Partner choice decision making and the integration of multiple cues

Ryan Schacht a,⁎, Mark Grote b

a Department of Anthropology, University of Utah, Salt Lake City, UT, 84112
b Department of Anthropology, University of California-Davis, Davis, CA, 95616

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Uncertainty about fitness-enhancing traits in a potential mate, as well as variability in social and ecological environments, favors the use of multiple cues in selecting a partner. Though how individuals respond with adaptive mating preferences is an open question. Here we investigate mate choice decision making among the Makushi of Guyana and compare two competing approaches: 1) a prioritized trait approach, in which preferences are determined by the independent evaluation of relevant partner traits; and 2) an integrative approach, in which preferences are determined by reducing multiple, interrelated traits to a few latent dimensions. Within these two approaches we measure the effects of several key factors — sex, adult sex ratio, and community-to-community variability — thought to pattern preferences. We find support for cue integration and contextual variability in preferences. Sex and adult sex ratio are weak predictors of preferences in the Makushi: preferences are best explained by unstructured community effects. These findings highlight two key issues in mate choice studies: 1) simple biologically-based models do not seem adequate to explain variation in preferences, either within or among populations; and 2) while context, generally speaking, matters in determining preferences, we lack theoretically-informed predictions about relevant contextual factors. The importance of cues, as well as what they signal in a potential partner, is likely to vary with location-specific factors that are yet unexplored.

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1. Introduction

In sexually reproducing species the choice of a mate is key to fitness (Andersson, 1994; Bateson, 1983). Research on mate choice has primarily focused on identifying preferred traits, insofar as these serve as signals of the potential benefits a mate may offer (reviewed in Andersson, 1994), be they direct (e.g., parental investment) or indirect (e.g., immunocompetence). Far from involving simple decisions, selecting a mate likely requires paying attention to multiple, potentially competing, signals. It is an open question how individuals utilize information from multiple cues to make an adaptive mate choice decision. In general, signals are thought to be organized in one of two ways: 1) as a collection of independently relevant traits, each reflecting a single property of a potential partner and varying in importance to the individual making the choice (the “chooser”; reviewed in Candolin, 2003); or 2) as suites of interrelated characters, in which relationships between traits are as important to the chooser as the traits themselves (e.g., Jennions & Petrie, 1997). We call the former the “prioritized traits” approach and the latter the “integrated traits” approach, acknowledging that these terms of convenience are imperfect. A central aim of our analysis is to learn whether individuals choosing mates seem to take a prioritized, or alternatively a more integrated, approach when evaluating traits of potential partners.

Within the two approaches, patterns of mate choice are often thought to rest on a long-standing model of sexual selection, which links differential parental investment to sex-differences in optimal mating rates (Trivers, 1972). A newer model pays attention to evolutionary feedbacks that can strongly influence sex roles and subsequent patterns of sex-differentiated behavior (Kokko & Jennions, 2008). In this paper we will explore mate choice decision-making by measuring the relative empirical support for the two approaches (prioritized vs. integrated traits) as a function of sex and population-level parameters.

1.1. Why multiple cues?

The emphasis, historically, within the study of mate choice was on the experimental manipulation of a single cue in homogenous environments (reviewed in Gerhardt, 1992). This work, while usefully highlighting the traits which could serve as cues of mate quality, poorly reflected actual animal displays that consisted of multiple cues (e.g., Dale & Slagvold, 1996; Hill et al., 1999; Kodric-Brown & Nicoletto, 2001). Additionally, studies revealed that individual reproductive decisions change by age, condition, experience and context (reviewed in Miller & Svensson, 2014). For example, in a well-known study among lark buntings, Chaine and Lyon (2008) found the traits associated with male pairing success to be highly variable from year to year, highlighting temporal flexibility in female choice. Thus, variation in the social and ecological environment, as well as among individuals, influences which traits are potentially fitness-enhancing, thereby favoring...
multiple signals and reinforcing the need to pay attention to multiple traits (Bro-Jorgensen, 2010).

Additionally, organisms have to make decisions under uncertainty, as individual traits may not be reliable signals of underlying quality or the condition of a potential mate (Brunswik, 1955). Because of this uncertainty, several traits, each related to underlying condition but likely only offering partial information, may need to be attended to. Thus variation in trait priorities, or in how preferences for different traits are combined, may arise due to individual and contextual factors (reviewed in Bro-Jorgensen, 2010).

Mate choice interactions are likely even more dynamic and sensitive to individual and contextual-level variables in species with mutual mate choice and biparental investment (Bergstrom & Real, 2000; Hoofer & Miller, 2008; Johnstone, Reynolds, & Deutsch, 1996; Kokko & Johnstone, 2002). For example, in humans, cues that may signal underlying male quality may also be associated with lower levels of parental investment (due to that male’s attractiveness to a larger number of mates) causing females to make trade-offs over multiple cues when selecting a mate (Scheib, 2001).

1.2. Patterning of choice (prioritized traits vs. integrated traits)

Mate choice studies of humans have successfully documented many important individual traits used in selecting partners (e.g., body mass index, waist to hip ratio, physical attractiveness, social status, kindness, and honesty; reviewed in Gangestad & Scheyd, 2005). The prioritized trait approach is useful for understanding mate selection in terms of the traits that are more or less important to the chooser. However, relationships between the chooser’s preferences across multiple traits may be lost in trait-by-trait comparisons (Miller, 1997). In a classic and approachable example of trait integration, Möller et al. (1998) find, when looking at male traits of song-rate and tail length among barn swallows (Hirundo rustica), that females do not simply have a greater preference for one trait over the other (i.e. they do not find support for a prioritized trait approach). Instead, the importance females place on male song-rate depends on male tail length (see Kodric-Brown & Nicoletto, 2001; Scheib, 2001 for similar findings in guppies and humans respectively).

