

Behaviour 151 (2014) 2059-2081

Female mate preference varies with age and environmental conditions

Kurtis R. Munro^a, Nancy J. Flood^a, Ann E. McKellar^b and Matthew W. Reudink^{a,*}

 ^a Department of Biological Sciences, Thompson Rivers University, Kamloops, BC, Canada V2C 0C8
^b Environment Canada, 115 Perimeter Road, Saskatoon, SK, Canada S7N 0X4
*Corresponding author's e-mail address: mreudink@tru.ca

Accepted 13 July 2014; published online 24 September 2014

Abstract

Sexual selection and mate choice are dynamic processes that can be influenced by a variety of environmental and social factors, which have been well studied in a range of taxa. However, in humans, the environmental factors that influence regional variation in preference for mate attributes remain poorly understood. In addition, underlying variation based on individual age may strongly influence mate preferences. In this study, we examined written descriptions of preferred mates from the online dating profiles of 1111 women from 26 cities across Canada. We grouped the words describing preferred mates into four categories: resource holding potential, physical attractiveness, activities and interests, and emotional appeal. We then asked whether variation in environmental (sex ratio, population size and population density), economic (population income) and individual factors (age) predicted variation in the relative importance of these four categories of female mate preference. Sex ratio was the best predictor of preference for the physical attractiveness and the activities and interests of potential mates, with women in male-biased cities placing more emphasis on physical attractiveness and less emphasis on activities and interests. Age was the best predictor of preference for resource holding potential, with younger individuals placing more emphasis on this trait. No factors were strong predictors of variation in preference for emotional appeal, perhaps because this trait was highly valued in all populations. This work supports a growing body of literature demonstrating that mate choice and mate preferences are often dynamic and can be influenced by individual and environmental variation.

Keywords

human, mate preference, sexual selection, resource holding, online dating.

1. Introduction

Sexual selection and mate preferences have been studied extensively across many taxonomic groups (Emlen & Oring, 1977; Johnstone, 1995; Jennions & Petrie, 1997; Petrie & Kempenaers, 1998). A majority of studies have focused on preferred mate characteristics in more or less constant environments with less attention paid to the influence of the environment in which mate choice is occurring. However, sexual signals and associated preferences are often dynamic and can change substantially with differing environmental or ecological conditions (Jennions & Petrie, 1997; Slabbekoorn & Smith, 2002; Wood et al., 2006; Gray et al., 2008; Robinson et al., 2008; Punzalan et al., 2010). For example, variation in environmental factors, such as the presence or absence of predators (Endler, 1980, 1983; Godin & Briggs, 1996; Houde, 1997), climate (Botero & Rubenstein, 2012), social influence (Rebar & Rodriguez, 2013), parasite pressure (Gangestad & Buss, 1993; Lee & Zietsch, 2011) and changes to the physical environment (Grether et al., 2005; Candolin et al., 2007; Little et al., 2007; Gray et al., 2008; DeBruine et al., 2010) may all significantly influence female mate preferences across a variety of taxa. Consequently, the optimal expression of sexually-selected traits and associated preferences can be highly context-dependent (Endler, 1983; Robinson et al., 2008).

One environmental factor that has received considerable attention with respect to its effects on mate choice and population dynamics is population density. Across taxonomic groups, variation in population density has been shown to influence patterns of sexual selection, mate choice, and promiscuity (Kokko & Rankin, 2006; Dreiss et al., 2010). Because large and/or dense populations are often limited in terms of resources, but plentiful in terms of potential mates, competition for both mates and resources can be intense, increasing the strength of sexual selection for high-quality (e.g., competitive) mates that have high resource holding potential (Qvarnstrom & Forsgren, 1998; Jirotkul, 1999a). Another factor that might be expected to produce similar consequences is population sex ratio. Specifically, individuals of the choosier sex might show greater preference for certain traits under conditions in which the less choosy sex is more numerous (Berglund, 1994; Jirotkul, 1999b; Stone et al., 2007; Dreiss et al., 2010). In addition, overall resource availability in a population can affect mate choice, since when resources are limited, mate searching tends to be more costly (e.g., Vitousek, 2009).

Individuals might focus on a variety of attributes when selecting a mate. One trait that has received considerable attention is the ability to win fights and control access to important resources (e.g., food, territories, mates), also known as resource holding potential (Eckert & Weatherhead, 1987; Koskimäki et al., 2004; Kelly, 2008). In humans, resource holding potential may be represented by financial stability, or the ability to acquire financial stability. Although women typically express a strong preference for this trait in long-term partners (Cameron et al., 1977; Pawlowski & Koziel, 2002; Valliant, 2006), the strength of this preference varies, and underlying environmental or economic conditions may influence this variation (McGraw, 2002; Hill & Reeve, 2004; Moore et al., 2006; Moore & Cassidy, 2007; De-Bruine et al., 2010; Anderson & Klofstad, 2012). Other traits of potential partners that have been examined in studies of human mate choice include physical attributes, emotional characteristics, and personal interests (Singh, 1995a, b; McGraw, 2002; Puts et al., 2012; Mautz et al., 2013). To date, most studies on human mate preference have focused on how preferences differ between the sexes (e.g., Bereczkei et al., 1997), among cultures (e.g., Sear & Marlowe, 2009), and between situations in which a short term versus longterm mate is being sought (e.g., Gangestad & Simpson, 2000). However, there has been increasing interest in examining the importance of environmental factors in influencing human mate preference (e.g., McGraw, 2002; Little et al., 2007; Dreiss et al., 2010; Lee & Zietsch, 2011; Anderson & Klofstad, 2012).

In the United States, McGraw (2002) found that female mate preference in humans varied geographically with local environmental factors such as population density and resource demands (cost of living). By examining 'lonely hearts' advertisements (LHAs) in newspapers from 23 cities across the United States, McGraw (2002) found that in more densely populated cities and cities with higher costs of living, in which there was presumably more competition for resources, women expressed a stronger preference for mates with high resource holding potential and placed less emphasis on either emotional attachment or on similarity of personal interests.

