Behavioral Ecology and Sociobiology (2018) 72: 83
https://doi.org/10.1007/s00265-018-2497-3

FEATURED STUDENT RESEARCH PAPER

Male aggressiveness as intrasexual contest competition in a cross-cultural sample

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Received: 19 October 2017 / Revised: 23 April 2018 / Accepted: 27 April 2018 / Published online: 7 May 2018

Abstract

Sexual selection favors traits that increase mating and, thus, reproductive success. Some scholars have suggested that intrasexual selection driven by contest competition has shaped human male aggression. If this is the case, one testable hypothesis is that beliefs and behavior related to male aggression should be more prevalent in societies where the intensity and strength of sexual selection is higher. Measured by factors such as (a) the presence and scope of polygyny; (b) the number of same-sex competitors relative to potential mates, and (c) the amount of effort males are available to allocate to mating. Using Bayesian item response models with imputation and data from 78 societies in the Standard Cross-Cultural Sample, we found robust support for this hypothesis when using variables related to male aggression. We ruled out some potential alternative explanations by controlling for geographic region and confounding variables such as political complexity and warfare.

Significance statement

Intersexual selection or mate attraction has been well studied in both evolutionary psychology and human behavioral ecology. Intrasexual selection or competition between members of the same sex for mates has been investigated much less. Of the current studies, there is still a divide in the literature as to whether intrasexual selection could have shaped human male aggression. For this reason, we tested the idea with data from a wide range of societies, the first systematic cross-cultural study to do so. Our results suggest that factors affecting the intensity of competition for mates led to the evolution of beliefs and behavior related to male aggression in small-scale human societies. This provides support for the hypothesis that intrasexual selection has been a driving force in shaping human male aggression.

Keywords Sexual selection · Polygyny · Sex ratio · Subsistence-mating tradeoff · Aggression · Human behavioral ecology

Introduction

Sexual selection is an evolutionary force favoring traits that lead to greater mating and, thus, reproductive success (Andersson 1994). Although it has the potential to drive evolution in both sexes (Clutton-Brock 2007; Brown et al. 2009), our paper focuses on sexual selection driven by mating competition between human males. Darwin (1871) referred to sexual selection via direct physical competition for mates as intrasexual selection. Today, several non-mutually exclusive mechanisms are recognized, but intrasexual selection through contest competition is the one most likely to lead to the evolution of armaments that males can use in combat with other males for access to potential mates (Andersson 1994; Emlen 2008; Puts 2010). Although some indications of sexual selection, such as sexual dimorphism, are lower among humans than in Australopithecines (Kramer and Russell 2015), many aspects of human male biology and behavior point to an evolutionary history consistent with contest competition. This leads some researchers to suggest that human male aggression has been shaped by intrasexual selection

Communicated by M. Raymond

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-018-2497-3) contains supplementary material, which is available to authorized users.

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(Archer 2009; Dixson 2009; Lindenfors and Tullberg 2011; Kruger and Fitzgerald 2012; Hill et al. 2013; Puts et al. 2015; Puts 2010).

Despite support for the intrasexual selection hypothesis, some have suggested alternatives. First, support for positive reproductive and mating consequences of aggression in small-scale societies is mixed (Beckerman et al. 2009). Second, intrasexual selection may lead to highly selective uses of aggression—i.e., only when it leads to reproductive advantage—rather than generalized aggression (Ainsworth and Maner 2014). Third, even if sexual selection has played a role in shaping male aggressive behavior, other evolutionary mechanisms could have also played a role (Buss 2009; McDonald et al. 2012; Plavcan 2012; Gómez et al. 2016). Finally, explanations of aggression as a product of sexual selection are opposed by explanations based in social role theory, or as Eagly and Wood (1999, p. 224) summarize it: "sex differences in aggression follow from the placement of women and men in the social structure." For these reasons, we feel that a test of the hypothesis with data from a wide range of societies is necessary.

