Male Aggressiveness as Intrasexual Contest Competition in 78 Societies.

Tara-Lyn Carter[1,2,3] & Geoff Kushnick[1,3]

[1] School of Archaeology and Anthropology, The Australian National University, Canberra

[2] School of Biological Sciences, Monash University, Melbourne, Australia

[3] Co-first authors

Corresponding author: Tara-Lyn Carter, email: tara-lyn.carter@monash.edu

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: (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 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 mixed support for the hypothesis using individual variables related to male aggression, but strong support when using a composite measure of male 'aggressiveness'. We ruled out some potential alternative explanations by controlling for spatial autocorrelation, 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

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study to do so. 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 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

1. Introduction

Sexual selection is an evolutionary force favoring traits that lead to greater mating and, thus, reproductive success (Andersson 1994; Clutton-Brock 2004). 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 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). Many aspects of human male biology and behavior point to an evolutionary history rife with contest competition, leading some 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 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; 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." For these reasons, we feel that a test of the idea with data from a wide range of societies is necessary.

To test the idea that male aggression has been shaped by intrasexual selection, we analyzed both individual measures related to male aggression, and a composite measure of 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

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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 behavioral ecology theory.

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 mixed-effects regression analysis, 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, but that the sign should be consistent across measures. 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.

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(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 (Georgiev et al. 2014; Gurven and Hill 2009; Quinlan and Quinlan 2007).

2. Material and Methods

2.1. Analytical Strategy

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 are 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 provide 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 re-coding 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 recoded binary for the following reasons. First, we wanted "to represent this information in quantitative terms without imposing unrealistic measurement assumptions of categorical variables" (Hardy 1993: 2). 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, 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 original coding used the information available in existing ethnographic texts.

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2.2. 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, 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 adult sex ratio. (c) *Other Factors:* Male Subsistence Effort (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, set 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; Mace and Holden 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 following independent variables: (a) Region (6 regions) was included as a random effect in the regression models; and, (b) spatially-lagged variables were constructed to capture spatial effects in both the dependent variable and the predictors of interest using a routine that allows for a spatial-weight matrix to be constructed using latitude and longitude coordinates (Kondo 2016), which are available in for each society in the SCCS.

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2.3. Dependent Variables/Composite

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 initially performed multilevel logistic regression analyses on the following variables we hypothesized to be good predictors of male intrasexual aggression: (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). We then chose to construct a composite variable for male intrasexual aggressiveness using tetrachoric principal components analysis (PCA), a data-reduction tool used with binary variables (Kolenikov and Angeles, 2009). We did so because the initial bivariate analyses simply did not have great enough statistical power when variables were analyzed individually, usually due to missing cases among variables. This is because not every society in the SCCS has recorded data for every variable. The results of these early analyses can be viewed in Table 1. The variables we included in the composite 'aggressiveness' variable were chosen because they are related to male-on-male aggression associated with mating, and initial bivariate analyses showed they were the best balance of two important factors: They were statistically associated with the study's predictors of interest and allowed for the greatest retention of cases (i.e., they had fewer missing values). Therefore, our composite variable 'aggressiveness' was constructed using the binary recodes of the above variables, excluding: (e) Male Sexual Aggressiveness; (f) Aggression Valued, and (g) Ideology of Male Toughness. Table S2 provides more details about the dependent variables used in the study.

To illustrate further our procedures for selecting dependent variables for the 'aggressiveness' composite, 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 for the composite. There is a clear cut off whereby the top-four variables are clearly better performers than the bottom-three with regards to association with the predictors of interest (20-80% versus 0-20% of the coefficients were reasonable predictors) and retention of cases (28 to 55, versus 78-126, missing of the 186 SCCS societies).

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Only societies with non-missing data for all four dependent variables used to construct the composite were included in the analyses, leaving 78 societies. Our composite dependent variable used to measure male 'aggressiveness' was constructed using the first principal component of the tetrachoric principal components analysis (Kolenikov and Angeles 2009), which explained 49% of the variance in these variables. The additional components had eigenvalues of one or less, so they were excluded (Quinn and Keough 2002). Our composite variable, thus, had 15 unique values ranging from 0.581 to -2.899 (N=78, M=-0.830, SD=1.104), as shown in Table 2.

