participants in the current study were interviewed individually in Bislama, either in their homes, farms, communal huts, or at markets. Participants first completed a questionnaire containing the 24 pairs of colour photographs of faces and were asked to select the face they considered to be most physically attractive from each pair. The exact phrasing for the attractiveness judgments in English and Bislama were as follows:

> English version of the attractiveness judgments instructions: You will look at lots of different female/male faces that are in the book. There are lots of pages as follows (researcher then gestures to the flipbook). On each single page there are two faces as follows (briefly gesture to first page with two faces, being careful not to point to either one, then quickly closes book). These faces are not real people, they are pretend faces. They were made before on a computer, and you do not know these people on these pages. You will have to look at the two faces, and you must think about the following: which one is more attractive than the other? Like this, which one do you like more? You choose which one is more attractive, and then you just point to it. Then, he will mark it on this paper. Then you look at another page, you chose another one, then another one, then all the way to the end of this book. Alright, did you understand everything? Ok, we can start.
>
> Bislama translation of the attractiveness instructions: Bambae yu luk fulup difren fes blong woman/man, we istap long buk. Igat fulup pej olsem (researcher then gestures to the flipbook). Lo wan wan pej igat tufala fes olsem (briefly gesture to first page with two faces, being careful not to point to either one, quickly closes book). Fes oli no ril man, i giaman fes nomo. Oli bin wokem lo komputa fastaem, mo yu no save man we istap long pej. Bambae yu mas luk lo tufala fes, mo yumas tingbaot wan samting olsem: wijwan hemi moa naes, bitim narawan? Olsem, wijwan yu yu laekem moa? Yu jusem wijwan hemi moa naes, afta yu poen lo hem nomo. Afta, mbae hemi putum lo pepa ia. Afta yu luk nara pej, yu jusem narawan, afta, narawan, afta, go go end blong buk ia. Oraet, yu yu kasem evri samting? Ok, yumi save stat.

The 24 images in the flipbook were comprised of 4 manipulations (facial shape, symmetry, adiposity, and skin tone), each of which had 6 pairs of faces. Questionnaires for men included only female faces and questionnaires for women included only male faces. The presentation of each manipulation on either the left or right side of the page was fully counterbalanced and the order in which manipulations appeared was randomized. Stimuli were printed on high quality photograph paper, laminated and placed in the flipbook. After making selections participants provided their age, island of residence, length of time living on the island of residence, level of education (none, primary school, secondary school, diploma/university). We also collected data on relationship status (single, married, unmarried but in a relationship), although we did not analyse these data as participants from the remote rural communities typically have arranged "kastom" marriages and discussing other kinds of relationship type, such as being in a co-residing but unmarried relationship, is taboo.

Study sites and participants

We recruited 492 Ni-Vanuatu people (Mean age = 30.99 ± 12.95 SD), of which 227 were men (M = 31.64 ± 13.50) and 265 were women (M = 30.44 ± 12.45) from the islands of Espiritu Santo, Efate, and Tanna (Figure 2). All participants had lived their entire lives on their respective island of residence and had some primary school (women = 43.8%, men = 52%) or high school (women = 38.1%, men = 32%) education. Some participants had University level education (women = 11.3%, men = 14.1%) that was primarily diplomas in tourism or teaching and the remainder had no education at all (women = 6.4%, men = 1.8%). Malariometric surveys reveal that parasite rates were 28% in the Northern island of Espiritu Santo, 14.1% in the central island of Efate and 8.3% on the southern island of Tanna (Figure 2, Kaneko et al. 1998). We used these islands as a between-subjects factor to test how face preferences vary with malarial parasite prevalence. However, within each of these islands economic development varies from more market economies in urban communities to remote rural communities where people are subsistence horticulturalists (VNSO 2009; Dixson et al. (forthcoming)). We tested whether current ecological conditions influenced preferences using categories of urban, peri-urban, and rural. However, we note that variation in urban development is not consistent across islands. Thus, we ran a second set of analyses comparing preferences among only those participants from remote