To test the hypothesis that male aggression has been shaped by intrasexual selection, we analyzed several factors related to male aggression. We employed dimension reduction models measuring behavior and beliefs related to male aggression (referred to hereafter as "aggressiveness"), in 78 of the Standard Cross-Cultural Sample's (SCCS) 186 societies. We adopted the comparative approach to studying adaptation used in behavioral ecology, whereby one tests hypotheses about function by looking at statistical association between a phenotype and aspects of the social and physical environment that might serve as selective agents (Davies et al. 2012). The underlying logic is that certain behavior and beliefs will arise in societies when conditions are present that would lead to individuals within that society maximizing fitness by adopting them. Our approach appreciates that human adaptation is shaped by selection on biological and/or cultural variants (Winterhalder and Smith 2000), but will not facilitate strong claims about the biological and/or cultural basis of aggression in human societies. Our aim is simply to demonstrate whether there is, or is not, an association between the variables of interest as a test of a hypothesis rooted in standard human behavioral ecological models.

Our overarching hypothesis was that aggressiveness should co-vary with factors influencing the strength of intrasexual selection. Put another way, aggressiveness should arise in societies with conditions whereby such behavior and beliefs provide a higher fitness payoff. To test this hypothesis, we used Bayesian Item Response Theory (IRT) analysis, which allowed us to control for potential confounding variables, such as political complexity and warfare, and geographic clustering.

More specifically, our hypothesis predicted associations between aggressiveness and the following factors:

(a) Increased intensity of mating competition reflected in the presence and scope of polygyny, because mating systems mediate the ability of males to monopolize mating opportunities (Emlen and Oring 1977; Shuster 2009).
(b) Since Emlen and Oring's (1977) landmark paper, conventional thinking states that both male-biased adult sex ratios (ASRs) and OSRs lead to an increase in male-male competition. More recently, however, Kokko and colleagues (Kokko and Jennions 2008; Klug et al. 2010; Kokko et al. 2012) have shown that under certain circumstances, male-biased adult sex ratios can lead to a decrease in competition—because some males will shy from competition when costs are high or probable benefits low. Moreover, Schacht et al. (2014) demonstrate that the relationship between sex ratios and violence is complex with cross-cultural studies of traditional societies showing that an excess of females is associated with an increase of male violence. Yet, studies using crime statistics worldwide find mixed results for the direction of the association. Therefore, our more specific prediction is that the relationship could plausibly go in either direction. Keeping in mind, our measures are closest to ASRs and an attempt to proxy for operational ones.
(c) Higher potential allocations to mating effort as reflected in lower contributions of males to subsistence tasks, based on the theoretical and empirical perspective that mating effort trades off against other aspects of individual fitness (Quinlan and Quinlan 2007; Gurven and Hill 2009; Georgiev et al. 2014).

Material and methods

Data

We used data from the SCCS to test for an association between "aggressiveness" and various factors that should influence the strength of intrasexual selection. The SCCS is a database of 186 societies each coded for various factors related to aspects of that society's social structure, environment, beliefs, and behavior at a "pinpointed" time in the past. These were chosen because of the availability of ethnographic accounts and the degree to which the factors reflect "traditional" ones (Murdock and White 1969). We have outlined the variables used in the study in more detail in Tables S1 and S2 and provided complete data in Table S3 in the Supplementary Materials.

One important issue that shaped our analytical strategy was the need to transform variables into a format that allowed for tractable and consistent multivariate analyses. Most SCCS variables are coded into multiple categories with a minority coded as binary or continuous. We started by recoding potential variables into binary format. For continuous variables, we set our cutoff point at the 50th percentile to avoid the statistical problems of doing it arbitrarily. We recoded binary for the following reasons. First, we wanted to represent categorical variables in quantitative terms without imposing unrealistic measurement assumptions. This was even the case for the continuous variables we used, like sex ratio, which is known to be imprecise (Ember 1974). Second, binary predictors of interest simplify the analysis into a comparison of groups.