A limitation of McGraw's (2002) study, however, was the lack of information provided about the individuals who placed the LHAs. For example, a potentially important factor that was not available from the LHAs he examined was the age of the individual placing the advertisement. Although age may sometimes have limited or no effect on mate preference (Buunk et al., 2002; Schwarz & Hassebrauck, 2012), age-related variation in mate preference was reported by Morgan et al. (2010) and Gil-Burmann et al. (2002) found that females under the age of 40 expressed a stronger preference for physically attractive mates, while females older than this expressed a stronger preference for males with high socioeconomic status. Thus, age may also contribute to variation in the type of mates preferred.

In recent years, with the advent of online dating sites, LHAs have significantly decreased in popularity (Madden & Lenhart, 2006; Valkenburg & Peter, 2007). The majority of people using online dating sites as a way to meet potential partners are 30-50 years of age, and participation does not appear to be related to income or education level (Valkenburg & Peter, 2007). Online personal advertisements provide a wealth of potential data on both stated mate preferences and methods used for mate attraction. In addition, because online advertisements can originate from a broad diversity of geographic locations, which may encompass significant variation in economic and ecological conditions, online advertisements allow us to examine the underlying social, ecological, and environmental factors that may influence variation in both mate attraction and mate preference. Several recent studies have used online advertisements from the United States to examine correlates of mate attraction and mate preference (e.g., Morgan et al., 2010; Klofstad et al., 2011). Most pertinent to this study, Anderson & Klofstad (2012) investigated the relationship between mate preference and a broad range of economic and environmental conditions at the level of zip code and observed a relationship between cost of living and a preference for mates with high resource holding potential (i.e., mates with high incomes). However, this pattern disappeared once the income of the individual placing the advertisement was included, leading the authors to suggest that assortative mating based on income, rather than environmental variation, best explained variation in preference for income. Thus, it is apparent that online profiles can offer a wealth of information about factors influencing variation in mate preferences and mate attraction.

Here, we aim to use information available from online dating advertisements to examine whether environmental (sex ratio, population size and population density), economic (population income) and individual (age) factors predict the mate preferences of females across Canada. We categorized stated preferences into four classes — physical attractiveness, resource holding potential, emotional appeal, and personal activities/interests — in order



Figure 1. Map of Canada showing the locations of the 26 cities included in the study. Point sizes are scaled to the population size of each city.

to test whether the relative emphasis placed on each class was dependent on the above factors. Like the United States, Canada is well-suited to such a study due to an extremely broad geographic distribution of cities, which encompass high variation in economic and environmental conditions (Figure 1).

2. Materials and methods

2.1. Economic and environmental data

The 2011 Canadian census provided data on population size, population density and male/female sex ratio (Government of Canada, 2012) for all cities from which we obtained online personal advertisements (see below). Because median total income for each city was not available from the 2011 census at the time this study was conducted, comparable information (for both sexes combined) from the 2006 census was used (Government of Canada, 2007). Economic and environmental data for all cities are given in Table A1 in the online version of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x. Data were obtained for city centers, rather for than census metropolitan areas, which can include outlying communities with different economic and environmental conditions.

2.2. Mate preference data collection

Mate preference data were collected from freely available online personal advertisements posted on an online dating site, the name of which we keep confidential to protect privacy. Although there are some limitations to the use of online personal advertisements, including possible issues with selfrepresentation (Gibbs et al., 2006; Toma & Hancock, 2010), online dating sites are incredibly popular across socioeconomic groups and appear to offer a fair representation of a large segment of the dating community, with online dating participation being unrelated to either income or education level (Valkenburg & Peter, 2007). The online advertisements that we used included a free-form section in which individuals described the preferred characteristics of potential mates, similar to what was included in the LHAs used by McGraw (2002). In both McGraw's (2002) study and ours, the preferences of each female were quantified by examining the descriptive words she used to express what characteristics she would like in a potential partner. Any selfdescriptive words were excluded unless followed by a statement indicating they were looking for the same characteristics in a mate (e.g., "I am an avid hiker and looking for someone who shares that passion"). We examined the same four sets of male attributes used by McGraw (2002) to classify female preferences: (1) physical attractiveness (e.g., muscular, tall, good-looking); (2) resource holding potential (e.g., college-educated, professional, wealthy); (3) emotional appeal (e.g., kind, affectionate, honest); and (4) personal activities/interests (e.g., hiking, reading, movies). This approach follows previous work done by Deaux & Hanna (1984), Wiederman (1993) and Greenlees & McGrew (1994), and is a highly repeatable method (McGraw, 2002). All descriptive words were categorized by a single observer (K.R.M.). For each female, the words from all categories were summed to find the total number of descriptive words used in her advertisement; following this, the number of words that fell into each of the four categories was divided by the total number of descriptive words she used in order to determine the proportion of

the overall description represented by each of these four categories of male attributes; these categories thus represented four states of a variable (proportion of descriptive words) indicating the relative mate preference of each female who placed an online advertisement.

Economic and mate preference data were collected for 26 cities across Canada, chosen based on the availability of economic and geographic data and to ensure a broad range of population sizes (from 14751 to 2615060 individuals) and geographic locations (Figure 1). Advertisements were collected during 2012 and 2013. Fifty personal advertisements written by self-identified heterosexual females were examined for each city, with the exception of Summerside, PEI and Yellowknife, NWT, for which there were only 42 and 33 such advertisements available, respectively (n = 1275 profiles across all cities). In cases where there were over 50 personal advertisements available, the first 50 were used; there was no apparent order to the profiles on the website. However, in some cases, individuals did not specify preferred characteristics, reducing our sample of stated mate preferences to 1111 advertisements. We then recorded the stated ages of all individuals from their online profiles.

2.3. Statistical analysis

We first wished to determine whether there were significant differences in the number of descriptive words from each of the four categories of male traits (physical attractiveness, resource holding potential, emotional appeal, and personal activities/interests) used by women when describing their mate preferences. We performed a multivariate analysis of covariance (MANCOVA) using the total number of words used in each category in each online advertisement as the response variable, and included city as an independent categorical variable and individual age as a covariate.