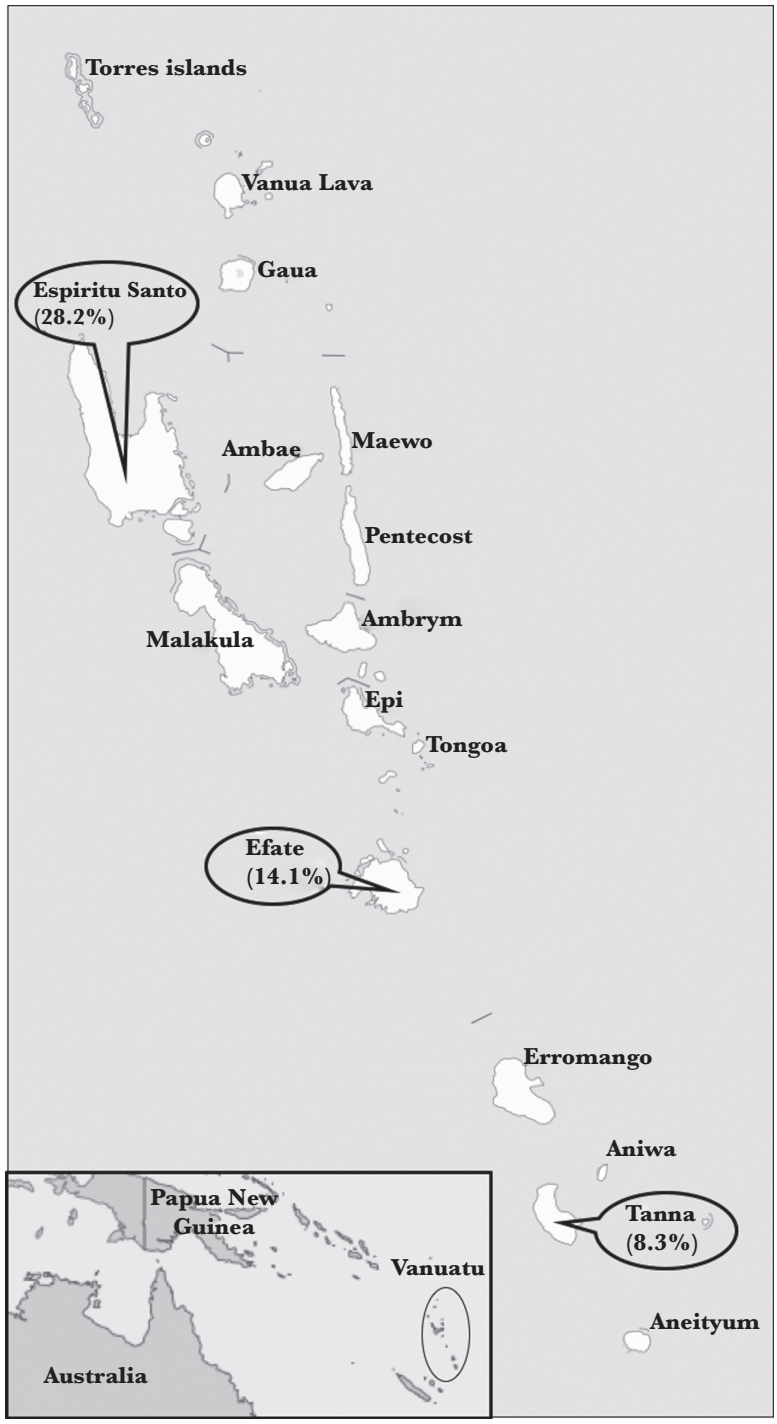

Figure 2
A map showing some of the main inhabited islands of Vanuatu. The study sites in the current study (Espiritu Santo, Efate, and Tanna) are highlighted along with data on malarial prevalence from malariometric surveys (Kaneko et al. 1998). The location of Vanuatu relative to Australia and Papua New Guinea is shown in the lower panel.

rural settlements from the island with the highest (Espiritu Santo island) and lowest (Tanna island) malarial prevalence.