Independent variables

Our analyses required three sets of independent variables: predictors of interest, potential confounders, and variables to adjust for potential phylogenetic and spatial autocorrelation. These variables are discussed below, with complete details included in Table S1 in the Supplementary Materials. The first set of independent variables were binary-recoded versions of the predictors of interest—variables that captured factors that we predicted should influence the strength of sexual selection: (a) *Polygyny:* polygyny (0 no, 1 yes); and wives variance, the variance in number of wives in the upper 50th percentile (0 no, 1 yes). (b) *Sex ratio:* sex ratio, the total number of males to females in a society, in the lower 50th percentile (0 no, 1 yes); and male war mortality (0 none or negligible, 1 higher than negligible). Neither of these is a perfect measure of OSR, or even ASR. (c) *Other factors:* male subsistence, the effort males contribute toward subsistence (0 women do more, 1 men do as much as women or more). Note that all percentiles were calculated using all non-missing values from the entire sample of 186 societies. The second set of independent variables were factors that might confound the hypothetical relationships (Ember et al. 2007). To adjust for these, we have included two binary-recoded control variables to adjust for these factors: political complexity (0 no state, 1 state) and warfare (0 absent or occasional, 1 frequent or endemic).

The third and final sets of independent variables were controls to adjust for phylogenetic and spatial autocorrelation. The sparse sampling of societies across language families in the SCCS, itself a measure taken when paring down the original Ethnographic Atlas to control for phylogenetic autocorrelation, precluded the use of phylogenetic methods (in the absence of a global “super”-tree) to control for shared cultural history which can lead to spurious cross-cultural correlation. This is referred to as “Galton’s problem” in cross-cultural studies such as this one (Eff 2004). Another potential source of non-independence in the data is spatial autocorrelation (Xu and Kennedy 2015) caused by societies which are geographically close sharing attributes because of shared ecology, diffusion, spill-over, and other processes. To adjust for these issues, we used the independent variable: geographic region (6 regions), included as a random effect in the IRT models.

Dependent variables

Our target dependent variable was a measure of behavior and beliefs related to male-on-male aggression with respect to competing for mates in each society but no one such variable exists within the SCCS. We therefore conducted an exhaustive search of the SCCS; identifying variables we hypothesized would be good predictors of male intrasexual selection. Initially, we performed multilevel logistic regression analyses on the following variables: (a) frequent interpersonal violence (0 absent, 1 present); (b) warriors have prestige (0 none or some, 1 great deal); (c) wives taken from hostile groups (0 no female captives taken, 1 women taken); (d) male scarification (0 absent, 1 present); (e) male sexual aggressiveness (0 men diffident and shy, 1 men forward and sometimes hostile); (f) aggression valued (0 little, 1 moderate or marked); and (g) ideology of male toughness (0 absent, 1 present). The variables we included to represent “aggressiveness” were chosen because they are related to male-on-male aggression associated with mating. Table 1 summarizes the results of our initial series of multilevel logistic regression models with random effects for region—one for each combination of predictor of interest and dependent variable considered. There is a clear distinction whereby the top six variables are clearly better performers than the last with regard to association with the predictors of interest (20–80% *versus* 0% of the coefficients were reasonable predictors). We chose in our analysis going forward to exclude this candidate variable, male sexual aggressiveness, because it captures male forwardness toward females during mating (ranging from “shy” to ‘hostile’), rather than agonistic interaction with males (Broude and Greene 1976).

We are confident the five variables are an efficacious measure of male “aggressiveness” for several reasons. First, the variables included in the analysis capture *male*-specific aggression related to competing with same-sex rivals. Although two of the included variables, warriors have prestige and frequent interpersonal violence, are not coded in a *male*-specific way, they still serve as important components of the composite variable. Although there are certainly varying degrees of female participation in war in human societies across history, warriors are predominately male (Goldstein 2003). Without trivializing male-on-female violence, male-on-male interpersonal violence is overwhelmingly the most common type in human societies (Archer 2009). Moreover, female violence is often indirect rather than physical (Vaillancourt 2013).

