Behavior and Beliefs Related to Male Aggression: Evidence of Intrasexual Selection in Humans?

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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, as measured by factors such as the presence and scope of polygyny, the number of same-sex competitors relative to potential mates, and the amount of effort males have available to allocate to mating. Using mixed-effect linear regression models with data from 78 societies from the Standard Cross-Cultural Sample, we found strong support for this hypothesis. We were able to rule out some potential alternative explanations by controlling for confounding variables such as political complexity, warfare and geographic clustering.

INTRODUCTION

Sexual selection is an evolutionary force favoring traits that lead to greater mating and, thus, reproductive success (Andersson, 1994; Clutton-Brock, 2004). Darwin (1871) referred to sexual selection via direct physical competition for mates as intrasexual selection. Today, a number of 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 they can use in combat with other males for access to potential mates (Andersson, 1994; Emlen, 2008; Puts, 2010). Many aspects of human male biology and behavior point to an evolutionary history rife with contest competition, leading some

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researchers to suggest that human male aggression has been shaped by intrasexual selection (Archer, 2009; Dixson, 2009; Hill et al., 2017; Hill et al., 2013; Kruger and Fitzgerald, 2012; Lindenfors and Tullberg, 2011; Puts et al,, 2015; Puts, 2010).

Despite this support, there are reasons to question the idea. First, support for positive reproductive and mating consequences of aggression in small-scale societies is mixed (Beckerman et al., 2009; Chagnon, 1988). 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; Gómez et al., 2016; McDonald et al., 2012; Plavcan, 2012). 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: 224) summarize it: “sex differences in aggression follow from the placement of women and men in the social structure.”

To test the idea that male aggression has been shaped by intrasexual selection, we analyzed a composite measure of behaviors and beliefs related to male aggression (referred to hereafter as ‘aggressiveness’) in 78 of the Standard Cross-Cultural Sample’s (SCCS) 186 societies. 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 those behaviors and beliefs provide a higher fitness payoff. To test this hypothesis, we used mixed-effects regression analysis,

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which allowed us to control for potential confounding variables, such as political complexity, 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) biased sex ratios (Clutton-Brock and Parker, 1992; Emlen and Oring, 1977; Kvarnemo and Ahnesjo, 1996; Weir et al., 2011). Because we are using proxy measures for operational sex ratio (OSR), our more specific prediction is that the relationship can have either sign. Since Emlen and Oring (1977) coined the term OSR as a key measure of the potential intensity of sexual selection, the standard prediction has been that male-biased adult sex ratios lead to an increase in male-male competition. More recently, however, Kokko and colleagues (Klug, et al., 2010; Kokko and Jennions, 2008; Kokko et al., 2012; Kokko and Monaghan, 2001; Kokko and Rankin, 2006) 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—leading to an adult sex ratio that is a poor measure of OSR.

(c) higher potential allocations to mating effort as reflected in decreased contributions of males to subsistence tasks, based on the theoretical perspective that mating effort trades off against other aspects of individual fitness (Georgiev et al., 2014; Gurven and Hill, 2009; Quinlan and Quinlan, 2007).

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Material and Methods

Data Source and Variables

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 chosen because of the availability of ethnographic accounts and the degree to which the factors reflect 'traditional' ones (Murdock and White, 1969). The variables used in the study are outlined in more detail in Table S1 of the Supplementary Materials.

One important issue that shaped our analytical strategy was the need to transform variables into a format that allowed for a tractable and consistent multivariate analysis. Most variables in the SCCS are coded into multiple categories with a minority coded as binary or continuous (Ember and Ember, 2009). We started by recoding potential variables into binary format. For continuous variables, we set our cut-off point at the 50th percentile to avoid the statistical problems of doing it arbitrarily. We did this for the following reasons. First and foremost, we wanted "to represent this information in quantitative terms without imposing unrealistic measurement assumptions of categorical variables" (Hardy, 1993). Second, binary predictors of interest simplify the analysis into a comparison of groups, which we felt was necessary to ensure we had sufficient statistical power to test for the effects of interests. We knew that some of the tests would have very small sample sizes. Not every one of the societies in the SCCS has values for every variable, as the

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original coding was done using the information available in existing ethnographic texts. Finally, we knew that sex ratio measures in the SCCS are imprecise (Ember, 1974).