In general, studies of mate choice take the prioritized trait approach, treating each cue as one of a list of independently relevant characteristics in a potential partner (e.g., Lippa, 2007). However, there is increasing interest in exploring how traits interact in a synergistic manner (Jennions & Petrie, 1997), focusing on variation and covariation in trait preferences. This has led to the integrated trait approach (Miller, 1997), which argues that relationships among traits are essential for understanding mate choice.

1.3. Variables influencing mate choice

The study of reproductive decision-making typically relies on the long-standing model of sexual selection developed by Trivers (1972). This model links mate choice preferences directly to differential investment in young by males and females. In humans, because investment by women is more obligatory (through gestation and lactation), they are expected to pay close attention to a partner’s ability to provide resources. In contrast, contrast, a woman’s reproductive value declines with age, men are expected to pay close attention to physical attractiveness, as it serves as a signal of fertility (Symons, 1979).

Variability in preferences driven by contextual factors and cultural norms (e.g. partner chastity; Buss et al., 1990) has long been acknowledged in studies of mate choice. However, and in line with predictions from traditional sexual selection theory, findings of men’s preferences for physical attractiveness and women’s preferences for traits are quite robust across the literature (Buss, 1989; Buss et al., 1990; Li et al., 2002; Schmitt, 2005; Shackelford, Schmitt, & Buss, 2005). So while gender differences in preferences are not expected across all traits, men’s preferences for reproductive capacity and women’s preferences for investment potential are generally treated as human universals. While the evidence is quite impressive, the methodology and theory underlying these findings can be productively criticized.

First, almost all of the work on human mate preferences has been based on questionnaire responses from college undergraduates (Asendorpf & Penke, 2005; Gray, Heaney, & Fairhall, 2003; Griffiths, 2001; Laland & Brown, 2011), generally from the US or western Europe. These populations are relatively easy to sample from and are worthy of study, however the generalizability of findings from such samples can be questioned (Henrich, Heine, & Norenzayan, 2010; Smith, Borgerhoff Mulder, & Hill, 2001). Additionally, some studies that purport to be cross cultural (Buss, 1989; Schmitt, 2005) draw on university students in developing nations, who may be even less representative of their local populations (Beckerman, 2005). Studies that do look outside the west generally find results counter to conventions: for example, among the Shuar (Pillsworth, 2008) and Hadza (Marlowe, 2004) there was little support for a difference between men and women in preferences for physical attractiveness. Additionally, a recent study using data from 12 societies, both industrialized and non-industrialized, found no consistent gender differences in partner preferences (Scott et al., 2014).

Second, a reformulated theory of sexual selection critiques the simplistic labeling of reproductive roles by gender based on inherent sex differences in parental investment (Kokko & Jennions, 2008). As in nonhumans (Clutton-Brock, 2007), patterns of sexual selection on men and women can be highly variable (Borgerhoff Mulder, 2008; Brown, Laland, & Mulder, 2009; Scelza, 2011). Reproductive strategies are not an invariant, species-specific characteristic, but rather facilitative responses to individual- and population-level social and ecological circumstances (e.g., Nettle, 2009; Owens & Thompson, 1994; Szekely, Webb, & Cuthill, 2000) requiring conditional decision-making (Gangestad & Simpson, 2000; Nettle, Coall, & Dickins, 2011).

To counter concerns of (1) western overrepresentation and (2) simplistic parental investment models, we conduct our study among the Makushi of Guyana, measuring the support for a sexual selection framework in which evolutionary feedbacks are predicted to influence sex roles and subsequent patterns of sex-differentiated investment in mating effort (Kokko, Klug, & Jennions, 2012). A key feature of this framework is its game-theoretical foundation (Kokko & Jennions, 2008), in which sex roles are partly determined by the relative scarcity of the sexes (e.g. Fromhage, Elgar, & Schneider, 2005). As a consequence, sex-structured pay-offs depending on the adult sex ratio (ASR) generate predictions of sex-differentiated behavior. For example, when females are in surplus, males may be able to leverage their relative scarcity, behaving promiscuously and offering little parental investment yet still obtaining mating opportunities. In contrast, when females are scarce, males may need to show a commitment to marriage and family in order to secure mating opportunities. The adult sex ratio is therefore expected to play an important role in the patterning of preferences (Schacht, Rauch, & Mulder, 2014; see Table 1). While some authors have explored sex ratio effects on reproductive decision making (Pedersen, 1991; Schmitt, 2005), they nevertheless assume that sex ratios will impact mating strategies as proposed by PI theory

<table>
<thead>
<tr>
<th>Traits of greatest importance to males and females choosing partners, according to traditional and reformulated sexual selection theories.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Traditional (sex)</strong></td>
</tr>
<tr>
<td><strong>Males</strong></td>
</tr>
<tr>
<td><strong>Physical attractiveness, faithfulness</strong></td>
</tr>
<tr>
<td><strong>Shifted ASR</strong></td>
</tr>
<tr>
<td><strong>Resources, social status</strong></td>
</tr>
</tbody>
</table>

Desired partner traits are in italics.
Table 2
Models and their predictions.