Although male scarification, at face value, would appear to be an ornament that functions to signal male quality to the opposite sex (Ludvico and Kurland 1995), newer evidence

Table 1 Summary of preliminary multilevel logistic regression analyses

Variable	SCCS	n	Missing	Predictors: $p \leq 0.10$
Included in the analysis:				
Wives taken from hostile groups	v870	158	28	3/5 (60%)
Warriors have prestige	v903	151	35	2/5 (40%)
Male scarification	v1694	145	41	1/5 (20%)
Frequent interpersonal violence	v666	131	55	4/5 (80%)
Ideology of male toughness	v664	108	78	1/5 (20%)
Aggressiveness valued	v625	81	105	1/5 (20%)
Excluded from analysis:				
Male sexual aggressiveness	v175	60	126	0/5 (0%)

suggests scarification might also serve as an armament that can be used to directly compete for mates with other males. A study of perceptions of tattoos on both males and females suggests that scarification may serve as an instrument of direct male-male competition because of its ability to intimidate same-sex rivals and to signal dominance (Wohlrab et al. 2009). The Maori, who are in the study's top-most grouping for aggressiveness (see Table S3), are an excellent ethnographic example. Maori facial and body tattoos (*tā moko*) may enhance the display during Haka, a dance which functions to intimidate same-sex rivals. Therefore, the inclusion of scarification is justified because it serves the dual purpose of ornament and armament.

Statistical analysis

To test hypotheses about the relationships between the factors that affect the intensity of sexual selection and "aggressiveness," we used Bayesian IRT models with imputation to account for the missing data. There are several reasons for doing so. Firstly, we hypothesized factors that are associated with aggressiveness both co-vary and may be interrelated. That is, a score on one item could predict a score on another item, in this way, these outcomes could be reduced to a smaller number—a theoretical unobserved dimension—referred to as the latent trait/outcome/dimension. In our case, the variables were reduced to one latent outcome we termed "aggressiveness," Secondly, although we attempted using a specialized principal component analysis (PCA), item response models are more favorable when dealing with variables that have binary outcomes and are being utilized more and more in human behavioral ecological models (Schacht and Grote 2015; Bunce and McElreath 2016). Thirdly, we were concerned that by using PCA with polychoric correlation to reduce the number of random variables by computing a set of principle variables (dimension reduction), there is always going to be uncertainty in the locations of the populations in the latent outcome. By treating the location of populations on the latent dimension as known, we were at risk of misrepresenting our true results. For previous analyses using PCA with polychoric correlation, please see the Supplementary Material.

IRT methods (within a Bayesian framework) still perform dimension reduction but allow one to reduce and more accurately represent the uncertainty (Schacht and Grote 2015; McElreath 2016). IRT models are commonly used by psychologists and in scholastic testing to determine latent traits such as "intelligence" or "test scores." The purpose of item response models is to link the manifestations (variation and covariation) of observable traits to the latent trait. Schacht and Grote (2015, p. 460) put it succinctly: "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." IRT thus allows us to include fixed and random effects for the variables warfare, political complexity, and geographic region respectively. Essentially, we can gauge the effects of our predictor variables (polygyny, wives variance, sex ratio, male war mortality, and male subsistence) on our latent trait of "aggressiveness" and fit these models utilizing IRT within a Bayesian MCMC (Markov Chain Monte Carlo) framework (Schacht and Grote 2015). We ran separate models for each predictor of interest, in addition to global models, which included all predictors. We followed the Bayesian IRT analysis procedure presented in Bunce and McElreath (2017), utilizing code (including code for imputation) made available to us by an anonymous reviewer (pers. comm.).

Only one of the 78 societies used in this study—the Kwoma—had non-missing data for all variables (see Tables S3 and S6 in the Supplementary Materials). Thus, we used Bayesian imputation to fill in missing values. Essentially, "imputation" estimates missing values in a data set by using the informative error of the existing predictors or outcomes. The Bayesian imputation methods we have used here again make use of the Hamiltonian MC algorithm, using RStan to specify parameters for each missing value. Bayesian imputation is a reliable and robust way to estimate missing values and provides greater statistical power (McElreath 2016). Statistical analyses were performed in R (R Core Team 2017) utilizing the RStan (Stan Development Team 2017) and Rethinking (McElreath 2016) packages. The plots were also created in R using the ggplots2 package; all dependencies are available from Github. For further information regarding priors and R code for both analysis and plots, please see the Supplementary Material.