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 such variable exists in the SCCS. We therefore constructed a composite variable using tetrachoric principal components analysis, a data-reduction tool used with binary variables (Kolenikov & Angeles, 2009). Our composite variable 'aggressiveness' was constructed using the following variables: (a) interpersonal violence; (b) warriors have prestige; (c) wives taken from hostile groups; and, (d) male scarification. We chose these variables because they were related to male-on-male aggression related to mating, and initial bivariate analyses suggested that they were statistically associated with the study's predictors of interest. Only societies with non-missing data for all were included in the analyses, leaving 78 societies (see Table S2 in the Supplementary Materials). Our composite dependent variable was constructed using the first principal component, which explained 49% of the variance in these variables. The additional components had eigenvalues of one or less. Our composite variable, thus, had 15 unique values ranging from 0.581 to -2.899 (N=78, M=-0.830, SD=1.104). The following were considered but not included in the final composite variable: (e) male sexual aggressiveness (v175); (f) aggressiveness valued (v625); and, (g) ideology of male toughness (v664).

The predictors of interest were variables that captured factors that we hypothesized should influence the strength of sexual selection: (a) *Polygyny:* Polygynous (0 no, 1 yes); and, 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 no, 1 yes). Neither of these is a perfect measure of OSR, or even adult sex ratio. (c) *Other Factors:* Males Expend Subsistence Effort (0 no, 1 yes). Note that all percentiles were calculated using non-missing values from the entire sample of 186 societies.

The second set of independent variables were factors (e.g., warfare and political complexity) that might confound the hypothetical relationships (Ember et al., 2007). The sparse sampling of societies across language families in the SCCS 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, referred to as 'Galton's Problem' in cross-cultural studies like this one (Mace and Holden, 2004). We have included three control variables to adjust for these factors: Political Complexity (0 no state, 1 state); Frequent Warfare (0 no, 1 yes); and, Region (6 regions).

Models and Hypothesis Tests

We conducted all statistical analyses in Stata 13. For each of the focal independent variables, we used two mixed-effects linear-regression models (Rabe-Hesketh and Skrondal, 2008) for inference estimated using maximum likelihood techniques: a bivariate version, and a multivariate version with controls for complexity and warfare. All of the models included a random-effects (intercept) term (Guassian) for region to control for shared history and environment. We ran separate models for each predictor of interest, then Bonferroni-adjusted p-values and confidence intervals, because there were insufficient observations to run global models. Only one of the 78 societies used in this study—the

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Kwoma—had non-missing data for all variables. We, thus, were not able to fully explore the interactions amongst the predictors of interest (Nakagawa and Cuthill, 2007). Yet, only one pair of these variables was correlated, as shown in Table S3 in the Supplementary Materials, suggesting that our estimates of the effects of individual predictors were reasonable measures of the true effects.

RESULTS

In Table 1, we provide a summary of the variables used in the study. One important thing to note is that, although the overall sample is 78 societies, for some of the independent variables of interest, the samples sizes are much smaller.

Table 1. Descriptive statistics (n=78 societies).

	n	Prop.
Dependent Variables:		
Frequent Personal Violence	78	0.69
Warriors Have Prestige	78	0.53
Wives Taken from Hostile Groups	78	0.49
Male Scarification	78	0.69
Independent Variables:		
Polygyny:		
Polygynous	78	0.88
Wives (Variance): Upper 50th %ile	44	0.50
Sex Ratio:		
Sex Ratio: Lower 50th %ile	41	0.44
Male Mortality from War	42	0.62
Other:		
Males Expend Effort Toward Subsistence	34	0.76
Control Variables:		
Political Complexity (State)	78	0.09
Warfare Frequent	74	0.68
Region:		
Africa	14	0.18
Circum-Mediterranean	11	0.14
East Eurasia	9	0.12
Insular Pacific	16	0.21
North America	19	0.24
South America	9	0.12

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We estimated associations between the predictors of interest and 'aggressiveness' using bivariate and multivariate versions of mixed-effect (random intercept) linear regression models. We provide the details of the models in Table 2; information about covariates included below and in Methods. Because we used multiple variables as measures of each of the first two effects (polygyny and sex ratio), we made Bonferroni corrections to p-values. Although the directionality and significance of the estimates were the same in both models, there were some differences in effect sizes. For this reason, we used the estimates derived from the multivariate models for inference.

Figure 1 illustrates the results of our hypothesis tests. Each bar is the size of the effect estimate for the variable of interest in the multivariate models—i.e., those that control for political complexity, warfare and region. The error bars are Bonferroni-adjusted confidence intervals (97.5% confidence intervals for the measures of polygyny and sex ratio, and 95% confidence intervals for the other predictor). The results can be described as follows:

(a) *Polygyny:* The first cluster in Figure 1 are the variables used to measure the presence and scope of polygyny. As predicted, aggressiveness is higher in societies with polygyny, as well as in those societies whose variance is in the upper 50th percentile for variance in number of wives, even after controlling for region, political complexity, and warfare.