Having found significant effects of age and city on the number of descriptive words in each category (see Results), we then wished to determine whether age and economic and environmental factors associated with each city (median total income sex ratio, population size, and population density) predicted variability in the emphasis that females placed on each of four categories. We constructed four categories of mixed models, one for each of the four categories of male traits. Specifically, we used the number of words associated with the particular male trait (physical attractiveness, resource holding potential, emotional appeal, or activities/interests) over the

total number of words in all four categories as a binomial response (i.e., where number of 'successes' was the number of words in that category). We used the binomial family and logit link function, and full models included individual age and population income, sex ratio, size and density as fixed effects, as well as all two-way interactions, and city as a random effect. For each category of model, we then examined all possible subsets of models and ranked them using Akaike's Information Criterion corrected for small sample size (AICc), considering models within 4 AICc units to be competitive (Burnham & Anderson, 2002). Due to the existence of high correlation (r > 0.5) between population size and density, population size and sex ratio, and income and sex ratio, those pairs of variables were never allowed in the same model. Thus, we ranked a total of 39 models for each of the four trait categories, including a null model with only the random effect. Though we performed four separate binomial analyses for each of the categories of traits, it should be noted that the four categories were not entirely independent as they each represented proportions of the total number of descriptive words used in each advertisement. However, we feel that our methods were appropriate in that (1) they allowed us to evaluate multiple predictor variables in a mixed model framework while maintaining interpretability of results, which would have been difficult in a multinomial framework and (2) they are consistent with previous work that analyzed each category separately (McGraw, 2002).

We standardized all fixed effect variables by subtracting each value from the mean and dividing by the standard deviation of that variable prior to analysis. We used R version 3.0.1 (R Development Core Team, 2013) for building and ranking models. We tested models for overdispersion and did not detect any (all p > 0.5), and after excluding models that included both population size and density, population size and sex ratio, or income and sex ratio, there was no evidence of multiple correlation (all r < 0.5).

3. Results

Our analysis included 1111 advertisements from 26 cities across Canada (mean \pm SD: 42.7 \pm 5.1 advertisements per city) which showed a range of median incomes (range \$21459–44567; mean \pm SD \$26486 \pm 4711), male/female sex ratios (range 0.86–1.03; mean \pm SD 0.94 \pm 0.04), population sizes (range 14751–2615060; mean \pm SD 407727 \pm 594159),

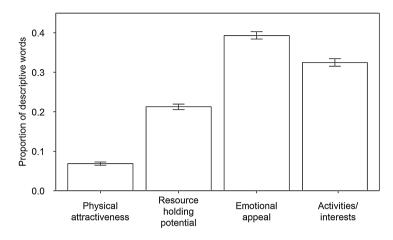


Figure 2. Mean proportion of descriptive words \pm SE used to describe traits of preferred partners from 1111 online advertisements in 26 Canadian cities.

and densities (range 56–5249 individuals/km²; mean \pm SD 1347 \pm 1465). Women who posted advertisements ranged in age from 18 to 80 years (mean \pm SD 40.7 \pm 11.8). On average, women used 5.61 \pm 5.16 descriptive words per advertisement. Out of the four categories of traits sought in male partners, emotional appeal was mentioned most often, followed by activities and interests, resource holding potential, and physical attractiveness (Figure 2). The number of descriptive words from each of the four categories of male traits varied significantly in association with both age ($F_{1,1084} = 10.1$, p < 0.01) and city ($F_{25,1084} = 1.3$, p = 0.015).

Female age and population income, sex ratio, size, and density all appeared in the top models explaining variation in the proportion of words used from each of the four categories (Table 1), as did interactions between age and each other variable and between population size and density, density and income, and density and sex ratio. The relative importance and significance of the variables differed among model categories (Table 2). Model-averaged parameter estimates and associated confidence intervals indicated that women from more male-biased populations placed more emphasis on physical attractiveness (Table 2). Interestingly, this relationship appeared to be associated with population density: an interaction between density and sex ratio suggested that a combination of male-biased sex ratio and high population, an interaction between density and female age indicated

Table 1.

Summary of the top six models explaining variation in preference for physical attractiveness, resource holding potential, emotional appeal, and activities and interests among online dating profiles in Canadian cities.

| Model category | Top model | AICc | ΔAICc | w_i |
|----------------------------|--|--------|-------|-------|
| Physical attractiveness | Age + density + sex ratio + age \times density + density \times sex ratio | 1085.8 | 0.00 | 0.44 |
| | Age + density + sex ratio + age \times density + density \times sex ratio + age \times sex ratio | 1087.3 | 1.47 | 0.21 |
| | Age + density + sex ratio + age \times density | 1087.7 | 1.88 | 0.17 |
| | Age + density + sex ratio + age \times density + age \times sex ratio | 1089.3 | 3.56 | 0.07 |
| | Age + density + age \times density | 1091.5 | 5.74 | 0.03 |
| | Age + density + income + age \times density | 1093.5 | 7.74 | 0.01 |
| Resource holding potential | Age + density | 1081.4 | 0.00 | 0.13 |
| | Age + density + age \times density | 1081.5 | 0.02 | 0.13 |
| | Age + density + sex ratio + age \times density | 1082.8 | 1.39 | 0.07 |
| | Age + density + sex ratio | 1082.9 | 1.46 | 0.07 |
| | Age + density + income + age \times density | 1083.4 | 1.94 | 0.05 |
| | Age + density + income | 1083.4 | 1.94 | 0.05 |

| Table 1. | |
|----------|--|
|----------|--|

(Continued.)