We are confident the composite variable is an efficacious measure of male 'aggressiveness' for several reasons. First, the variables included in the composite 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 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). Female violence is often indirect rather than physical (Vaillancourt 2013). Further, we excluded another candidate variable, Male Sexual Aggressiveness, because it captures male forwardness towards females during mating (ranging from 'shy' to 'hostile'), rather than agonistic interaction with males (Broude and Greene 1976).

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 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. So, the inclusion of scarification is justified because it serves the dual purpose of ornament and armament.

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Table 1 Summary of preliminary multilevel logistic regression analyses

Variable	SCCS	n	Missing	Predictors: p≤0.10
Included in composite:				
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%)
Excluded from composite:				
Ideology of Male Toughness	v664	108	78	1/5 (20%)
Aggressiveness Valued	v625	81	105	1/5 (20%)
Male Sexual Aggressiveness	v175	60	126	0/5 (0%)

2.4. Models and Hypothesis Tests

To test hypotheses about the relationships between the factors that affect the intensity of sexual selection and 'aggressiveness' we used mixed-effects linear-regression models estimated using maximum likelihood techniques (Rabe-Hesketh and Skrondal 2008). All models included a random effects (intercept) term (Gaussian) for Region as one adjustment for the effects of phylogenetic and spatial autocorrelation. We ran separate models for each predictor of interest, then Bonferroni-adjusted p-values, because there were insufficient observations to run global models. Only one of the 78 societies used in this study—the Kwoma, had non-missing data for all variables (see Table S3 in the Supplementary Materials). Thus, we were not able to explore fully the interactions amongst the predictors of interest (Nakagawa and Cuthill 2007). Yet, only one pair of the predictors of interest displayed a significant correlation, as shown in Table S4 in the Supplementary Materials, suggesting that our estimates of the effects of individual predictors were reasonable measures of the true effects.

Our inference from the regression models included two steps. In the first, we built two sets of regression models for each predictor of interest to decide whether these independent variables had a confounding effect on the relationships of interest and, thus, should be included in models used for inference: (a) bivariate models (predictor of interest on 'aggressiveness') and (b) multivariate models (with Political Complexity and Warfare added). In the second, we built three sets of regression

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models for each predictor of interest to examine whether spatially-lagged models were better suited for inference than models without spatial adjustment (following the example in Kondo 2016): (a) bivariate models (with no spatially-lagged variables); (b) spatially-lagged models (with adjustment for spatial autocorrelation in the composite dependent variable); and, (c) spatially-lagged models (with adjustments for autocorrelation in the dependent variable and the predictors of interest).

Table 2 Societies (n=78) by male 'aggressiveness' (a composite variable constructed using the first principal component of four variables from the SCCS that together measure behavior and beliefs related to male aggression.) Highlighted societies discussed in text of Discussion

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

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3. Results

3.1. Descriptive Statistics

In Table 3, we provide descriptive statistics for the variables used in the study. One important thing to note is that, although the overall sample for which we could calculate the composite dependent variable is 78 societies, for some of the independent variables of interest, the samples sizes are much smaller.

Table 3 Descriptive statistics (n=78 societies)

	n	0	1	Prop.
Dependent Variables:				
Frequent Interpersonal Violence	78	24	54	0.69
Warriors Have Prestige	78	37	41	0.53
Wives Taken from Hostile Groups	78	40	38	0.49
Male Scarification	78	24	54	0.69
Independent Variables:				
Polygyny:				
Polygynous	78	9	69	0.88
Wives (Variance): Upper 50th %ile	25	12	13	0.52
Sex Ratio:				
Sex Ratio: Lower 50th %ile	24	8	16	0.67
Male War Mortality	42	16	26	0.62
Other:				
Male Subsistence Effort	34	8	26	0.76
Control Variables:				
Political Complexity	78	71	7	0.09
Warfare	74	24	50	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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3.2. Model Building