<table>
<thead>
<tr>
<th>Cognition underlying mate choice</th>
<th>Integrated traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intervening variables (variables patterning the variation)</td>
<td>Suites of traits widely important by community</td>
</tr>
<tr>
<td>Community</td>
<td>Differences in importance of individual traits by context</td>
</tr>
<tr>
<td>Sex</td>
<td>Differences in importance of individual traits by sex</td>
</tr>
<tr>
<td>ASR × Sex</td>
<td>Differences in importance of individual traits by sex and ASR</td>
</tr>
</tbody>
</table>

A community effect is included in all models, and the fixed effect for sex is included in models containing the ASR × sex interaction. Thus, a nested sequence of increasingly complex models is produced by moving from top to bottom in the table.

(Emlen & Oring, 1977), namely that men will invest more in mating effort when they are more numerous than women.

The predictive variables and contrasting approaches for patterning choice can be thought of as existing in distinct theoretical domains. The traditional sex-based and newer evolutionary feedback frameworks are both compatible with either the prioritized or integrated trait approaches. For example, integrated traits may be strongly patterned by sex alone, or prioritized traits may be best explained by both sex and ASR.

We will measure the support for models of mate choice involving nested combinations of a) community effects, b) sex, and c) ASR, in two ways (prioritized vs. integrated traits; Table 2). In doing so, we not only examine variables that influence mate choice but also tackle the newer issue of how humans evaluate traits in potential partners: as separate pieces of information or as an integrated package.

2. Methods

2.1. Study population

The Makushi inhabit the Rupununi savannas of south-western Guyana, region 9. Living along the border with Brazil, this ethnic group shares many cultural traits with other groups from the Xingu Basin. These include shifting cultivation, a focus on bitter cassava, matrilocality, marriage, the performance of bride-service before marriage, and fairly egalitarian gender relationships (Schacht, 2013). While premarital sex is not disapproved, and is an expected avenue to secure a partner (Myers, 1993), the Makushi generally marry monogamously and extended families typically share one residential area (Forte, 1996). Makushi marriages are generally endogamous, in that mates are usually selected from within the village community (Myers, 1993). As elsewhere in Guyana, outmigration has led to considerable between-community variation in ASR, as men and women search for economic opportunities. Principle activities for men are mining, cattle ranching, agricultural work and logging, activities which occur mainly in the more remote areas of the Rupununi or in the forested regions at the center of the country, whereas women are attracted to urban areas (such as the capital of Roraima in neighboring Brazil) and the larger interior Guyanese towns (such as Lethem) in search of shop and domestic work (Gafar, 2004).

Community-level ASR strongly structures marital options for endogamous marriage, but men are still expected to perform bride-service in order to marry. This traditionally involved a year of service by the prospective husband, in which he clears and farms fields for his in-laws while building a new dwelling nearby for himself and his wife. Men and women typically marry only once or twice, and conventions are similar across all marriages, with men providing bride-service and thereafter bearing considerable responsibility to provide for their wives and children (including stepchildren who are valuable helpers) through farming, fishing and various forms of wage labor (Myers, 1993). At divorce, children remain largely the responsibility of the mother and her family (although a father may take sons) but are expected to be provided for by a stepfather if the mother remarries.

2.2. Data collection

We conducted the mate choice preference survey across eight Makushi communities (Fig. 1). We first conducted a full census to determine the community composition. We then randomly sampled a minimum of 30 individuals from each village for a total of 148 men and 152 women aged 18–45 (Table 3). We asked respondents to answer questions regarding the importance of partner traits operationalized through 10 items: financial resources, physical attractiveness, faithfulness, parenting qualities, social status, health, desire for children, devotion, hardworking, and strength of family bonds. These traits were selected based on their ubiquity in the mate-choice literature (see Bustom & Emlen, 2003) and pilot-tested to ensure cultural appropriateness. Respondents rated each item with an item score, using a five-point scale (1 = not at all important, through 5 = very important). In order to minimize response bias and other potential data-quality problems, our study protocol incorporated: a) a long (16 month) period of fieldwork during which community rapport could be built across each of the villages, b) gender-matched interviewers and interviewees and c) the use of a nonverbal response card method (Lindstrom et al., 2010) to guarantee the privacy of the interviewee’s response, even from the interviewer. Furthermore, we asked questions using regional colloquial language, after pilot-testing the wording of questions for salience. In this way we tried to make sure respondents understood what was being asked of them.

Table 3
Descriptive statistics for each community.

<table>
<thead>
<tr>
<th>Community</th>
<th>ASR</th>
<th>Men/Women (18–45 years)</th>
<th># Men interviewed</th>
<th># Women interviewed</th>
<th>Total population</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0.93</td>
<td>125:135</td>
<td>29</td>
<td>29</td>
<td>745</td>
</tr>
<tr>
<td>H</td>
<td>1.11</td>
<td>70:63</td>
<td>15</td>
<td>15</td>
<td>415</td>
</tr>
<tr>
<td>F</td>
<td>1.13</td>
<td>70:62</td>
<td>15</td>
<td>15</td>
<td>407</td>
</tr>
<tr>
<td>E</td>
<td>1.16</td>
<td>87:75</td>
<td>18</td>
<td>19</td>
<td>596</td>
</tr>
<tr>
<td>G</td>
<td>1.22</td>
<td>73:60</td>
<td>20</td>
<td>20</td>
<td>432</td>
</tr>
<tr>
<td>D</td>
<td>1.33</td>
<td>80:60</td>
<td>19</td>
<td>19</td>
<td>406</td>
</tr>
<tr>
<td>B</td>
<td>1.35</td>
<td>72:20</td>
<td>15</td>
<td>15</td>
<td>162</td>
</tr>
<tr>
<td>C</td>
<td>1.43</td>
<td>57:40</td>
<td>17</td>
<td>20</td>
<td>310</td>
</tr>
</tbody>
</table>
2.3. Statistical approach