Results

Hypothesis tests

To test the study's focal hypotheses, we used Bayesian IRT analysis and imputation; we ran models both for the individual predictors of interest and a global model considering all predictors together. For this study, we establish that a single dimension well represents the six outcomes from the SCCS related to male aggressiveness. We can more easily compare the predictors of interest while viewing the outcomes concurrently. Figure 1 illustrates the results for the individual models, and Fig. 2 illustrates the global models. Table 2 presents the posterior mean coefficient estimates from the IRT analysis and 90% credible intervals (CI) for individual predictor models and the global model. A posterior mean coefficient estimate is mean of the posterior distribution. In Bayesian analysis, the posterior distribution is equal to the prior distribution plus new evidence (termed likelihood). The credible intervals are interpreted as a 90% probability that in the population the parameter lies between the two values provided. A 90% credible interval is the default when applying Bayesian statistics and is considered more computationally stable than using a 95% credible interval. It also reduces the likelihood of Type-S errors (see the rstanarm documentation for further rationale).

Let us consider the predictors of interest used for each of the three hypotheses. They are described as follows:

(a) *Polygyny:* The variables in Figs. 1 and 2 used to measure the presence and scope of polygyny are polygyny, wives variance, and male war mortality. As predicted, aggressiveness is higher in societies with polygyny, as well as in those societies who are in the upper 50th percentile for variance in number of wives, even after controlling for geographical region, political complexity, and warfare. This holds true in both the individual and global models, although the effects were stronger when polygyny (posterior mean = 0.64, CI = 0.11, 1.16) and male war mortality (posterior mean = 0.46, CI = − 0.07, 0.96) were considered individually (see Table 2), whereas the effects of the predictor wives variance were greater when taken together in the global model with all other predictors (posterior mean = 0.52, CI = − 0.13, 1.26).

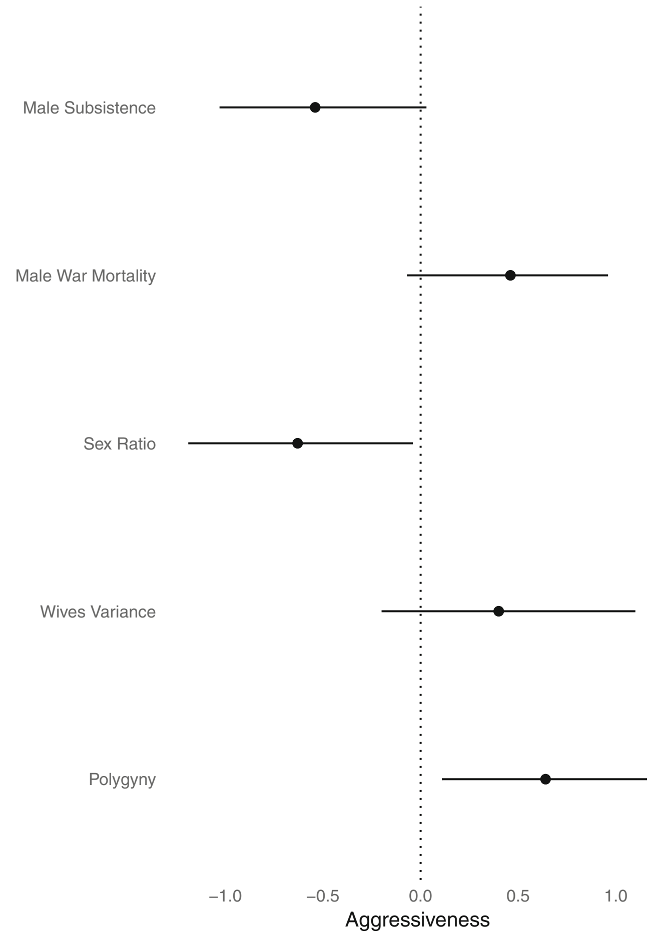

Fig. 1 Posterior means (dots) and 90% credibility intervals (tails) for the predictors of interest, individual models for each predictor. Outcomes of male aggressiveness are reduced to a single dimension "aggressiveness" and uncertainty surrounding each predictor is represented. The best individual predictor of aggressiveness is "polygyny." We controlled for geographical region, warfare, and political complexity in each of these models

(b) *Sex ratio:* The variables in Figs. 1 and 2 used to measure biased sex ratios were sex ratio and male war mortality. As predicted, aggressiveness was associated with biased sex ratios, even after controlling for geographical region, political complexity, and warfare. Societies with relatively more female-biased sex ratios—measured as both being in the lower 50th percentile for sex ratio (individual model, posterior mean = − 0.63 CI = − 1.19, − 0.04; global model, posterior mean = − 0.49, CI = − 1.16, 0.19), and higher male war mortality (individual model, posterior mean = − 0.46 CI = − 0.07, 0.96; global model, posterior mean = − 0.34, CI = − 0.24, 0.88)—had higher levels of aggressiveness.