In the first step of building models to be used for hypothesis testing, we estimated associations between the predictors of interest and 'aggressiveness' using bivariate and multivariate versions to assess confounding (see Table 4). The coefficients for the predictors of interest show evidence that Political Complexity and Warfare confounded the relationships of interest. When we added the potential confounders, there were substantive changes in the estimated coefficients for the predictors of interest ranging from -49 to +16%. For this reason, we used the multivariate versions of the models to test our focal hypotheses.

In the second step, we estimated associations between the predictors of interest and 'aggressiveness' using multivariate versions of the models, while including spatially-lagged variables to assess and control for phylogenetic and spatial autocorrelation (see Table 5). With the addition of spatially-lagged control variables that adjust for spatial autocorrelation in the dependent variable (Table 5b) and dependent variables plus predictors (Table 5c), there are changes in estimated coefficients for the predictors of interest of up to 24% (relative to the non-spatial models in Figure 5a). For this reason, we used the models that included spatially lagged versions of the dependent variable and predictors of interest for hypothesis testing—i.e., those in Table 5c.

Table 4 Confounding: Coefficients for predictors of interest in multilevel mixed effect models with random effects (intercept) terms (Gaussian) for Region: (a) bivariate models include the predictors of interest on the composite dependent variable, (b) multivariate models include controls for Political Complexity and Warfare

Predictor of Interest	**(a)**			**(b)**			$\Delta\beta_{a \to b}$
	n	β		**n**	β		
Polygyny:							
Polygyny	78	0.89	*	74	1.03	***	+16%
Wives (Variance): Upper 50th %ile	25	1.46	***	24	0.74	*	-49%
Sex ratio:							
Sex Ratio: Lower 50th %ile	24	-0.63		22	-0.80	†	-25%
Male War Mortality	42	1.31	***	40	0.93	**	-42%
Other:							
Male Subsistence Effort	34	-0.90	*	32	-0.73	*	-19%

***p<0.001, **p<0.01, *p<0.05, †p<0.10.

3.3. Hypothesis Tests

To test the study's focal hypotheses, we used estimates from the models in Table 5c. The results are illustrated in Figure 1, where the estimates are bound by Bonferroni-adjusted confidence intervals. In this case, our adjustments were for the number of predictors of interest used for each of the three hypotheses. They can be described as follows:

(a) *Polygyny:* The first cluster in Figure 1 comprises the variables used to measure the presence and scope of polygyny. As predicted, aggressiveness is higher in societies with polygyny (contrast=1.04, z=3.52, adjusted p<0.001), as well as in those societies who are in the upper 50th percentile for variance in number of wives (contrast=0.79, z=2.81, adjusted p=0.005), even after controlling for region, political complexity, warfare, and spatial autocorrelation. Because we used two hypothesis tests, the confidence intervals are Bonferroni-adjusted, as are the p-values for our test of difference between the estimates.

(b) *Sex Ratio:* The second cluster in Figure 1 comprises the variables used to measure biased sex ratios. As predicted, aggressiveness was associated with biased sex ratios, even after controlling for region, political complexity, warfare, and spatial autocorrelation. Societies with relatively more female-biased sex ratios—measured as both being in the lower 50th percentile for sex ratio (contrast= -0.79, z= -1.92, adjusted p=0.054), and higher male war mortality (contrast=1.15, z=3.47, adjusted p=0.001)—had higher levels of aggressiveness. Because we used two hypothesis tests, the confidence intervals are Bonferroni-adjusted, as are the p-values for our test of difference between the estimates.

(c) *Other:* The third, and right-most, cluster in Figure 1 comprises the variable 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 mating, showed lower levels of aggressiveness, even after controlling for region, political complexity, warfare, and spatial autocorrelation (contrast= -0.72, z= -2.41, p=0.016). Because we test only one hypothesis, we made no Bonferroni adjustment to confidence intervals or p-values for the test of difference.