In order to weigh the evidence in our sample for different notions about the cognition underlying mate choice, we evaluate the relative support for nine theoretically-informed models fitted to the observations. Here, and in the Supplementary Online Materials S1–S4 (available on the journal’s website at www.ehbonline.org), we describe our approach to estimation and comparison of prioritized trait models (I–III) and integrated trait models (IV–IX). All models are fitted by computationally-intensive Bayesian methods. Bayesian methods are a practical (more than an ideological) choice here, for two main reasons: 1) the models are relatively “large”, containing many parameters to infer, yet our main interests lie in a small subset of these parameters or in whole-model comparisons; 2) the integrated trait models (IV–IX) present problems of identification (see S2), which can be partly remedied by appropriate choices of prior distributions. Computational Bayesian methods naturally accommodate these needs. All models I–IX contain basic linear equations (see S1) of familiar regression form.

2.3.1. Prioritized traits

Within the prioritized trait approach we consider three nested ordered logit models (community, sex, and ASR; Table 2; S1). Ordered logit regression models are used when the responses — here, item scores — are ordered categories. All items and individuals are included in each model. The direction and magnitude of effects in these models are allowed to vary freely and are unique to each item. For example, we do not require sex-specific differences in the importance of social status and financial resources to conform to expected patterns of strong female preference (e.g., Buss, 1989; Shackelford et al., 2005; Stewart, Stinnett, & Rosenfeld, 2000). However, if those preferences do exist in the sample they will be reflected by the estimated effects. We take this approach in order to give models the greatest latitude to find sex differences if they exist.

2.3.2. Integrated traits

Here we consider six models using a dimension reduction approach. In using dimension reduction, we assume that an individual’s response profile expresses interrelated preferences across items that can be reduced to a smaller number of variables. These variables are unobserved, and we refer to them as latent traits; they are theoretical constructs analogous to intelligence or leadership ability (e.g., Gardner, 1983; Stogdill & Coons, 1957). It is unclear whether dimension reduction of interrelated preferences should aim for a unidimensional or multidimensional trait. For example, is one axis ranging from low to high adequate to explain variation in response profiles? Previous findings suggest that this may be overly simplistic (Botwin, Buss, & Shackelford, 1997) and that there may be multiple axes in play (e.g., individuals may be placed low on one axis yet high on another). Accordingly we examine both one and two dimensional models. We return to the question of additional dimensions in the Discussion.

A traditional dimension reduction approach used in psychometrics is factor analysis. This is most suitable when the observed variables — here items — have Gaussian distributions. However, a preliminary check showed that ordinary factor analysis would be a poor choice for our sample: the item score distributions are discrete and very skewed (see Fig. 2); and the variance/covariance matrix computed from the item scores had several negative eigenvalues. A slightly better option is to build a factor model on the polychoric correlation matrix, which treats the item scores as thresholded continuous variables (Grilli & Rampichini, 2003). However, again the matrix was ill-conditioned, and it was clear that an approach better suited to our ordinal variables was needed.
Item response models were developed by quantitative psychologists due to the need for appropriate dimension reduction techniques for data sets sharing features of ours (Hambleton, Swaminathan, & Rogers, 1991). Like factor analysis, item response models contain a linear prediction equation involving one or more latent variables, and aim to connect variation and covariation in the observed variables to the latent variables. However, unlike factor analysis, an appropriate link function is required to transform the linear predictor to the scale of the manifest variables. The item response model establishes the position of each individual in a latent space, and derives probabilities of responses to multiple observed manifest variables as a function of item parameters and the individual’s position in the space. Essential to the questions at hand is the possibility to include fixed effects, such as sex and ASR, as well as contextual (“random”) effects in the linear predictor (see Table 2 and S1). This facility allows us to estimate the effects of community, sex and ASR on the latent trait. Bayesian methods built on Markov Chain Monte Carlo (MCMC) algorithms make it possible to fit and compare these item response models (structured as in Table 2; Zhu & Stone, 2012).

### 2.3.3. Community effects

All community predictors in Table 2 are random intercepts, included to capture unmeasured community-to-community heterogeneity in trait preferences. The intercepts are community-specific (as well as trait-specific in the prioritized trait models), and act to adjust community-average preferences to a theoretical population baseline. These predictors are “unstructured”, in the sense that they are not derived from direct measurements of community-level variables such as ASR. They can be used interpretively to ask whether unobserved community-level (“contextual”) factors may act as important sources of variation in preferences. We understand the inclusion of community random effects to be both facilitated, and required by, the multi-level nature of our dataset (consisting of individuals nested within eight communities). Merlo et al. (2005) motivate the use of community random effects as tools for detecting contextual phenomena in datasets of similar form.