Espiritu Santo is the largest island in Vanuatu and has the highest levels of malarial prevalence in our sample (Figure 2). We collected responses from 72 women (M = 27.44 ± 9.46) and 54 men (M = 34.48 ± 12.55). Data were collected from a remote rural community of horticulturalists in Tanafo village and from 2 coastal rural villages of Hog harbour and Port Olry (female = 63; male = 50) and the urban centre of Luganville (female = 9; male = 4). Our second study site was Tanna island, which has the lowest levels of malaria (Figure 2). Here, all participants were recruited from the remote rural region of Niprainitata and live almost exclusively as subsistence horticulturalists (female = 103, M = 30.79 ± 13.15; male = 83, M = 30.53 ± 14.43). We also collected data from Efate

island, which has intermediate levels of malaria compared with Espiritu Santo and Tanna (Figure 2). Participants were 90 women (M = 32.44 ± 13.36) and 90 men (m = 30.97 ± 13.08). Data were collected primarily in the capital Port Vila, which is a densely populated urban centre (female = 55; male = 47), and peri-urban communities where people partially subsist from farming local gardens (female = 30; male = 39). Outside of Port Villa, people live in small rural communities and subsist predominantly via horticulture (female = 5; male = 4).

STATISTICAL ANALYSIS

We calculated for each female rater, the proportion of symmetrical, heavy, masculine, and dark skin faces selected and for each male rater the proportion of symmetrical, heavy, feminine, and light skin faces selected. We then ran Analyses of Variance (Anovas) for the four preference measures, with malarial parasite rates as a fixed effect, from the lowest pathogen levels on Tanna to the highest on Santo. We ran a second set of Anovas for each preference measure with island development (fixed effect; rural, peri-urban, and urban). All effect sizes in Table 1 are partial eta square (η_p^2) and analyses were undertaken in SPSS 22.

RESULTS

Men's preferences for female facial traits

Men's preferences were greater than chance (0.50) for symmetrical faces (t_{226} = 4.505, P < 0.001), feminized face shapes (t_{226} = 3.796, P < 0.001), and lighter skin tones (t_{226} = 8.146, P < 0.001), while preferences were greater for thinner than heavier faces (t_{226} = −13.411, P < 0.001).

Island malarial parasite rates were associated with male preferences for symmetry in opposite sex stimuli (Table 1; Figure 3). Preferences for symmetry were significantly higher among men from the island with the highest compared to the island with the lowest malarial prevalence (Levene's Test: F = 7.19, P = 0.008; $t_{99.155}$ = 2.803, P = 0.006, d = 0.49) and among men from the island with intermediate compared with lowest malarial prevalence (Levene's Test: F = 16.191, P < 0.001; $t_{158.621}$ = 2.394, P = 0.018, d = 0.36). Preferences did not differ significantly between men from the islands with the highest and intermediate malarial prevalence (t_{142} = 0.421, P = 0.674, d = 0.07, Figure 3). There was also a significant effect of island development on men's preferences for symmetry (Table 1), reflecting that participants from urban areas had higher preferences for symmetrical faces than participants from rural areas (t_{186} = 3.017, P = 0.003, d = 0.50). Comparisons were non-significant between urban and peri-urban participants (Levene's Test: F = 15.03, P < 0.001; $t_{57.777}$ = 1.437, P = 0.156, d = 0.31) and between peri-urban and rural areas (Levene's Test: F = 23.19, P < 0.001; $t_{46.188}$ = 0.229, P = 0.820, d = 0.04, Figure 3).

Women's preferences for male facial traits

Women's preferences were greater than chance (0.50) for symmetrical faces (t_{264} = 4.297, P < 0.001), while preferences were lower than chance for masculine faces (t_{264} = −5.758, P < 0.001) and heavier looking faces (t_{264} = −6.952, P < 0.001). Preferences for skin tone were equivocal (t_{264} = −0.387, P = 0.699).

Island malarial parasite rates were associated with female preferences for symmetry (Table 1; Figure 4). Preferences for symmetry were significantly higher among women from the island with the highest compared to the lowest malarial prevalence (t_{173} = 2.606, P < 0.010, d = 0.40) and between participants from the island with intermediate compared to the lowest malarial prevalence (t_{191} = 2.033, P = 0.043, d = 0.29, Figure 4). Preferences between participants from islands with the highest and intermediate malarial prevalence did not differ significantly (t_{160} = 0.810, P = 0.419). There was also a main effect of island development on women's skin tone preferences (Table 1). Preferences for dark skin tones were lower among women in peri-urban areas than women in rural (t_{199} = -3.614, P < 0.001, d = −0.48) and urban areas (t_{92} = −2.190, P = 0.031, d = −0.48, Figure 4). Preferences between urban and rural participants were not statistically significant (t_{233} = −1.134, P = 0.258, d = −0.17).