(b) *Sex Ratio:* The second cluster in Figure 1 are the variables used to measure biased sex ratios. As predicted, aggressiveness was associated with biased sex ratios, even after controlling for region, political complexity, and warfare. Societies with female-biased sex

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Table 2. Details of the mixed-effect linear regression models, including two models (bivariate and multivariate) for each predictor of interest. Each of the ten models includes a random-effects term for region. p-values have been adjusted using the Bonferroni correction.

Model	A. Bivariate			B. Multivariate		
	β	*P*(adj)	*n*	*β*	*P*(adj)	*n*
Polygyny:						
1. *Polygyny:*						
Constant	-1.63	--	78	-2.64	--	74
Polygynous	0.89	0.038		1.03	<0.002	
Complexity	--	--		-0.02	0.998	
Warfare	--	--		1.42	<0.002	
2. *Variance in # of Wives:*						
Constant	-1.43	--	25	-2.26	--	24
Wives (Variance): Upper 50th %ile	1.46	<0.002		0.74	0.020	
Complexity	--	--		0.67	0.262	
Warfare	--	--		1.72	<0.002	
Sex Ratio:						
3. *Sex Ratio:*						
Constant	-0.71	--	24	-0.91	--	22
Sex Ratio: Bottom 50th %ile	-0.63	0.154		-0.79	0.107	
Complexity	--	--		-1.18	0.120	
Warfare	--	--		0.99	0.079	
4. *War Mortality:*						
Constant	-1.70	--	42	-1.85	--	40
Male War Mortality	1.31	<0.002		0.93	0.010	
Complexity	--	--		0.23	0.941	
Warfare	--	--		0.76	0.044	
Other:						
5. *Subsistence Effort:*						
Constant	-0.05	--	34	-0.84	--	32
Male Effort Toward Subsistence	-0.90	0.015		-0.73	0.011	
Complexity	--	--		-0.54	0.300	
Warfare	--	--		1.05	<0.001	