| Model category | Top model | AICc | ΔAICc | w_i |
|----------------------|--|--------|-------|-------|
| Emotional appeal | Null | 1026.9 | 0.00 | 0.09 |
| | Age | 1027.0 | 0.06 | 0.09 |
| | Size | 1027.0 | 0.11 | 0.08 |
| | Age + density + age \times density | 1027.7 | 0.71 | 0.06 |
| | Density | 1027.7 | 0.74 | 0.06 |
| | Age + size | 1027.7 | 0.78 | 0.06 |
| Activities/interests | Sex ratio | 1399.6 | 0.00 | 0.16 |
| | $Age + size + age \times size$ | 1400.1 | 0.50 | 0.12 |
| | Density + sex ratio | 1400.6 | 0.97 | 0.10 |
| | Density + sex ratio + density \times sex ratio | 1400.8 | 1.15 | 0.09 |
| | Age $+$ sex ratio | 1401.0 | 1.40 | 0.08 |
| | Age + density + sex ratio | 1402.1 | 2.48 | 0.05 |

Key words from online profiles of 1111 women from 26 cities were grouped into the above categories, and the models describe the proportion of total key words used that were within that category.

Table 2.

Model-averaged parameter estimates and 95% CI for variables included in the top-ranked models (<4 AICc units of best model) explaining variation in preference for physical attractiveness, resource holding potential, emotional appeal, and activities and interests among online dating profiles in Canadian cities.

| | Physical attractiveness | Resource holding potential | Emotional appeal | Activities/interests |
|----------------------------|-------------------------|----------------------------|------------------------------|---------------------------|
| Age | 0.06 (-0.031, 0.15) | -0.1 (-0.158, -0.043)* | 0.031 (-0.015, 0.078) | 0.016 (-0.035, 0.067) |
| Size | | 0.037(-0.014, 0.088) | -0.027 (-0.07 , 0.016) | -0.046(-0.096, 0.005) |
| Density | 0.029(-0.081, 0.149) | 0.054(-0.001, 0.109) | -0.024(-0.069, 0.021) | -0.025(-0.071, 0.021) |
| Income | | 0.013 (-0.055, 0.081) | -0.005(-0.054, 0.044) | -0.003(-0.05, 0.044) |
| Sex ratio | 0.184 (0.066, 0.302)* | 0.021 (-0.034, 0.076) | -0.009(-0.054, 0.037) | $-0.06 (-0.11, -0.011)^*$ |
| Age \times size | | 0.034(-0.031, 0.099) | 0.0011 (-0.044, 0.066) | $-0.079(-0.138, -0.02)^*$ |
| Age \times density | 0.152 (0.062, 0.241)* | 0.038 (-0.015, 0.091) | -0.035(-0.08, 0.01) | -0.026(-0.073, 0.023) |
| Age \times income | | -0.016(-0.082, 0.049) | 0.01 (-0.039, 0.06) | |
| Age \times sex ratio | -0.029(-0.111, 0.052) | -0.028(-0.083, 0.028) | 0.018 (-0.027, 0.063) | 0.022 (-0.026, 0.07) |
| Density \times income | | 0.038 (-0.06, 0.136) | -0.035(-0.116, 0.046) | |
| Density \times sex ratio | 0.166 (0.006, 0.325)* | -0.011 (-0.085, 0.063) | | -0.045 (-0.111, 0.02) |

* 95% CI did not overlap zero.

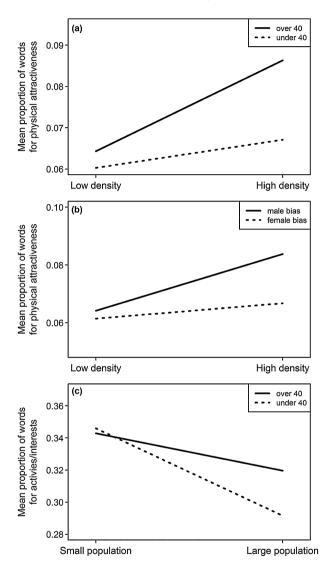


Figure 3. Significant interaction effects from top models explaining variation in preference for physical attractiveness and activities/interests (see Table 2). With increasing population density, (a) older women showed greater preference for physical attractiveness relative to younger women and (b) women from male-biased populations showed greater preference for physical attractiveness relative to women from female-biased populations. With increasing population size, (c) younger women showed lower preference for personal activities/interests relative to older women. For visualization purposes, population density, size, and sex ratio were ranked as high or male-biased if above the median and low or female-biased if below the median, and age was divided by women over and under 40 years.

that as population density increased, older women placed more emphasis on physical traits relative to younger women (Figure 3a). Female age seemed to be the most important factor associated with the emphasis placed on resource holding potential, with younger women placing greater emphasis on this trait. No clear patterns emerged for models explaining the emphasis that women placed on emotional appeal: confidence intervals on all parameter estimates overlapped zero and the null model was considered competitive (Table 1). Women from more female-biased populations placed more emphasis on activities and interests (Table 2). Also, an interaction between age and population size indicated that as population size increased, younger women placed less emphasis on activities and interests than did older women (Figure 3c).

4. Discussion

In this study, we asked if individual and population-level environmental variables were associated with variation in human female mate preference across Canadian cities. We found that variation in population sex ratio and individual age, as well as interactions between several variables predicted female mate preferences. These results add to a large and growing body of literature, spanning a range of taxa, demonstrating that mate preferences are not static, but can be influenced by underlying environmental conditions (Endler, 1983; Robinson, 2008).

4.1. Resource holding potential

The top model describing female preference for resource holding potential included age and population density (Table 1), with younger women and women in higher density cities placing a greater emphasis on resource holding potential (although the confidence interval for the model-averaged parameter estimate for population density overlapped zero; Table 2). We suggest two possible explanations for the finding that age was negatively related to preference for resource holding potential. First, for both men and women, incomes tend to increase with age, generally resulting in older individuals being more financial stable (Government of Canada, 2007). More financially stable women may require fewer resources from their mates and thus place less relative emphasis on resource holding potential in their online dating profiles. A second hypothesis is that women's self-perception of desirability may change with age, resulting in a shift in what they feel they can expect from potential mates (Waynforth & Dunbar, 1995; Bereczkei et al., 1997). For example, Bereczkei et al. (1997) found that females in better physical condition (young, physically attractive and fertile) were able to expect more resource holding potential in a mate.