Additional analyses

In our samples, island development did not vary systematically with island malarial prevalence. To eliminate differences in island development within islands and compare the effects of island malarial prevalence, we compared preferences among only those participants

Table 1

Univariate Anovas testing effects of malarial parasite level and island development on men and women's preferences for facial shape, symmetry, skin tone and adiposity

	Men's preferences for female stimuli							
	Malarial parasite level				Island development			
	F	Df	P	η_p^2	F	Df	P	η_p^2
Shape	0.53	2, 224	0.589	0.005	0.71	2, 224	0.491	0.006
Symmetry	4.17	2, 224	0.017	0.036	3.56	2, 224	0.030	0.031
Skin tone	0.86	2, 224	0.426	0.008	1.05	2, 224	0.351	0.009
Adiposity	1.50	2, 224	0.225	0.013	2.53	2, 224	0.082	0.022
	Women's preferences for male stimuli							
	Malarial parasite level				Island development			
	F	Df	P	η_p^2	F	Df	P	η_p^2
Shape	0.75	2, 262	0.473	0.006	0.11	2, 262	0.895	0.001
Symmetry	4.03	2, 262	0.019	0.030	0.85	2, 262	0.430	0.006
Skin tone	0.82	2, 262	0.442	0.006	6.22	2, 262	0.002	0.045
Adiposity	1.41	2, 262	0.245	0.011	0.19	2, 262	0.831	0.001