### 2.3.4. Model comparisons

We perform posterior predictive calculations, consequently producing evidence ratios and model weights, in order to compare the relative support for models I–IX (see Ntzoufras, 2009 sections 10.4, 11.10). We understand comparison of the different models — which themselves mirror different notions about how mates are chosen — as an attractive alternative to traditional hypothesis testing. This weight-of-evidence strategy keeps all models in play, but highlights those that are better supported by the observations. Gelfand, Dey, and Chang (1992) give a rationale for the specific approach to model comparison used here, and point to advantages provided by computational Bayesian estimation. The basic quantity calculated is a conditional predictive ordinate (CPO) for each observed person-and-item score (see S4). COPs are specific to each model, and can be combined across persons and items to produce model-wide summaries broadly analogous to information measures such as the deviance information criterion (DIC; Spiegelhalter et al., 2002).

### 3. Results

#### 3.1. Item score distributions

To begin our investigation we examine the item score distributions by sex (Fig. 2). What is initially striking is that the modal response for all items, except desire for children, is “very important”, the highest category. A visual inspection suggests that preferences vary by sex (males in light gray, females in dark gray) for at least some traits: more men than women rate physical attractiveness as “very important” and more women than men rate financial resources and strength of family bonds as “very important”. The frequent use of the response “very important” produces highly skewed score distributions for most items and pre-empts the use of traditional analytic tools built on Gaussian distributions (such as factor analysis). Sampling strategies involving “forced choices”, in which respondents rank items in order of importance or allocate points to each item out of a fixed total, may help to circumvent such ceiling effects. The ordered logit and item response models we use here are not troubled by ceiling effects, provided that item scores are at least moderately variable.

Fig. 2 aggregates responses for each item across individuals by sex, in effect breaking each person’s multivariate response profile (consisting of a sequence such as financial resources = “very important”, physical attractiveness = “fairly important”, etc.) into univariate parts. Looking at Fig. 2, it could be imagined that a small number of common response profiles are shared by many individuals, but this is not the case: each of the n = 300 response profiles in the sample is unique. We understand this to mean that preferences do indeed vary across the sample, and that individuals evaluated how their preferences differ across traits.

#### 3.2. Model comparisons

In Table 4 we display pseudo Bayes model weights, which allow us to compare the relative support for each model. Our principle finding is that the prioritized trait models (I–III) and unidimensional (1-D) integrated trait models (IV–VI) are not competitive when compared to the two dimensional (2-D) integrated trait models (VII–IX; Table 4). Of the 2-D models, model VII, with random effects for community, is the best-supported model. Notably, our best model does not include the respondent’s sex as a predictor of preferences, even though sex has been found important in many previous studies of mate choice. An additional surprise is that models containing the adult sex ratio as a predictor are relatively uncompetitive, in spite of recent findings showing a relationship between mating effort and ASR in this population (Schacht & Borgerhoff Mulder, 2015).

#### 3.3. What about sex differences?

In mate-choice studies, sex is often argued to be a primary determinant of reproductive strategies. Here we examine this claim, investigate the relationship between sex and trait preferences in our sample and offer an explanation as to why sex is not a predictor in our best model.

##### 3.3.1. Prioritized trait models

According to the prioritized trait approach, each trait is one of a list of independently relevant individual characteristics. Within this approach we measure the effects of three variables (community, sex, and ASR; Table 2). Based on logCPO values (Table 4), model II, with a unique

<table>
<thead>
<tr>
<th>Model</th>
<th>logCPO</th>
<th>ΔlogCPO</th>
<th>Model weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>I (Community)</td>
<td>-3580.0</td>
<td>-307.1</td>
<td>0.000</td>
</tr>
<tr>
<td>II (Sex)</td>
<td>-3558.3</td>
<td>-285.4</td>
<td>0.000</td>
</tr>
<tr>
<td>III (ASR)</td>
<td>-3651.1</td>
<td>-288.2</td>
<td>0.000</td>
</tr>
<tr>
<td>IV (Community)</td>
<td>-3000.9</td>
<td>-280.9</td>
<td>0.000</td>
</tr>
<tr>
<td>V (Sex)</td>
<td>-3298.6</td>
<td>-25.7</td>
<td>0.000</td>
</tr>
<tr>
<td>VI (ASR)</td>
<td>-3299.2</td>
<td>-26.3</td>
<td>0.000</td>
</tr>
<tr>
<td>VII (Community)</td>
<td>-3272.9</td>
<td>0.0</td>
<td>0.921</td>
</tr>
<tr>
<td>VIII (Sex)</td>
<td>-3275.6</td>
<td>-2.7</td>
<td>0.002</td>
</tr>
<tr>
<td>IX (ASR)</td>
<td>-3276.9</td>
<td>-4.0</td>
<td>0.017</td>
</tr>
</tbody>
</table>

