Original Article

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

A B S T R A C T

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, selection of 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 & Slagsvold, 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; Hooper & 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, Moller 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, because 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 resources 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 critiqued.

First, almost all of the work on human mate preferences has been based on questionnaire responses from college undergraduates (Aspendorf & 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, 2009; Brown, Laland, & Mulder, 2009; Scelza, 2011). Reproductive strategies are not an invariant, species-specific characteristic, but rather facultative 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 1
Traits of greatest importance to males and females choosing partners, according to traditional and reformulated sexual selection theories.

	Traditional (sex)	Reformulated (sex * ASR)	
Males	*Physical attractiveness, faithfulness*	Male-biased ASR: *faithfulness, good parent*	Female-biased ASR: *physical attractiveness, health*
Females	*Resources, social status*	Male-biased ASR: *faithfulness, good parent*	Female-biased ASR: *physical attractiveness, health*

Desired partner traits are in italics.