(c) *Male subsistence effort:* In Figs. 1 and 2, the variable male subsistence was used to measure the ability of males to invest in mating effort. As predicted, societies in which males expend relatively more subsistence effort and thus had lower ability to invest in

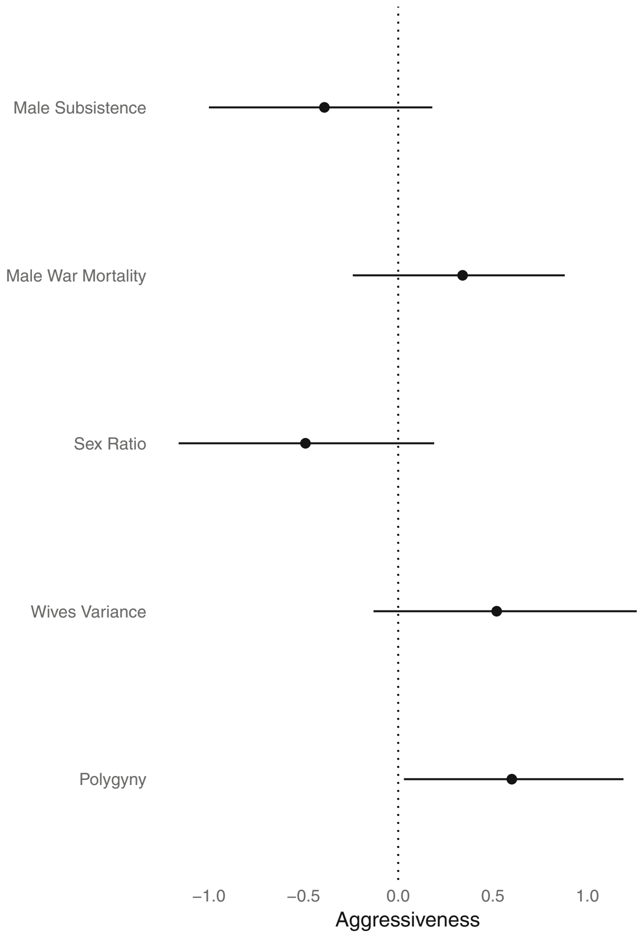

Fig. 2 Posterior means (dots) and 90% credibility intervals (tails) for the predictors of interest, in a global model considering all predictors. Outcomes of male aggressiveness are reduced to a single dimension "aggressiveness" and uncertainty surrounding each predictor is represented. Again, in the global models, the best predictor of aggressiveness is "polygyny." We controlled for geographical region, warfare, and political complexity in this model

mating showed lower levels of aggressiveness, even after controlling for region, political complexity, and warfare, (individual model, posterior mean = − 0.54 CI = − 1.03, 0.03; global model, posterior mean = − 0.39, CI = − 1.00, 0.18).

Discussion

What the results show (and what they do not)

The results of our study show that when intrasexual selection is strong, male aggressiveness is most intense. We interpret these results as support for the hypothesis that intrasexual selection has shaped male aggressiveness in human societies. We appreciate that this aspect of human sociality is shaped by complex interactions between biological and social factors and made no claim to have illuminated its genetic, cultural, or social interactions. What we have shown is that in societies with conditions that increase the intensity of male mating competition, there are often higher levels of aggressiveness, measured as behavior and beliefs related to male aggression. We have, thus, added to the ever-growing body of literature using cross-cultural data from the SCCS to test evolutionary hypotheses (e.g., Ludvico and Kurland 1995; Quinlan and Quinlan 2007).