Although the effect of density is not strong, the finding that this variable is part of our top model is consistent with work on other taxa suggesting that in dense populations, resources are likely to be limited even though the number of potential mates is high; as a result, there is increased competition among males for mates and in females, an increase in preference for males with high resource holding ability (e.g., Jirotkul, 1999a; Casalini et al., 2010). In humans, McGraw (2002) found that population density and cost of living were important predictors of female preference for resource holding potential. Based on his results, McGraw (2002) suggested that in densely populated American cities, in which there is a high demand for both mates and resources, women seeking mates may place more priority on individuals with high resource holding potential (*sensu* Qvarnstrom & Forsgren, 1998).

Some recent work has suggested that relationships between environmental variation and mate preference may be better explained by assortative mating by income (Anderson & Klofstad, 2012), whereby females in some cities place higher emphasis on resource holding potential in a mate because these females have higher incomes themselves, rather than because of the nature of the city. Anderson & Klofstad (2012) used a direct approach, examining the stated preferred income of a potential mate (which was available in the advertisements on the online dating site they used); however, in our study, as in McGraw's (2002) paper, we are interested in the relative emphasis that individuals place on resource holding ability compared to other attributes of potential mates. Though we were unable to assess its influence in this study, assortative mating is likely also an important explanatory variable; however, we suggest that our findings indicate that environmental variation in population density may be a predictor of the *relative* importance females place on resource holding ability in potential mates.

4.2. Emotional appeal, physical attractiveness, activities and interests

Similar to McGraw (2002), we found that women used words associated with emotional appeal to describe the preferred characteristics of potential mates more than they did words in any other category (Figure 2); this pattern of strong preference for emotional appeal appeared to be universal, not varying across cities or with age or any environmental or economic variables. These findings are also consistent with Buss (1989), who found that emotional appeal was the most highly valued aspect of a potential mate across 37 cultures in 33 countries.

The amount of emphasis that females placed on the physical attractiveness of potential mates was positively related to male-to-female sex ratio over the 26 cities. Our results suggest that as the relative proportion of males increased, females placed more importance on physical attractiveness in a potential mate. Population density was also present among the top models, though the confidence intervals for this parameter estimate overlapped zero (Table 2). However, significant interaction effects suggested that older women in male-biased populations placed the most emphasis on physical traits when residing in high-density populations (Figure 3a, b). The importance of density is consistent with work on other taxa, which has demonstrated that the intensity of sexual selection on ornamental traits increases with increasing population density (Eshel, 1979; Jann et al., 2000; Kokko & Rankin, 2006; Taff et al., 2013). Women living in densely-populated areas may experience a higher number of interactions, and have a greater selection of potential mates, and may, therefore, be more selective about physical appearance when choosing a mate. This situation would be compounded in male-biased populations: with more males available, females would have more potential mates to choose from and would be free to be more selective about the physical qualities of their mate. For example, female guppies (Poecilia reticulata) show greater preference for male ornamentation under male-biased sex ratios (Jirotkul, 1999b). However, the reason why preference for physical traits increased with increasing population density more strongly in older women than younger women remains unclear. Perhaps younger women maintain a relatively consistent number of social interactions regardless of population density (e.g., through social media), whereas for older women the number of interactions, and thus the potential for being selective about physical appearance, is increased substantially at higher densities.

The emphasis that females placed on the personal activities and interests of potential mates was negatively related to male-to-female sex ratio; as the relative number of males increased, females seemed to place less emphasis on this aspect of potential mates. This result suggests females are being

less choosy about certain traits when the population sex ratio is male-biased, perhaps because in these situations the emphasis shifts to other traits, such as the physical characteristics discussed above. Interestingly, an interaction between age and population size suggested that when they resided in larger cities, younger women placed relatively less emphasis (compared to older women) on the activities and interests of potential mates (Figure 3c). Perhaps sharing personal activities or interests is of less importance to younger women in larger cities, where there is more choice in the activities available. In smaller cities, or in rural areas, in contrast, personal interests may be much more important. For example, Rudzitis (1999) suggested that the second most important reason, aside from employment, for moving to a rural area in the western United States was to partake in outdoor recreation. Similar trends were also observed in New Zealand, where environmental and lifestyle factors were major drivers of moves from urban to rural areas (Government of New Zealand, 2007).

4.3. Limitations

Although the findings of this study are compelling, our results have several limitations. First, there is the potential for self-misrepresentation (Pawlowski & Dunbar, 1999; Gibbs et al., 2006; Toma & Hancock, 2010), as female advertisers may benefit from reporting a younger age than is true, due to male preference for younger mates (Buss, 1989; Kenrick & Keefe, 1992). However, if this pattern is consistent across advertisers, it is unlikely to influence our results. Second, there may be differences between the preferences stated by advertisers and their true, 'revealed' (by the actual mate choice) preferences. For example, Hitsch et al. (2010) examined both stated preferences in online advertisements and 'revealed' preferences by examining characteristics of potential mates that were contacted by advertisers and found significant differences with regards to race preferences in both men and women. However, there is no reason to expect differences between stated and revealed preferences to vary across samples. Finally, our conclusions regarding the causal effects of environmental factors on mate preference are limited due to the correlative nature of the study. For example, non-random migration of individuals into certain cities, rather direct environmental effects of those cities, could help explain observed preferences. One possibility is that highly attractive females may be more likely to live in high-density, malebiased cities. As women are known to mate assortatively by attractiveness

(Little et al., 2001), this could help explain why older women in high-density cities express a greater preference for physical attractiveness.