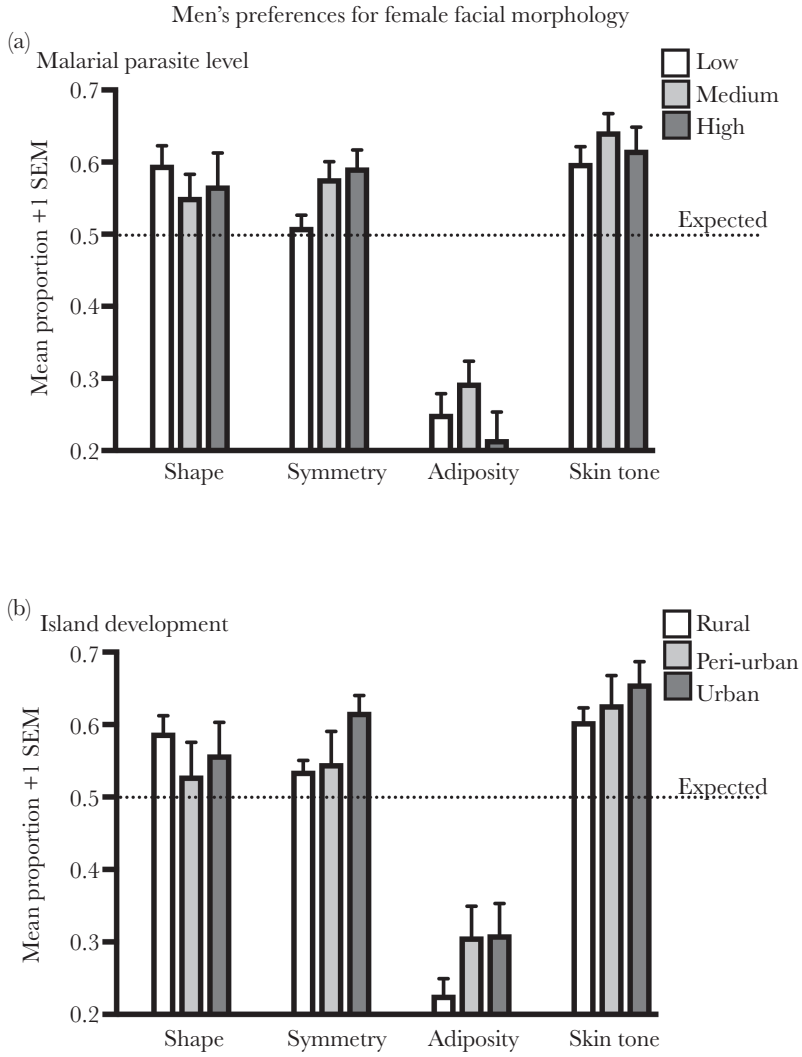

Figure 3

Mean proportions (+1 SEM) of feminised, symmetrical, heavier, and lighter toned female faces selected as most attractive by men living in islands varying in malarial parasite level (a) and island development (b). The dashed line represents the expected proportion of men preferring a given trait.

living in the remote rural communities from the islands of Espiritu Santo (50 men: mean age = 35.00 ± 12.77; and 63 women: M = 27.48 ± 9.49) and Tanna (83 men: M = 30.53 ± 14.43; and 103 women: M = 30.79 ± 13.15), which have the highest and lowest malarial prevalence respectively (Figure 2).

Men's preferences for facial symmetry were influenced by malarial prevalence ($F_{1,131}$ = 6.31, P = 0.013; η_p^2 = 0.046), so that preferences were higher for symmetry in the high malaria (M = 0.583, SD = 0.182) than the low malaria island (M = 0.510, SD = 0.150). However, malarial prevalence did not influence preferences for facial shape ($F_{1, 131}$ = 0.29, P = 0.594; η_p^2 = 0.002; high: M = 0.570, SD = 0.327 and low: M = 0.596, SD = 0.240), skin tone ($F_{1, 131}$ = 0.15, P = 0.702; η_p^2 = 0.001; high: M = 0.613, SD = 0.234 and low: M = 0.598, SD = 0.207), or adiposity ($F_{1, 131}$ = 1.61, P = 0.206; η_p^2 = 0.012; high: M = 0.193, SD = 0.253 and low: M = 0.251, SD = 0.254). Likewise, women's preferences for facial symmetry were influenced by malarial prevalence ($F_{1,164}$ = 8.80, P = 0.003; η_p^2 = 0.051), so that preferences were higher for symmetry in the high (M = 0.624, SD = 0.243) than the low malaria island (M = 0.513, SD = 0.229). However, malarial prevalence did not influence preferences for facial shape ($F_{1,164}$ = 0.44, P = 0.508; η_p^2 = 0.003; high: M = 0.407, SD = 0.284 and low: M = 0.432, SD = 0.194), skin tone ($F_{1,164}$ = 0.44, P = 0.508; η_p^2 = 0.003; high: M = 0.532, SD = 0.250 and low: M = 0.506, SD = 0.231), or adiposity ($F_{1,164}$ = 2.78, P = 0.098; η_p^2 = 0.017; high: M = 0.354, SD = 0.255 and low: M = 0.419, SD = 0.234).

DISCUSSION

The current study reports preferences for facial morphology among women and men from three small-scale island communities in Vanuatu. These islands vary in malarial prevalence from pronounced in the northern islands to almost absent in the southern islands (Flint et al. 1985; Kaneko et al. 1998, 2014; Ubalee et al. 2005). We found that women and men from islands with higher rates of malaria expressed the strongest preferences for symmetrical faces, which is consistent with the hypothesis that symmetry as a cue of health is enhanced in high pathogen settings (Little et al. 2007). We also found that symmetry was preferred among men in urban areas compared to peri-urban and rural areas. Women from peri-urban areas had stronger preferences lighter skin in men than women from urban and rural