LogCPO is calculated for each model as described in S4. Models are nested within classes; for example, model IV is nested within models V and VI in the class of integrative 1-dimensional models. Δlog CPO is the natural logarithm of the pseudo Bayes factor (a type of evidence ratio) for each model compared to model VII, the best-supported model in the set. Pseudo Bayes weights are calculated from Δlog CPO as described in S4. Model weights may exaggerate the support for model VII in comparison to the other two-dimensional models (VII and IX). The logCPO scores of the 2-D models are very similar; however model VII is the best model by a small amount.
sex effect for each item, is the best of the three prioritized trait models (ordering the logCPOs of models I–III from most- to least-negative produces an ordering of least-supported to best-supported models). This is a reassuring finding given the apparent sex differences in several item score distributions (Fig. 2). In Fig. 3 we display estimated linear predictors for item scores in model II. For a given item the linear predictor is the sum of a community effect and a sex effect (see S1). Items rated higher by males tend to have positive linear predictors whereas those rated higher by females tend to have negative linear predictors. Although most of the variation in item scores is attributable to community effects, we nonetheless recover sex differences for three items: strength of family bonds, financial resources, and physical attractiveness (the first two have a higher female rating and the last has a higher male rating). For each of these items, the sex effect ($\alpha_i$), an additive term in the linear predictor, is statistically well supported and distinguishable from zero. We have thus confirmed, within the prioritized trait approach, two key predictions of PI theory following Buss et al. (1990): females prefer partners who can provide resources, and males prefer physically attractive, fertile partners. While high female ratings for strength of family bonds are not suggested by PI theory, they do fit quite neatly with a general reliance of Makushi women on extended kin to meet household resource needs.

3.3.2. Integrated trait models: one latent dimension

Under the 1-D approach, item responses are functions of a single latent variable capturing interrelated preferences. Among the 1-D models, the model with community and sex effects (model V) is best supported by logCPO (Table 4). Here the apparent utility of sex as a predictor resembles our finding from the prioritized trait approach.

To continue our evaluation of sex and its effects on preferences, we turn to Fig. 4. Here we show the response probability curves for the item physical attractiveness in the top panel and densities of the latent variable by sex and location in the bottom. Physical attractiveness was selected because mate-choice studies typically find a robust sex difference in preferences for this trait, and because we found a sex effect for this item using the prioritized trait approach. For each value on the horizontal axis (lower panel), the curves of the upper panel give the probabilities of each response option. Therefore a person with a position close to 0 on the latent trait will respond “very important” with probability near 0.5, and “fairly important” with probability near 0.3. The superimposed densities of the bottom panel show where male and female respondents of each community lie on the axis. Left-to-right shifts of the densities reflect sex and community differences in placement along the axis. The response probability curves for other items will vary depending on item-specific parameters; but because the latent variable and the male–female contrast $\alpha$ are shared across items in the 1-D model, the lower panel is the same for all items.

We see considerable overlap in the distributions of males and females across communities. If male–female differences were large and communities were not important sources of variation, we would see two sets of distributions, well separated by sex but indistinguishable by community. Instead, in this sample demanding individuals of either sex find physical attractiveness “very important” in a partner. Thus, if the goal is to predict the importance of physical attractiveness, the sex of the respondent is of limited value.

3.3.3. Integrated trait models: two latent dimensions

Fig. 5 shows response probability curves for physical attractiveness and densities for the two latent dimensions of the 2-D model with sex. As a feature of the model, the response probability curves for physical attractiveness, as well as the densities, are different for dimensions one and two. As for the 1-D model, within a dimension the latent variable and the male–female contrast are shared across all items, while the response probability curves vary across items as a function of item-specific parameters. A slight separation between male and female densities is present in dimension 1, but sex differences are
difficult to detect in dimension 2. Physical attractiveness tends to be “very important” to individuals positive on dimension 1; interestingly, a few female respondents occupy the positive extremes of this dimension. The polarity is reversed along dimension 2, where individuals in the positive extremes appear to be relatively indifferent to physical attractiveness in a potential partner. As in the 1-D model, sex is of limited value in predicting placement along the axes.

3.4. The “best” model: 2-dimensions with community effect

While we have focused on the predictor sex, our best model (model VII) does not include it. To understand this result graphically we turn to Fig. 6. Here we plot individual placement along the two dimensions, for the 2-D model including only random intercepts for community. We do not see distinct groupings by sex, as would be expected if the sex of the respondent were informative about their position in the latent space. Instead the latent positions of males and females appear to be well mixed across the two dimensions. We return to model VII interpretively in the next section.

4. Discussion

Our findings address two questions outlined at the beginning: 1) How can we better describe the decision-making process of individuals choosing mates (prioritized vs. integrated traits)? and 2) Which variables (community, sex, ASR or some combination thereof) best predict mate preferences? In answer to question 1, and in line with researcher calls for exploring the interaction of multiple cues (e.g., Miller & Svensson, 2014), we find strong support for preferences built upon trait integration. Regarding question 2, we detect meaningful variation in preferences, but find that neither the traditional nor reformulated models of sexual selection persuasively explain the observations.

Our best model (model VII) includes community-level random intercepts within two dimensions of preference. Fig. 7 gives a schematic interpretation of model VII based on response profiles for virtual individuals in the four quadrants (indicated by light grey vertical and horizontal lines). We label the horizontal dimension (D-1) “general demand” because positively placed individuals are more likely to use the response option “very important” when rating items. However, individuals negatively placed in D-1 are not simply undemanding, but instead are selective in their preferences, rating some traits “very important” but other traits notably less important. Therefore the two dimensions should not be interpreted independently of each other. We label the vertical dimension (D-2), “natal tendencies”, with individuals positive on the dimension rating the desire for children as “very important”.