4.4. Conclusions

In this study, we asked whether variation in women's mate preference was associated with geographic variation in environmental and economic conditions, as well as with the age of the individual placing the advertisement. By examining online advertisements from 26 cities across Canada, which spanned a large geographic range and encompassed a broad range of environmental and economic conditions, we found significant variation in the attributes preferred in potential mates. We suggest that our results support the hypothesis that female mate preferences are dynamic and may be influenced by environmental factors, such as population density and sex ratio. In addition, though the effects of age may sometimes be weak (Buunk et al., 2002; Schwarz & Hassebrauck, 2012), we found that in fact age was an important predictor of preference for resource holding potential. Thus, we suggest that it may be important in future studies of human mate preference to examine age-specific patterns or to control for age when examining patterns of mate preference.

Data available from online dating profiles present a wealth of information useful for studies of human mate preference and mate attraction. Many other personal attributes, aside from age (e.g., personal income; Anderson & Klofstad, 2012), may also help explain variation in human mate preference; for instance, future studies could examine the influence of employment status, marital status (i.e., single, divorced, widowed), and number of children on mate preference. Because environmental variation and age were associated with the relative preference for mate characteristics in this study, it may be important for future studies investigating sexual selection and mate choice in humans to not only ask which traits are being selected, but also to investigate the environmental conditions in which selection is acting on those traits (Cornwallis & Uller, 2009; Gordon, 2011).

Acknowledgements

We thank C. Ross Friedman, T. Dickinson and R. Germain and for insightful comments and discussion of this manuscript and A. Pillar for creating Figure 1. We also thank the editor and reviewers for helpful comments and suggestions. Funding was provided by the Thompson Rivers University CUEF U-REAP fund for an undergraduate research scholarship to K.R.M.

References

- Anderson, R.C. & Klofstad, C.A. (2012). For love or money? The influence of personal resources and environmental resource pressures on human mate preferences. — Ethology 118: 841-849.
- Bereczkei, T., Voros, S., Gal, A. & Bernath, L. (1997). Resources, attractiveness, family commitment; reproductive decisions in human mate choice. — Ethology 103: 681-699.
- Berglund, A. (1994). The operational sex ratio influences choosiness in a pipefish. Behav. Ecol. 5: 254-258.
- Botero, C.A. & Rubenstein, D.R. (2012). Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. — PLoS ONE 7: e32311.
- Burnham, K.P. & Anderson, D.R. (2002). Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. — Springer, New York, NY.
- Buss, D.M. (1989). Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. — Behav. Brain Sci. 12: 1-49.
- Buunk, D.P., Dijkstra, P., Fetchenhauer, D. & Kendrick, D.T. (2002). Age and gender differences in mate selection criteria for various involvement levels. — Pers. Relat. 9: 271-278.
- Cameron, C., Oskamp, S. & Sparks, W. (1977). Courtship American style: newspaper ads. Fam. Coord. 26: 27-30.
- Candolin, U., Salesto, T. & Evers, M. (2007). Changed environmental conditions weaken sexual selection in sticklebacks. — J. Evol. Biol. 20: 233-239.
- Casalini, M., Reichard, M. & Smith, C. (2010). The effect of crowding and density on male mating behaviour in the rose bitterling (*Rhodeus ocellatus*). — Behaviour 147: 1035-1050.
- Cornwallis, C. & Uller, T. (2009). Towards and evolutionary ecology of sexual traits. Trends Ecol. Evol. 25: 145-152.
- Deaux, K. & Hanna, R. (1984). Courtship in the personals column: the influence of gender and sexual orientation. — Sex Roles 11: 363-375.
- DeBruine, L.M., Jones, B.C., Crawford, J.R., Welling, L.L.M. & Little, A.C. (2010). The health of a nation predicts their mate preferences: cross-cultural variation in women's preferences for masculinized male faces. — Proc. Roy. Soc. Lond. B: Biol. Sci. 277: 2405-2410.
- Dreiss, A.N., Cote, J., Richard, M., Federici, P. & Clobert, J. (2010). Age- and sex-specific response to population density and sex ratio. — Behav. Ecol. 21: 356-364.
- Eckert, C.G. & Weatherhead, P.J. (1987). Competition for territories in red-winged blackbirds: is resource-holding potential realized? — Behav. Ecol. Sociobiol. 20: 369-375.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. — Science 197: 215-223.
- Endler, J.A. (1980). Natural selection on color patterns in *Poecilia reticulata*. Evolution 34: 76-91.

- Endler, J.A. (1983). Natural and sexual selection on color patterns in Poeciliid fishes. Environ. Biol. Fish. 9: 173-190.
- Eshel, I. (1979). Sexual selection, population density, and availability of mates. Theor. Popul. Biol. 16: 301-314.
- Gangestad, S.W. & Buss, D.M. (1993). Pathogen prevalence and human mate preferences. Ethol. Sociobiol. 14: 39-54.
- Gangestad, S.W. & Simpson, J.A. (2000). The evolution of human mating: trade-offs and strategic pluralism. — Behav. Brain Sci. 23: 573-644.
- Gibbs, J.L., Ellison, N.B. & Heino, R.D. (2006). Self-presentation in online personals: the role of anticipated future interaction, self-disclosure, and perceived success in Internet dating. — Commun. Res. 33: 152-177.
- Gil-Burmann, C., Peláez, F. & Sánchez, S. (2002). Mate choice differences according to sex and age. — Hum. Nature — Int. Bios. 13: 493-508.
- Godin, J.-G.J. & Briggs, S.E. (1996). Female mate choice under predation risk in the guppy. — Anim. Behav. 51: 117-130.
- Gordon, D.M. (2011). The fusion of behavioral ecology and ecology. Behav. Ecol. 22: 225-230.
- Government of Canada SC (2007). Statistics Canada: 2006 Community Profiles. Available online at http://www12.statcan.gc.ca/census-recensement/2006/dp-pd/prof/92-591/.
- Government of Canada SC (2012). Statistics Canada: 2011 Census Profile. Available online at http://www12.statcan.gc.ca/census-recensement/2011/dp-pd/prof/index.cfm? lang=e.
- Government of New Zealand (2007). Statistics New Zealand: urban and rural dwellers' reasons for moving. Available online at http://www.stats.govt.nz/browse_for_stats/ population/Migration/internal-migration/reason-for-moving-within-between-urban-rural-areas/moving-to-new-residence.aspx.
- Gray, S.M., Dill, L.M., Tantu, F.Y., Loew, E.R., Herder, F. & McKinnon, J.S. (2008). Environment-contingent sexual selection in a color polymorphic fish. — Proc. Roy. Soc. Lond. B: Biol. Sci. 275: 1785-1791.
- Greenlees, I.A. & McGrew, W.C. (1994). Sex and age differences in preferences and tactics of mate attraction: analysis of published advertisements. — Ethol. Sociobiol. 15: 59-72.
- Grether, G.F., Kolluru, G.R., Rodd, F.H., De La Cerda, J. & Shimazaki, K. (2005). Carotenoid availability affects the development of a colour-based mate preference and the sensory bias to which it is genetically linked. — Proc. Roy. Soc. Lond. B: Biol. Sci. 272: 2181-2188.
- Hill, S.E. & Reeve, H.K. (2004). Mating games: the evolution of human mating transactions. — Behav. Ecol. 16: 398-402.
- Hitsch, G.J., Hortacsu, A. & Ariely, D. (2010). What makes you click? mate preferences in online dating. — Quant. Mark. Econ. 8: 393-427.
- Houde, A.E. (1997). Sex, color, and mate choice in guppies. Princeton University Press, Princeton, NJ.
- Jann, P., Blanckenhorn, W.U. & Ward, P.I. (2000). Temporal and microspatial variation in the intensities of natural and sexual selection in the yellow dung fly *Scanthophaga stercoraria*. — J. Evol. Biol. 13: 927-938.