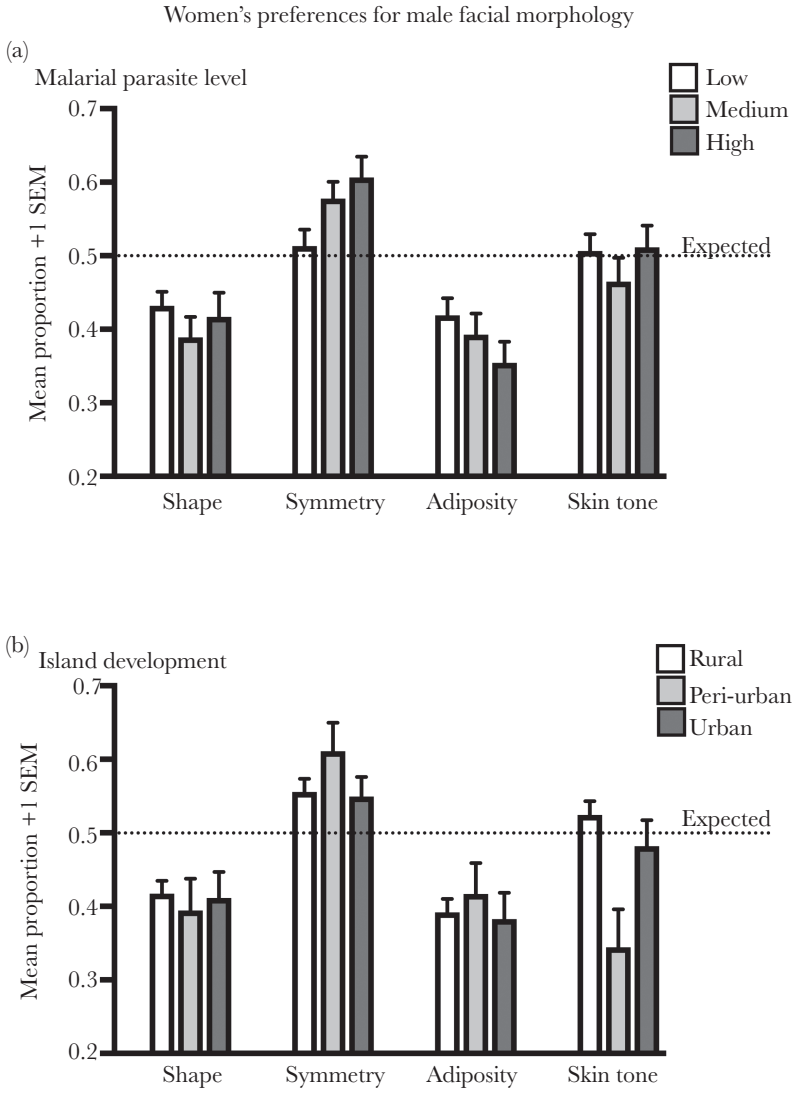

Figure 4
Mean proportions (+1 SEM) of masculinised, symmetrical, heavier and darker toned male faces selected as most attractive by women living in islands varying in malarial parasite level (a) and island development (b). The dashed line represents the expected proportion of women preferring a given trait.

areas. Our findings suggest that preferences for some facial cues that may reflect aspects of underlying quality are stronger under environmentally harsh conditions.

To our knowledge, very few studies have tested preferences for symmetry in small-scale societies. Our findings that symmetry was preferred in harsher environmental conditions compliment those of Little et al. (2007), who reported preferences for facial symmetry were stronger among Hadza hunter gatherers of Tanzania than among men and women from the UK. However, the evidence for a relationship between fluctuating asymmetry (FA) and human health is, at best, weak (Van Dongen and Gangestad 2011). Longitudinal evidence on adolescent development in the UK found no support for a relationship between FA and health (Pound et al. 2014). Of particular relevance to the current study, facial FA in infants and adolescents from rural communities in Senegal was not associated with the number of malarial infections (Thomas et al. 2015). While we found that preferences for symmetry were higher in islands with higher levels of malaria, given the mixed associations between facial symmetry and health we interpret this finding with caution. Future studies assessing health, facial FA and perceptions of health and attractiveness across study sites that vary systematically in prevailing parasitic exposure would be valuable.

We found no support for the theory that women's preferences for masculine male faces and men's preferences for feminine female faces are associated with the prevalence of disease (DeBruine et al. 2010a, 2010b, 2012; Little et al. 2011). Our quasi-experimental design is restricted to one important disease, malaria, an infectious mosquito-borne disease that imposes substantial mortality and morbidity burdens (Breman 2001; Carter et al. 2016). If preferences serve to identify mates with superior genotypes for coping with prevailing disease, then we would expect people from high-malaria islands to express strong preferences for sexually dimorphic faces. Malaria is not, however, contagious; and if preferences serve to avoid person-to-person infection, then we would not expect inter-island variation in preferences. Thus, there is a need to extend the current research to include multiple vectors of contagious and non-contagious diseases within an inter-island framework to fully

test if facial masculinity and femininity vary according to the type of prevailing pathogenic risks.