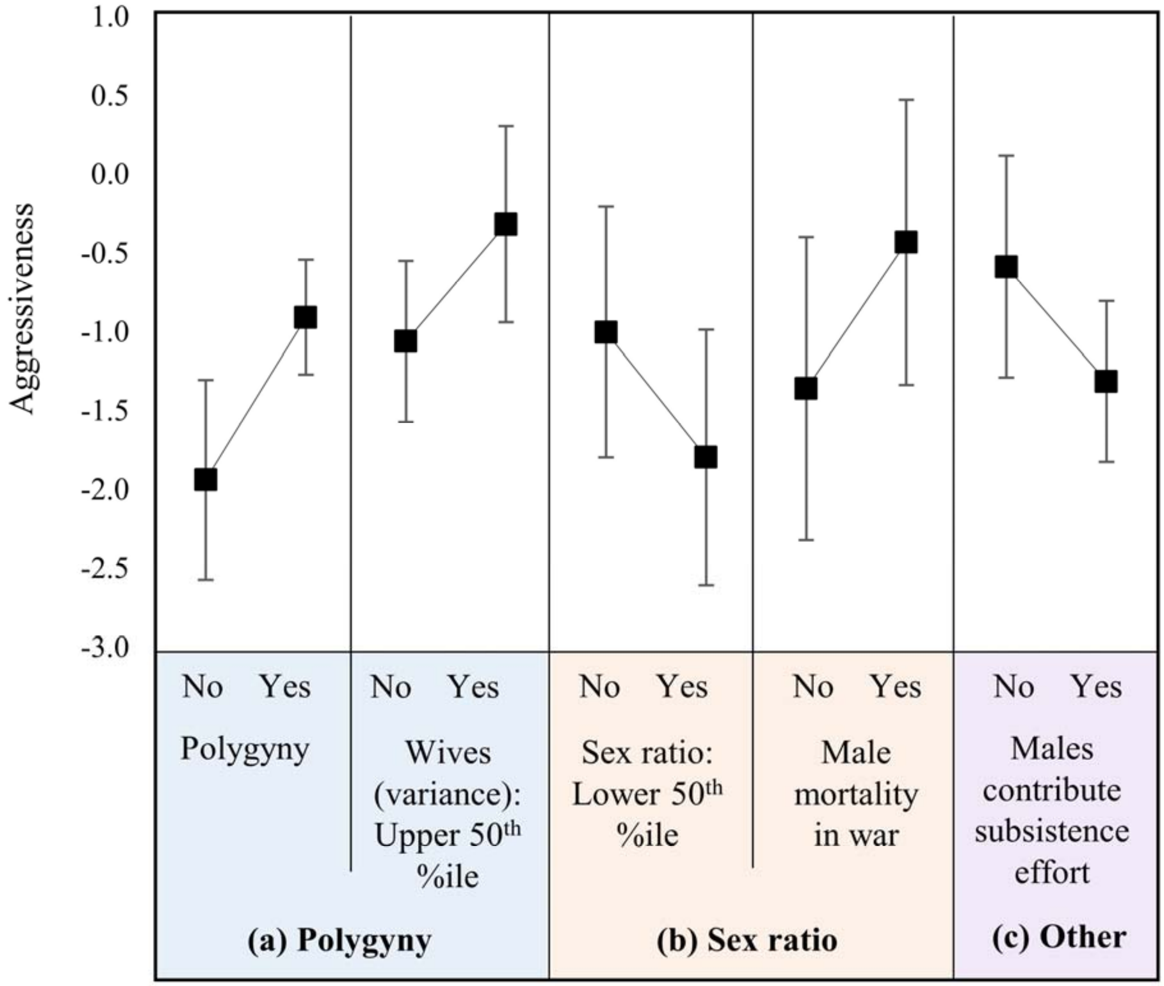

Figure 1. Estimates of the effects of various factors that influence the strength of sexual selection on ‘aggressiveness', a composite measure of behavior and beliefs related to male aggression. We drew inference from mixed-effects linear regression models, controlling for political complexity, presence of frequent warfare, and geographic region. Confidence intervals were Bonferroni-corrected.

ratios (those with sex ratios in the lower 50th percentile or male mortality at war) had higher levels of aggressiveness.

(c) *Other:* The right-most bar in Figure 1 is the variable used to measure the ability of males to invest in mating effort. As predicted, societies in which males contribute to subsistence, and thus had lower ability to invest in mating, had lower levels of aggressiveness.

DISCUSSION

Although all of the results of our analyses support the hypothesis that intrasexual selection has shaped male aggression, the first two results are more straightforward than the third. First, aggressiveness was higher in societies where polygyny is allowed, 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 non-human animals (Emlen and Oring, 1977; Shuster, 2009). Second, aggressiveness was lower when males expended effort toward subsistence, which is consistent with a tradeoff between mating effort and effort directed toward other aspects of fitness (Gurven and Hill, 2009; Quinlan and Quinlan, 2007). This has been documented in chimpanzees (Georgiev et al., 2014) and in human societies where pairbonds are more stable with male-female substistence complementarity (Quinlan and Quinlan, 2007).

The sex ratio results are 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 (Clutton-Brock and Parker, 1992;

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Emlen and Oring, 1977; Kvarnemo and Ahnesjo, 1996) but supports the suggestion that, under certain conditions, the converse may be true (Kokko and Jennions, 2008; Kokko et al., 2012; Kokko and Monaghan, 2001; Kokko and Rankin, 2006). On one hand, a male-biased OSR 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 (Fromhage et al., 2005; Kokko et al., 2012). On the other hand, male-biased adult sex ratios may lead to potential same-sex rivals focusing their efforts away from mating altogether because the competitive environment is unfavorable (i.e., the 'scope for competitive investment' is low) (Kokko et al., 2012). Our results are consistent with the latter. This is not unexpected, as a recent review by Schacht et al. (2014) suggests that human male violence may increase with female-biased adult sex ratios.

One 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 adult sex ratio for that matter. For the vast majority of 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 an increased levels of aggressiveness in males.

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Another challenge was that the SCCS has no direct measure of behavior and beliefs related to male aggression as they pertain to contest competition for mates. In response, we constructed a composite ('aggressiveness') using principal components analysis. We are confident that it is an efficacious measure for the following reasons: First, with the exception of interpersonal violence, all of the variables used to create the composite were chosen because they capture *male*-specific aggression that would primarily be targeting sexual rivals. Without trivializing male-on-female violence or the ability of females to behave violently, male-on-male violence is overwhelmingly the most common type in human societies (Archer, 2009) and aggression by females is usually indirect rather than physical (Vaillancourt, 2013). Second, we excluded potential variables for failing to meet minimum requirements. For example, we did not use variables that showed no statistical relationship to the predictors of interest in a preliminary analysis, which used Bonferroni corrections to mitigate the problems of increased Type-I error probability. Further, we excluded variables, such as male sexual aggressiveness, that better encapsulated male forwardness and hostility toward females during mating than antagonistic interactions with males. Third, many have paid attention to male scarification as an ornament (e.g., a signal of mate quality), but much less attention has been paid to scarification as an armament (Ludvico and Kurland, 1995). 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).