- Jennions, M.D. & Petrie, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. Biol. Rev. Camb. Philos. 72: 283-327.
- Jirotkul, M. (1999a). Population density influences male-male competition in guppies. Anim. Behav. 58: 1169-1175.
- Jirotkul, M. (1999b). Operational sex ratio influences female preference and male-male competition in guppies. — Anim. Behav. 58: 287-294.
- Johnstone, R.A. (1995). Sexual selection, honest advertisement and the handicap principle reviewing the evidence. Biol. Rev. Camb. Philos. 70: 1-65.
- Kelly, C.D. (2008). The interrelationships between resource-holding potential, resource-value and reproductive success in territorial males: how much variation can we explain? — Behav. Ecol. Sociobiol. 62: 855-871.
- Kenrick, D.T. & Keefe, R.C. (1992). Age preferences in mates reflect sex differences in reproductive strategies. — Behav. Brain Sci. 15: 75-133.
- Klofstadt, C.A., McDermott, R. & Hatemi, P.K. (2011). Do bedroom eyes wear political glasses? The role of politics in human mate attraction. — Evol. Hum. Behav. 33: 100-108.
- Kokko, H. & Rankin, D.J. (2006). Lonely hearts or sex in the city? Density-dependent effects in mating systems. — Phil. Trans. Roy. Soc. B 361: 319-334.
- Koskimäki, J., Rantala, M.J., Taskinen, J., Tynkkynen, K. & Suhonen, J. (2004). Immunocompetence and resource holding potential in the damselfly, *Calopteryx virgo* L. — Behav. Ecol. 15: 169-173.
- Lee, A.J. & Zietsch, B.P. (2011). Experimental evidence that women's mate preferences are directly influenced by cues of pathogen prevalence and resource scarcity. — Biol. Lett. 7: 892-895.
- Little, A.C., Burt, D.M., Penton-Voak, I.S. & Perrett, D.I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. — Proc. Roy. Soc. Lond. B: Biol. Sci. 268: 39-44.
- Little, A.C., Cohen, D.L., Jones, B.C. & Belsky, J. (2007). Human preferences for facial masculinity change with relationship type and environmental harshness. — Behav. Ecol. Sociobiol. 61: 967-973.
- Madden, M. & Lenhart, A. (2006). Online dating. Pew internet and American life project. Available online at http://www.pewinternet.org.
- Mautz, B.S., Wong, B.B.M., Peters, R.A. & Jennions, M.D. (2013). Penis size interacts with body shape and height to influence male attractiveness. — Proc. Natl. Acad. Sci. USA 110: 6925-6930.
- McGraw, K.J. (2002). Environmental predictors of geographic variation in human mating preferences. — Ethology 108: 303-317.
- Moore, F.R. & Cassidy, C. (2007). Female status predicts mate preferences across nonindustrial societies. — Cross-Cult. Res. 41: 66-74.
- Moore, F.R., Cassidy, C., Smith, J.J.L. & Perrett, D.I. (2006). The effects of female control of resources on sex-differentiated mate preferences. — Evol. Hum. Behav. 27: 193-205.