![Fig. 5. Model VIII, 2-D sex: response probability curves for the item physical attractiveness along with community- and sex-specific densities for the latent variables on dimensions 1 and 2. These graphs display model VIII, but details of their construction are as in Fig. 4.](image)

![Fig. 6. Model VII, 2-D community: individuals are plotted by posterior means of the latent traits (λ̂, φ̂) and shaded by sex.](image)
In general, individuals positive on D-1 rate traits “very important”. Here are our interpretations of these individuals based on their placement along D-2:

1. Individuals positive on both dimensions find all items “very important”. These are demanding individuals wanting a partner who “has it all”.
2. Individuals positive on D-1 but negative on D-2 find all items “very important” except desire for children, which is “not at all important”. A desire for a family is not driving these individuals’ mate choice decisions, partner quality is.

Individuals negative on D-1, are not demanding across all items. However, this is not to say that they are generally unchoosy: devotion, parenting qualities, health and hardworking are consistently rated as “very important”. However the importance of other traits depends on their placement on D-2:

1. Individuals negative on D-1 but positive on D-2 find, in addition to the traits outlined above, desire for children and faithfulness in a partner “very important”. We understand these individuals to prefer mates exhibiting “Partner and Child Commitment”.
2. Individuals negative on both dimensions, find family bonds “very important” and desire for children “not at all important”. We understand these individuals to prefer “Kin Support”.

What we uncover through an examination of the quadrants is not a simple story about choosy vs. unchoosy individuals. Instead, and especially for those negative on D-1, we see mixed preferences, with some key traits being ”very important” while others are not.

It is possible that more than two dimensions are needed to fully characterize mate preferences. A preliminary check in this sample suggested, however, that very little could be learned by adding a third dimension. In trial computing experiments, we found that person- and item-specific parameters for a third dimension reproduced those of the first or second dimension (bringing to mind a repeating mirror). Although we cannot rule out the existence of additional dimensions of mate preference (especially in other samples) we believe that two dimensions are adequate for these data, and that three or more dimensions would unduly strain the available variation.

In response to question 2, we find that community random effects best explain patterning in preferences. Sex is often argued to be a primary determinant of reproductive strategies due to potential differences in optimal mating rates, leading women to place a greater importance on cues that signal ability to acquire resources and men to place a greater importance on cues that signal fertility and reproductive value (e.g., Buss, 1989). Had we concluded our analysis after fitting only the prioritized trait models, we would have confirmed yet again the importance of sex (model II). Sex differences in three traits align in the predicted direction (see Fig. 3).

Sex differences are not unimportant in Makushi reproductive strategies, but they are likely not as straightforward as conventionally argued. The Makushi offer a useful comparison to “typical” studies of mate choice focusing on college undergraduates in western industrialized settings (Henrich et al., 2010). In the west, cultural institutions create traditional sex roles where males control most of the resources (Eagly & Wood, 1999). Unsurprisingly, this is also associated with robust and consistent sex differences across mate choice studies. The Makushi are quite different. Kinship is matrilineal, marriage is matrilocal, and men must perform bride-service in order to marry (Schacht, 2013). Makushi women generally provide most calories for subsistence, and as a consequence sex roles are quite egalitarian, with women having considerable power in household decision-making. The relative economic autonomy of Makushi women may explain why preferences do not diverge strongly across the genders; instead, situationally-dependent preferences may be adopted by both males and females (Fig. 7).

Similar work among the Shuar of Ecuador finds that resource preferences are patterned by community market integration (Pillsworth, 2008). Like the Makushi, the Shuar are traditionally matrilineal and matrilocal with subsistence centered on cassava propagation and female food production and processing. Pillsworth found that in a traditional village, where families depend on women’s food production, men expressed a greater preference for partner resource provisioning than did women. In the market integrated village, where families were heavily dependent on purchased goods, western-style ‘traditional’ preferences emerged. Therefore, put plainly, preferences for a resource-provider do not seem to be rigid and simply based on sex, but instead vary facultatively based on who provides the bulk of the resources in a particular community.

Newer sexual selection models show as well that sex does not automatically act as a predictor of behavior, because sex roles coevolve with sex-structured pay-offs to mating strategies, time spent in parental care and sex-biased mortality differentials (Kokko et al., 2012). We hypothesized that sex might be an important predictor of preferences in interaction with ASR, based on earlier work (Schacht & Borgerhoff Mulder, 2015) investigating mating effort among males. However, ASR contributed essentially nothing to the models here. It seems that partner preference is less sensitive than mating effort to the availability of partners. Why? This is an open question, but it may be that the traits of an ideal mate are those associated with successful long-term relationships. These traits may be related to ecological conditions that are possibly less labile over time, thus unlikely to change with short-term fluctuations in ASR. What we can say, however, is that predictions based only on sex and partner availability are inadequate.

Social scientists should welcome this attention to variable sex roles insofar as cross-cultural variability in human reproductive and mating behavior seems to be the rule rather than the exception (Brown et al., 2009). It has long been argued that sexual stereotyping arises from models inappropriately linking men’s and women’s reproductive strategies to the constraints of parental care (Eagly & Wood, 1999; Gowaty, 1997; Hrdy, 1997). Several studies have tested alternative models for mate preferences and have found that income inequality (Eagly & Wood, 1999), cultural affiliation (Boyd & Silk, 2006), self-ratings (Buston & Emlen, 2003), socioeconomic status (Buss, 1989) and trait matching (McClintock, 2014) are often better predictors of
preferences than gender. Thus, the apparent robustness of gender differences may be an artifact of the focus on gender at the expense of other, possibly more meaningful, variables.

Subsequently to our main investigation, we explored three individual-level variables: age, income, and relationship status (the latter at the suggestion of a reviewer); and one community-level variable: market integration. These post-hoc checks were not included in our planned analyses, so we understand them to serve an interpretive, rather than inferential, function.