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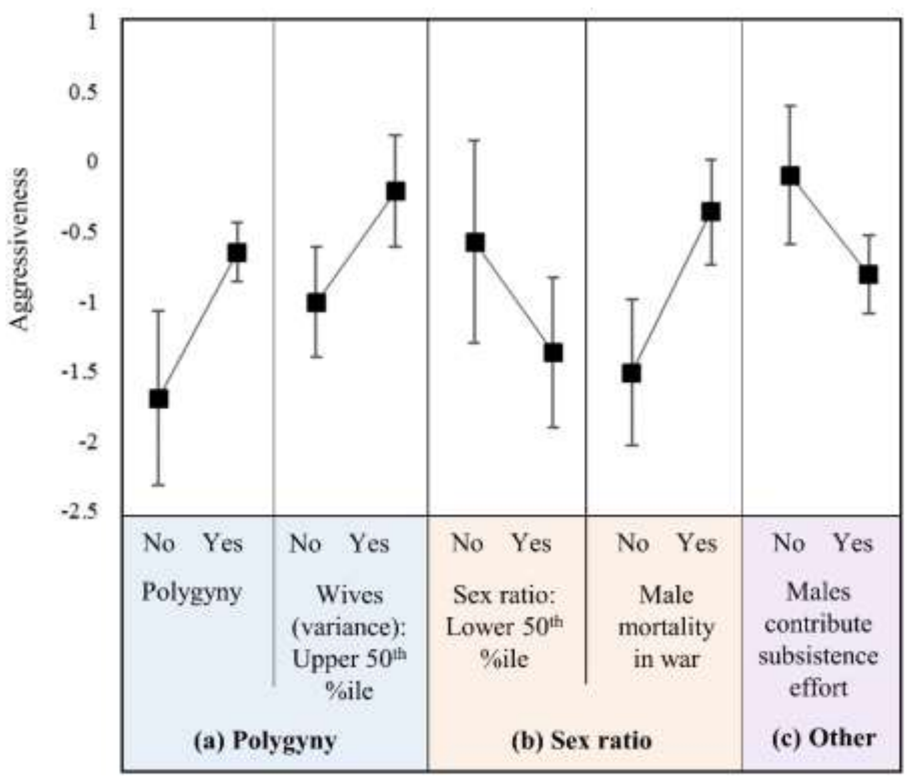
Table 5 Details of the mixed-effect linear regression models with random effects (intercept) terms (Gaussian) for Region: (a) multivariate model with no spatial variables added; (b) multivariate model with spatially-lagged dependent variable; and, (c) multivariate model with spatially-lagged dependent variable and predictor of interest