- Morgan, E.M., Richards, T.C. & VanNess, E.M. (2010). Comparing narratives of personal and preferred partner characteristics in online dating advertisements. — Comput. Hum. Behav. 26: 883-888.
- Pawlowski, B. & Dunbar, R.I.M. (1999). Withholding age as putative deception in mate search tactics. — Evol. Hum. Behav. 20: 73553-73569.
- Pawlowski, B. & Koziel, S. (2002). The impact of traits offered in personal advertisements on response rates. — Evol. Hum. Behav. 23: 139-149.
- Petrie, M. & Kempenaers, B. (1998). Extra-pair paternity in birds: explaining variation between species and populations. — Trends Ecol. Evol. 13: 52-58.
- Punzalan, D., Rodd, F.H. & Rowe, L. (2010). Temporally variable multivariate sexual selection on sexually dimorphic traits in a wild insect population. — Am. Nat. 175: 401-414.
- Puts, D.A., Jones, B.C. & DeBruine, L.M. (2012). Sexual selection on human faces and voices. — Annu. Rev. Sex Res. 49: 227-243.
- Qvarnstrom, A. & Forsgren, E. (1998). Should females prefer dominant males? Trends Ecol. Evol. 13: 498-501.
- R Core Team (2013). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available online at http://www.R-project.org/.
- Rebar, D. & Rodriguez, R.L. (2013). Genetic variation in social influence on mate preferences. Proc. Roy. Soc. Lond. B: Biol. Sci. 280: 1471-2954.
- Robinson, M.R., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Kruuk, L. (2008). Environmental heterogeneity generates fluctuating selection on a secondary sexual trait. — Curr. Biol. 18: 751-757.
- Rudzitis, G. (1999). Amenities increasingly draw people to the rural West. Rur. Dev. Perspect. 14: 9-13.
- Schwarz, S. & Hassebrauck, M. (2012). Sex and age differences in mate-selection preferences. Hum. Nat. 23: 447-466.
- Sear, R. & Marlowe, F.W. (2009). How universal are human mate choices? Size does not matter when Hadza foragers are choosing a mate. — Biol. Lett. 5: 606-609.
- Singh, D. (1995a). Female judgment of male attractiveness and desirability for relationships: role of waist-to-hip ratio and financial status. J. Pers. Soc. Psychol. 69: 1089-1101.
- Singh, D. (1995b). Female health, attractiveness, and desirability for relationships: role of breast asymmetry and waist-to-hip ratio. — Ethol. Sociobiol. 16: 465-481.
- Slabbekoorn, H. & Smith, T.B. (2002). Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. — Evolution 56: 1849-1858.
- Stone, E.A., Shackelford, T.K. & Buss, D.M. (2007). Sex ratio and mate preferences: a crosscultural investigation. — Eur. J. Soc. Psychol. 37: 288-296.
- Taff, C.C., Freeman-Gallant, C.R., Dunn, P.O. & Whittingham, L.A. (2013). Spatial distribution of nests constrains the strength of sexual selection in a warbler. — J. Evol. Biol. 26: 1392-1405.
- Toma, C.L. & Hancock, J.T. (2010). Looks and lies: the role of physical attractiveness in online dating self-presentation and deception. Commun. Res. 37: 335-351.

- Valkenburg, P.M. & Peter, J. (2007). Who visits online dating sites? Exploring some characteristics of online daters. — Cyberpsychol. Behav. 10: 849-852.
- Valliant, N. (2006). Sex differences in stipulated preferences and mate search by clients of a French marriage bureau. — Psychol. Rep. 98: 285-290.
- Vitousek, M.N. (2009). Investment in mate choice depends on resource availability in female Galápagos marine iguanas (*Amblyrhynchus cristatus*). — Behav. Ecol. Sociobiol. 64: 105-113.
- Waynforth, D. & Dunbar, R.I.M. (1995). Conditional mate choice strategies in humans: evidence from "lonely hearts" advertisements. — Behaviour 132: 755-779.
- Wiederman, M.W. (1993). Evolved gender differences in mate preferences: evidence from personal advertisements. — Ethol. Sociobiol. 14: 331-352.
- Wood, W.E., Yezerinac, S.M. & Dufty, J. (2006). Song sparrow (*Melospiza melodia*) song varies with urban noise. — Auk 123: 650-659.

Appendix

Table A1.

Environmental predictors collected from 26 cities across Canada.

| City | Median income (Canadian dollar) | Population size | Sex ratio (M/F) | Density (individuals/km ²) | Average age (years) |
|----------------------------|--|--------------------|-----------------------|---|---------------------------|
| Abbotsford-Mission, BC | 22990 | 133 497 | 0.97 | 356 | 39.52 |
| Calgary, AB | 30542 | 1096833 | 1.00 | 1329 | 36.02 |
| Charlottetown, PEI | 22230 | 34 587 | 0.86 | 805 | 40.96 |
| Edmonton, AB | 27734 | 812 201 | 0.99 | 1187 | 34.48 |
| Guelph, ON | 30078 | 121688 | 0.94 | 1395 | 39.38 |
| Halifax, NS | 27 198 | 297 943 | 0.92 | 1106 | 40.72 |
| Hamilton, ON | 26267 | 519949 | 0.95 | 465 | 38.18 |
| Kamloops, BC | 26075 | 85678 | 0.96 | 286 | 41.82 |
| Kelowna, BC | 25134 | 117312 | 0.92 | 554 | 43.40 |
| Montréal, QC | 21459 | 1649519 | 0.94 | 4518 | 36.76 |
| Peterborough, ON | 24212 | 78698 | 0.89 | 1234 | 43.88 |
| Québec, QC | 26178 | 516622 | 0.93 | 1138 | 40.64 |
| Regina, SK | 29100 | 193 100 | 0.95 | 1328 | 41.86 |
| Saint John, NB | 22510 | 70063 | 0.89 | 222 | 42.18 |
| Saskatoon, SK | 25868 | 222189 | 0.96 | 1060 | 43.12 |
| St. Catharines-Niagara, ON | 25114 | 131 400 | 0.91 | 1367 | 41.70 |
| St. John's, NL | 22852 | 106172 | 0.91 | 238 | 38.10 |
| Summerside, PEI | 22382 | 14751 | 0.87 | 520 | 45.12 |
| Thunder Bay, ON | 27 395 | 108 359 | 0.94 | 330 | 42.96 |
| Toronto, ON | 24 544 | 2615060 | 0.92 | 4150 | 35.64 |
| Vancouver, BC | 23682 | 603 502 | 0.96 | 5249 | 36.72 |
| Victoria, BC | 24651 | 80017 | 0.89 | 4109 | 44.78 |
| Whitehorse, YT | 34337 | 23 276 | 0.98 | 56 | 41.02 |
| Windsor, ON | 25 4 4 3 | 210891 | 0.94 | 1441 | 39.06 |
| Winnipeg, MB | 26015 | 663 617 | 0.94 | 1430 | 38.02 |
| Yellowknife, NWT | 44 567 | 19234 | 1.02 | 182 | 44.27 |

Information on population size, sex ratio and population density was collected from the 2011 Canada Census; median income was not available from the 2011 census at the time of the study and was collected instead from the 2006 census. Average age was collected from self-reported ages of online profiles for each city.