Our results did not support the recent suggestion that urbanisation predicts variation in preferences for facial dimorphism (Scott et al. 2014; Dixson et al. 2017a). However, we did find that women living in peri-urban areas preferred lighter-skinned stimuli. Among the Yali of Papua, preferences for lighter skin were stronger among participants from regions that were in closer contact with more developed urban areas in which contact with Western tourism was greater (Sorokowski et al. 2013). In a similar vein, within developing areas of El Salvador access to the Internet was positively associated with women's facial masculinity preferences (Batres and Perrett 2014). Tourism and access to the Internet may be associated with Western economic development and exposure to Western advertising, potentially influencing perceptions of beauty towards a more Western ideal among our sample of peri-urban Ni-Vanuatu people. However, skin tone preferences were very similar among women from the most urban and most rural communities, suggesting that effects of urbanisation do not fully explain our findings. Debate surrounds whether sexual dimorphism in skin colour is sexually selected (Aoki 2002), and studies report cross-cultural differences in skin tone preferences (Dixson et al. 2007a, 2007b, 2010a). Until further evidence on the possible effects of Western media exposure on skin tone preferences within small-scale societies is available, we suggest caution when interpreting our findings.

Preferences for facial adiposity were low across all islands. This finding does not support our hypothesis that people living in environments with higher malaria rates, which causes acute periods of nausea, vomiting and weight loss (Anstey et al. 2009; Breman 2001), should have stronger preferences for facial adiposity. It is possible that changes in facial adiposity are less important than changes in other characteristics associated with malarial infection, such as skin complexion and body weight. For example, skin tone became lighter and more yellow among Caucasian participants injected with lipopolysaccharide, which causes acute sickness, suggesting that sickness is observable via subtle changes in skin complexion (Henderson et al. 2017). Studies using stimuli that depict actual changes in facial health occurring due to malarial infection would be more ecologically valid than our current methods. However, given that our participants generally prefer less corpulent faces, and preferences for body weight, shape and other characters associated with adiposity vary cross-culturally (Dixson et al. 2010b, 2011; Singh et al. 2010), it is possible that facial adiposity may simply not be a cue that is prioritized in this particular culture.

The current study has some important limitations. For example, we did not take account of relationship context when asking people's preferences for different facial attributes. Several studies have shown that women's preferences for sexually dimorphic traits are stronger when judging short-term than long-term relationships (Little et al. 2011; but see Dixson et al. 2016). However, a cross-cultural study of 12 cultures, 10 of which were small-scale societies, found no consistent pattern in preferences for facial masculinity for short and long-term relationships (Scott et al. 2014). Nonetheless, preferences may have differed when assessing mate qualities for a short and long-term partner and additional studies addressing this issue would be valuable. Further, we used only a limited number of faces and manipulations derived for morphometrics of people of European ethnicity to alter the facial dimensions in our stimuli. Thus, while our stimuli capture objective variation in masculinity, adiposity, symmetry and tone, creating transforms using morphometrics generated from the actual study population would be ideal. Ecological validity of stimuli is often cited as a shortcoming in cross-cultural research on human mate preferences (Dixson and Vasey 2012; Patterson et al. 2015, 2016) and developing stimuli from within the communities being surveyed should ideally be undertaken in future studies.

In summary, our findings suggest some variation in face preferences as a function of historical malarial parasite richness and contemporary transitions towards market economic development. We found that women and men stated higher preferences for symmetrical faces under conditions of higher malarial parasitic exposure, and preferences for lighter skin and symmetry were stronger under conditions of urban development among women and men respectively. While our methods were relatively coarse-grained, we suggest that the study of human mate preferences conducted within cultures, including Western settings, can illuminate subtle economic and ecological effects that may maintain some of the variation in mate preferences.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Dixson et al. (2017b).

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