Our analyses have ruled out several alternative explanations. For instance, the positive association between male mortality in warfare and aggressiveness could be explained by the presence of warfare without the need to invoke sexual selection. It could be that warfare, societal complexity, or some combination of the two confounds the relationships of interest (Ember 1974). It also could be that simpler societies are more likely to allow polygyny and value aggression without necessitating a causal link between the two. Our analytical approach allowed us to show that the relationships of interest still existed even when controlling for the confounding effects of societal complexity and warfare. Similarly, shared cultural histories and environments can lead to spurious cross-cultural correlation (Eff 2004). Our results stood up to statistical control for geographical region. Finally, others have suggested that aggressive beliefs may serve to socialize boys, and aggressive behavior may be the product of that socialization, in societies where war is part of life (Chick and Loy 2001). This observation, however, is compatible with evolutionary perspectives on socialization and development (e.g., Low 1989). Additionally, the direction of our results was

Table 2 Summary of posterior mean coefficient estimates and 90% credible intervals for individual and global models

	Polygyny	Wives variance	Sex ratio	Male war mortality	Male subsistence
6 outcomes*	0.64 (0.11, 1.16)				
6 outcomes		0.40 (− 0.20, 1.10)			
6 outcomes			− 0.63 (− 1.19, − 0.04)		
6 outcomes				0.46 (− 0.07, 0.96)	
6 outcomes					− 0.54 (− 1.03, 0.03)
6 outcomes	0.60 (0.03, 1.19)	0.52 (− 0.13, 1.26)	− 0.49 (− 1.16, 0.19)	0.34 (− 0.24, 0.88)	− 0.39 (− 1.00, 0.18)

*The 6 outcomes reduced to the latent outcome of "aggressiveness" are as follows: (1) wives taken from hostile groups; (2) warriors have prestige; (3) male scarification; (4) frequent interpersonal violence; (5) ideology of male toughness; (6) aggressiveness valued maintained under the global model, looking at all of the predictors simultaneously. There were some interactions however that we were not able to investigate. For instance, Ember et al. (2007) found that male war mortality and pathogen stress are good predictors of polygyny. We were also not able to rule out alternative hypotheses related to the direction of causality. For instance, sex ratio (as measured by male mortality) may lead to more competition between males, but causality may be bidirectional (Kruger 2010).

Polygyny, sex ratio, and male contribution to subsistence

Although our results support the intrasexual selection hypothesis, two of the results are more straightforward than the third. First, aggressiveness was higher in societies where polygyny is sanctioned, and where it leads to the most intense competition, as measured by variance in number of wives. The effects are consistent with theory and empirical findings from nonhuman animals (Emlen and Oring 1977; Shuster 2009). Second, aggressiveness was lower when males expended at least as much or more effort toward subsistence as do females, which is consistent with a tradeoff between mating effort and effort directed toward other aspects of fitness (Quinlan and Quinlan 2007; Gurven and Hill 2009). This has been documented in chimpanzees (Georgiev et al. 2014) and in human societies where pair-bonds are more stable with intermediate male contributions to subsistence (Quinlan and Quinlan 2007; Kushnick 2016).

The third result, related to sex ratio, is less straightforward. As predicted, relatively biased sex ratios were associated with aggressiveness. Nonetheless, the results run counter to the intuitive and long-held assumption that sexual selection will be stronger when there are more same-sex rivals relative to potential mates in the population (Emlen and Oring 1977; Clutton-Brock and Parker 1992; Kvarnemo and Ahnesjö 1996). To the contrary, it supports the suggestion that, under certain conditions, the converse may be true (Kokko et al. 2012). One possible reason is that a male-biased ASR can lead to an increase in agonistic male-male encounters and a shift away from courtship effort (Weir et al. 2011) but perhaps only when females are easily monopolized into harems (Kokko et al. 2012). Male-biased adult sex ratios can lead to potential same-sex rivals focusing their efforts away from competition for multiple mating opportunities and instead concentrate on a single mate because the competitive environment is unfavorable (i.e., the "scope for competitive investment" is low) (Kokko et al. 2012).