Age and income did not appear to be related to placement in the D-1/D-2 latent space, but some patterning with relationship status can be seen (Fig. 8). Single individuals tend to be negative on D-1, therefore perhaps less demanding of a potential mate, having a smaller set of traits that are deemed to be “very important”. Both Makushi men and women desire to secure a long-term marriage partner (Myers, 1993; Schacht, 2013). A stable partner is not only necessary to meet household needs according to the gender division of labor, but also to gain respect from community members as a result of reaching adult status. Unmarried individuals in our sample may have traits that make them less attractive as marriage partners, in contrast to married individuals who were desirable enough to secure a mate. Numerous studies have found that individuals express preferences for, and pair with, mates of similar value across traits (Buss, 1989; Buston & Emlen, 2003; McClintock, 2014; Stevens, Owens, & Schaefer, 1990). Additionally, individuals who score favorably on a particular trait are even more discriminating in their preferences for that trait in a partner (Buss, 1989; Buston & Emlen, 2003). Positive assortative mating (reviewed in Buller, 2005) for mate quality may help to explain why single individuals in our sample appear to have less stringent preferences.

Next, we turned to a community level variable: market integration (i.e. reliance on wage labor), measured as community distance to the regional capital. A display of individuals, shaded by community membership, reveals moderate but detectable clustering of light and dark points (Fig. 9). In the lower left quadrant we see lighter shading: these individuals live in communities farther away from wage labor opportunities. They are also characterized by desiring kin support (i.e. they rate strength of family bonds to be “very important”: Fig. 7). The lack of available wage labor opportunities, which can provide a buffer in times of resource shortage, may cause individuals in these communities to be more reliant on their extended families to meet household needs. Turning to the upper right quadrant, we find a greater concentration of darker points (these individuals tend to be in closer proximity to wage labor). These are also individuals who tend to rate all items as “very important”. These preferences may be in response to relatively recent market integration and the need to pay attention to many traits because of uncertainty about the relationships between traits and mate quality in novel environments (see Candolin, 2003).

Additionally, individuals in communities closer to the regional capital are generally more pronatal. This is surprising and is counter to typical predictions from both competitive market and demographic transition models (e.g., Kaplan 1996). Generally, as population measures of market integration increase, natal preferences decrease due to the importance of education and rising costs to having multiple children. However, among the Makushi, success is largely independent of education. Most jobs available for men and women are low-skill, wage labor positions. These jobs therefore are new-found sources of wealth that can be used to support more children. However, over time, as success becomes more tightly linked to education, predictions from competitive market and demographic transition models may hold, as individuals begin investing more in fewer children as opposed to many.

In sum, neither sex nor its interaction with ASR is included in our best model; this appears to be because community-to-community variation dominates other factors predicting mate preferences. While the drivers of community-level variability are yet unknown, we do uncover “types” of preferences from the two-dimensional model. Some individuals make very few concessions when choosing a partner, whereas others are selective, targeting differing combinations of the 10 traits. Additionally, or more precise, measures of individual- (e.g. mate value) and population-level (e.g. market integration) variables may help to more clearly explain trait preferences and their integration into the patterns we observe.

5. Conclusion

Integrative trait models allow us to ask which variables predict preferences as well as examine relationships between preferences for different traits. We recover two underlying dimensions explaining variation in preferences: a general-demand dimension and a pronatal dimension. A model in which unstructured community-level effects
predict individual placement on these dimensions is better-supported than models incorporating more familiar predictors of trait preferences. Changes in social and ecological environments, as well as uncertainty about traits that accurately signal partner quality, may prompt individuals choosing a mate to use different combinations of traits in different contexts. These ephemeral sources of variation may contribute to the low repeatability, or what may be labeled ‘noise’, in preferences that we see across mate choice studies (Candolin, 2003; Jennions & Petrie, 1997). Our study highlights the need to incorporate unstructured variation (random effects) in predictive models along with more traditional individual and contextual covariates (fixed effects). Unstructured variation could arise from community-level heterogeneity as here, or from unmeasured time-varying factors in a longitudinal study (Chaine & Lyon, 2008).

Optimal mating strategies are likely influenced by sex-specific payoffs to behaviors, but assortative mating and situationally-dependent factors could result in an apparent lack of sex differences in preferences. The robust literature surrounding sex differences largely makes use of a prioritized trait approach that may miss much of the relevant complexity underlying partner choice decision-making. We do not claim that sex differences found in previous studies are ‘wrong’, as far as they go. But, as we have shown here, these studies may be methodologically incapable of revealing the rich tapestry of factors necessary to predict situationally-dependent mating behavior.

We have investigated an alternative model for mate choice in humans (the integrated trait model), and have compared it to a more conventional prioritized trait model, using computational Bayesian methods. In this sample the integrative model performs markedly better than the prioritized trait model. We believe that the underlying psychology shaping mate choice is unknown and open to investigation; however, we offer the integrative approach as a promising way to understand mate choice. The weak support for sex differences is not unexpected in this sample, given the background ethnography and previous findings for this population (Schacht & Borgerhoff Mulder, 2015). Perhaps most interesting is the fact that the patterning of mate choice may be related to community membership – possibly more specifically to market-economy access – suggesting a direction for further investigation.

Supplementary materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolveumbehav.2015.05.001.

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