	n	(a)		(b)		(c)	
		β	***p***	***β***	***p***	***β***	***p***
Polygyny:							
1. Polygyny							
Constant	74	-2.64	--	-2.77	--	-3.52	--
Polygynous		1.03	<0.001	1.06	<0.001	1.04	<0.001
Political Complexity		-0.02	0.952	<0.01	0.993	-0.03	0.921
Warfare		1.42	<0.001	1.44	<0.001	1.44	<0.001
Aggressiveness (Spatial)		--	--	-0.11	0.594	-0.18	0.410
Polygynous (Spatial)		--	--	--	--	0.83	0.295
2. Variance in # of Wives:							
Constant	24	-2.26	--	-2.45	--	-2.76	--
Wives (Variance): Upper 50th %ile		0.74	0.010	0.76	0.007	0.79	0.005
Political Complexity		0.67	0.141	0.68	0.126	0.69	0.117
Warfare		1.72	<0.001	1.73	<0.001	1.72	<0.001
Aggressiveness (Spatial)		--	--	-0.26	0.249	-0.35	0.150
Wives (Var.): Upper 50th %ile (Spatial)		--	--	--	--	0.40	0.361
Sex Ratio:							
3. Sex Ratio:							
Constant	22	-0.91	--	-1.32	--	-1.62	--
Sex Ratio: Lower 50th %ile		-0.80	0.055	-0.73	0.078	-0.79	0.054
Political Complexity		-1.18	0.062	-1.12	0.054	-1.21	0.048
Warfare		0.99	0.018	0.99	0.016	0.86	0.047
Aggressiveness (Spatial)		--	--	-0.47	0.412	-0.34	0.555
Sex Ratio: Lower 50th %ile (Spatial)		--	--	--	--	1.11	0.367
4. War Mortality:							
Constant	40	-1.85	--	-1.48	--	-1.15	--
Male War Mortality		0.93	0.005	1.05	0.001	1.15	0.001
Political Complexity		0.23	0.755	0.14	0.851	0.19	0.797
Warfare		0.76	0.022	0.63	0.055	0.59	0.069
Aggressiveness (Spatial)		--	--	0.42	0.106	0.38	0.135
Male War Mortality (Spatial)		--	--	--	--	-0.75	0.195
Other:							
5. Subsistence Effort:							
Constant	30	-0.84	--	-0.98	--	0.21	--
Male Subsistence Effort		-0.73	0.011	-0.71	0.014	-0.71	0.016
Political Complexity		-0.54	0.300	-0.51	0.334	-0.51	0.370
Warfare		1.05	<0.001	1.04	<0.001	1.04	0.001
Aggressiveness (Spatial)		--	--	-0.17	0.533	-0.17	0.533
Male Subsistence Effort (Spatial)		--	--	--	--	<0.01	0.994

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 the fixed effects of political complexity, warfare, and spatially-lagged versions of the dependent variables and predictors of interest, and random effects of region. Confidence intervals were Bonferroni-corrected



4. Discussion

4.1. What the Results Show (and What They Do Not)

The results of our study lend support to the hypothesis that intrasexual selection has shaped male aggressiveness in human societies. Although our initial analyses of individual variables related to male aggression provided mixed support, our analyses of a composite dependent variable that better encapsulated 'behavior and beliefs related to male aggression' provided strong support. We appreciate that this aspect of human sociality is shaped by complex interactions between biological and social factors, and make no claim to have illuminated its genetic or cultural underpinnings. What we have shown is that, in societies with conditions that increase the intensity of male mating

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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).

By using multivariate methods, we 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 (Mace and Holden 2004). Our results stood up to statistical control for spatial autocorrelation. 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., Belsky et al. 1991; Lo, 1989).

We were not, however, able to rule out alternative explanations that would require looking at two or more of the predictors simultaneously. We had an insufficient number of cases with non-missing data to run a global model, or even models to explore just two predictors at once. For this reason, we were only able to explore the interrelationship of predictors using bivariate tetrachoric correlation. Only one set of predictors were correlated. Nonetheless, there are reasons to believe that some of the variables might have displayed interesting dynamics if we were able to explore them. 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 bi-directional (Kruger 2010).

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4.2. 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 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 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 (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 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 (Clutton-Brock and Parker 1992; Emlen and Oring 1977; Kvarnemo and Ahnesjo 1996). To the contrary, it 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). One possible reason: 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). Another possible reason: 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 may be consistent with the latter. Although it would be impossible to test with the regression framework employed in our study as sample sizes are too small to look at interactions between the independent variables, 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 very small sample of societies where we have information about

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both variables, as predicted, there is relatively little scope for competitive investment. For the variable Sex Ratio: Lower 50th Percentile, all the societies (9 of 9, 100%) have males who contribute relatively more to subsistence; for the variable Male War Mortality, a great majority have 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 adult sex ratios, 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 adult sex ratio 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.

4.3. 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. Our initial analyses, where we used individual variables related to male aggression as dependent variables provided mixed support for the overarching hypothesis. In response, we constructed a composite ('aggressiveness') using principal components analysis. We provided justification in the 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 Table 1). 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

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Yanomamö of Venezuela, among whom Chagnon (2013: 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 (Chagnon 1988). 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 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 amongst the male participants have not been observed occur (Geertz 1972).

4.4. 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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