Our results may be consistent with the latter. Although we did not test this within the framework employed in our study, one might expect an interaction between sex ratio and male contribution to subsistence in shaping aggressiveness. When males contribute relatively more to subsistence, they have less scope for competitive investment and, thus, would only engage in competition if the odds were in their favor (i.e., there were relatively more females than males in the population). Interestingly, in the sample of societies where we have information about both variables (prior to imputation), as predicted, there is relatively little scope for competitive investment. For the variable sex ratio: lower 50th percentile, all the societies have males who contribute relatively more to subsistence. For the variable male war mortality, societies have a great majority of males who contribute relatively more to subsistence. Taken together, our findings are consistent with Schacht et al.'s (2014) review of the evidence that human male violence increases with female-biased ASRs and again the importance of male subsistence effort in shaping the evolution of male reproductive strategies (Quinlan and Quinlan 2007; Kushnick 2016).

Another challenge was that our first measure of sex ratio is an imprecise proxy for OSR, the balance of males to females in the mating pool, or even ASR for that matter. For most SCCS societies, the information on sex ratio is based on the entire society rather than the breeding population (Ember and Ember 1992). For this reason, our second measure, male mortality at war, may have provided a better measure because most males in battle are of reproductive age, and previous studies have shown that it relates to polygyny (Ember 1974; Ember et al. 2007; Quinlan and Quinlan 2007). Notwithstanding this challenge, the two measures of sex ratio used were related to male aggression in a similar way. That is, female-biased sex ratios were associated with increased levels of aggressiveness in males.

Measuring male aggressiveness

One challenge for our study was the lack of a direct measure in the SCCS for behavior and beliefs related to male aggression as they pertain to contest competition for mates. We addressed this by using Bayesian IRT to reduce the individual variables related to male aggression to one latent dimension of "aggressiveness." We provided justification in the "Material and Methods" section for the inclusion (and exclusion) of candidate variables and are confident that our measure is a good one. An examination of two additional ethnographic examples of societies in our sample provides additional support.

Here are two examples, one from each of the extreme categories (see our previous analysis Table S5 in the Supplementary Material). In the highest aggressiveness category are societies in which there is frequent personal violence, warriors have a great deal of prestige, wives are taken from neighboring groups, and male scarification, such as piercing, tattooing, cicatrization, or removal of skin, is present. Exemplifying this group are the Yanomamö of Venezuela, among whom Chagnon (2013, p. 220) claims, "fights over women are a major cause of

Yanomamö fighting" and *unokais*, adult males who have killed another adult, have more wives and higher reproductive success on average. In the lowest aggressiveness category are societies with very low levels of interpersonal violence, where warriors do not have prestige, wives are not taken from hostile groups, and male scarification is absent. Exemplifying this group are the Balinese of Indonesia, among whom appropriate male behavior surrounding courtship is described by Jennaway (2002) as being neither "violent nor aggressive" (p. 82). Although male status competition plays out in ultraviolent cockfighting, the relationship of this aspect of Balinese culture to actual behavior is wholly symbolic, and fights among the male participants have not been observed to occur (Geertz 1972).

Conclusion

Our results suggest that factors affecting the intensity of competition for mates are associated with the evolution of beliefs and behavior related to male aggression in small-scale human societies. We argue that this provides support for the hypothesis that intrasexual selection has been a driving force in shaping human male aggression (Archer 2009; Dixson 2009; Lindenfors and Tullberg 2011; Hill et al. 2013; Puts et al. 2015; Puts 2010). Our comparative approach, in seeking a large enough sample to conduct multivariate analyses, used data that overlooked intra-societal variation. For complementarity, future analyses should compare a smaller subset of societies, or communities within a single society, using richer behavioral, ethnographic, and demographic data.

Acknowledgments We thank Carol Ember for providing data on male mortality from war. We thank Michael Jennions and anonymous reviewers for useful feedback on an earlier version of the manuscript. We also thank Caleb Carter for assistance with computation.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This research does not require ethics board approval as it makes use of data from the Standard Cross Cultural Sample, an open source collection of cross-cultural data from 186 cultures.

Informed consent The data in this study comes from a historical and fully web-accessible database; individuals cannot be identified and as such informed consent is not applicable.

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