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Fourth and finally, by examining ethnographic accounts of the societies in our sample, it is clear that the aggressiveness values ascribed to each by our composite variable are approximately correct (see Table 3). Here are two examples, one from each of the extreme categories. 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, cicatrisation or removal of skin is present. Exemplifying this group are the Yanomamo of Venezuela, who Chagnon (1988) described as have mating competition where males "represent themselves as aggressively as possible, indicating to potential competitors that affronts, insults, and cuckoldry will be immediately challenged and met with physical force." 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, amongst whom appropriate male behaviour 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 amongst the male participants never occur (Geertz, 1972).

By using multivariate methods, we were able to rule out a number of alternative explanations. First, it could be that warfare, societal complexity, or some combination of the two confounds the relationships of interest (Ember, 1974). That is, the positive association between aggressiveness and male mortality in warfare could be explained by the presence of warfare without the need to invoke sexual selection. Similarly, it has been

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Table 3. Societies by a 'aggressiveness' (a composite variable constructed using the first principal component of four variables from the SCCS that together measure behaviour and beliefs related to male aggression.) Highlighted societies discussed in text.

Category:	HIGHEST	INTERMEDIATE	LOWEST
Aggressiveness:	Greater than 0	Less than 0, but greater than -1	Less than -1
Societies:	0.581 Aleut, Aranda, Azande, Comanche, Fon, Maori, Masai, Mende, Mundurucu, Omaha, Teda, Thonga, Tiwi, Tupinamba, ***Yanomamo*** 0.061 Ashanti, Ganda, Jivaro, Kikuyu, Lolo, Orokaiva	-0.273 Abipon, Chiricahua, Creek, Gheg Albanians, Huron, Ifugao, Kurd, Kwoma, Nama, Hottentot, Riffians, Rwala Bedouin -0.407 Hidatsa, Ingalik, Kaska, Mbau Fijians, Tiv, Western Samoans, Yapese -0.536 GrosVentre, Otoro Nuba -0.793 Nyakyusa, Trobrianders -0.928 Ainu, Gilyak, Wolof, Yukaghir	-1.057 Tuareg -1.262 Goajiro, Marquesans, Montagnais, Paiute (North), Pomo (Eastern), Tikopia -1.391 Amhara, Haitians, Iban, Papago -1.525 Havasupai, Natchez -1.782 Aweikoma, Egyptians, Manus -2.045 Pastoral Fulani -2.379 Kung Bushmen, Mbuti, Santal, Siamese, Trukese, Trumai, Yurok -2.899 ***Balinese***, Copper Eskimo, Lapps, Lepcha, Vedda, Yokuts (Lake), Yurak Samoyed

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). It also could be that simpler societies are more likely to allow polygyny and value aggression without necessitating a causal link between the two. Finally, shared cultural histories and environments can lead to spurious cross-cultural correlation. Our results stood up to statistical control of these factors. There were insufficient cases with non-missing data to run a global model, or even models to explore just two predictors simultaneously, so we were only able to explore the interrelationship of predictors using bivariate tetrachoric correlation.

Our analyses focused, for the most part, on small-scale societies. As shown in Table 1, only 9% of the 78 SCCS societies that we used were state-level societies. Although the frequency of male-male aggressiveness (and lethal violence) in small-scale societies contrasts with the state societies (Walker and Bailey, 2013) male-male violence is still problematic in modern societies especially where there are high levels of economic inequality (Daly, 2016). Pinker (2011) suggests that a number of factors, present in modern progressive societies, can lead to a decrease in aggressive behavior and violence, as even early Western civilization was plagued by these social ills (Gottschall, 2008). These perspectives suggest that although sexual selection has created human males who use aggression and violence to gain reproductive advantage, we are not cursed to a future of aggression and violence. To the contrary, we may be able to decrease the amount of violence in our society by embracing progressive values and policies that decrease inequality.

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In conclusion, our results suggest that factors affecting the intensity of competition for mates lead to the evolution of beliefs and behavior related to male aggression in small-scale human societies. This provides support for the hypothesis that sexual selection has been a driving force in shaping human male aggression (Archer, 2009; Dixson, 2009; Hill et al., 2013; Lindenfors and Tullberg, 2011; 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 (along the lines of the research described in Apicella and Barrett, 2016).

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