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

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Abstract

Sexual selection favours 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 behaviour 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 male contribution to subsistence. Using data from a global sample of 78 societies, we found strong support for this hypothesis. We discuss potential alternative explanations for the relationships, ruling out some using multivariate methods to control for confounding variables such as political complexity, warfare and geographic clustering.

Introduction

Sexual selection is an evolutionary force favouring traits that lead to greater mating and reproductive success (Darwin 1871, Andersson 1994, Clutton-Brock 2004). Darwin (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 sexual dimorphism in body size or armamentation, usually in males (Andersson 1994, Emlen 2008). Many aspects of human male biology and behavior point to an evolutionary history rife with contest competition (Hill, Hunt et al. 2013, Puts, Bailey et al. 2015), leading some scholars to suggest that human male aggression has been shaped by intrasexual selection (Archer 2009). To

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address this notion, we analyse the distribution of aggressive behaviours and beliefs across 78 small-scale societies.

Our overarching hypothesis is that behavior and beliefs related to male aggression should covary with factors influencing the strength of intrasexual selection. Specifically, we predict the following to be associated with higher levels of aggression: (a) increased intensity of mating competition reflected in the presence and scope of polygynous practices (Emlen and Oring 1977, Shuster 2009); (b) increased intensity of mating competition as reflected in male-biased sex ratios (Emlen and Oring 1977, Kvarnemo and Ahnesjo 1996, Weir, Grant et al. 2011); and, (c) higher potential allocations to mating effort as reflected in decreased contributions of males to subsistence tasks (Gurven and Hill 2009). These relationships should hold when controlling for potential confounding variables, such as political complexity, warfare and geographic clustering.

METHODS

We used data from the Standard Cross-Cultural Sample (SCCS) to test for an association between behavior and beliefs related to male aggression 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 behaviour (Murdock and White 1969). The variables we used for this study are summarized below, and complete details are included in Table S2 in the SEM. Descriptive statistics are provided in Table 1.

To obtain a single, composite measure of the level of aggressiveness in male behaviours and beliefs for each society, we conducted a principal components analysis with a routine that uses polychoric (tetrachoric) correlation to accommodate binary variables (Kolenikov and Angeles

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2009): Frequent Interpersonal Violence (0 no, 1 yes); Warriors Have Prestige (0 no, 1 yes); Wives Taken from Hostile Groups (0 no, 1 yes); and, Male Scarification (0 no, 1 yes). Only societies with non-missing data for all were included in the analyses, leaving 78 societies. The first principal component, which we used as the dependent variable, explained 49% of the variance in these variables. The additional factors had eigenvalues of 1 or less.

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

	Yes	No	M	SD
Dependent Variables:				
Frequent Personal Violence	54	24	–	–
Warriors Have Prestige	41	37	–	–
Wives Taken from Hostile Groups	38	40	–	–
Male Scarification	54	24	–	–
Independent Variables:				
Polygyny:				
Polygynous	69	9	–	–
Mean # of Wives	–	–	1.5	0.14
Variance in # of Wives	–	–	0.4	0.08
Sex Ratio:				
Sex Ratio (m/f x 1000)	–	–	110.3	4.54
Male Mortality from War	26	16	–	–
Other Factors:				
Males Expend Effort Toward Subsistence	26	8	–	–
Control Variables:				
Political Complexity	7	71	–	–
Warfare Frequent	50	24	–	–
Region [1]	–	–	–	–

[1] Eight dummy variables for 9 regions.

The first set of independent variables were those that captured factors that we hypothesized should influence the strength of sexual selection: (a) *Polygyny:* Polygynous (0 no, 1 yes); Mean Number of Wives in the Upper 50th percentile (0 no, 1 yes); and, Variance in Number of Wives

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in the Upper 50th percentile (0 no, 1 yes). (b) *Sex Ratio:* Sex Ratio in the Lower 50th percentile (0 no, 1 yes); and, Male War Mortality (0 no, 1 yes). (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. The sparse sampling of societies across language families in the SCCS precluded the use of phylogenetic methods to control for shared cultural history (Mace and Holden 2004), which can lead to spurious cross-cultural correlation. 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 (10 regions with 9 dummy variables).

We conducted all statistical analyses in Stata 13. For each of the focal independent variables, we used two ordinary least-squares linear regression models for inference: a bivariate model, and a multivariate model with controls for complexity, warfare, and any region variables that were significant predictors of the outcome in a separate regression model.

RESULTS

The direction and statistical significance of associations between the focal independent variables and level of aggression were essentially identical in the bivariate and multivariate models. We thus drew inference from the multivariate models. The complete details of all models are provided in Table S3 in the SEM.

The associations between the focal independent variables and aggression, while controlling for political complexity, warfare, and region (when appropriate) are shown in Figure 1. As predicted, the presence of polygyny, higher mean number of wives, and higher variance in number of wives had positive associations with male aggressiveness, and males exerting effort toward subsistence had a negative association. Both sex ratio variables ran counter to prediction. Male mortality from war, which indicates a female-biased sex ratio, showed a positive association with levels of aggression, and sex ratio in the upper 50th percentile for male bias showed a negative association.

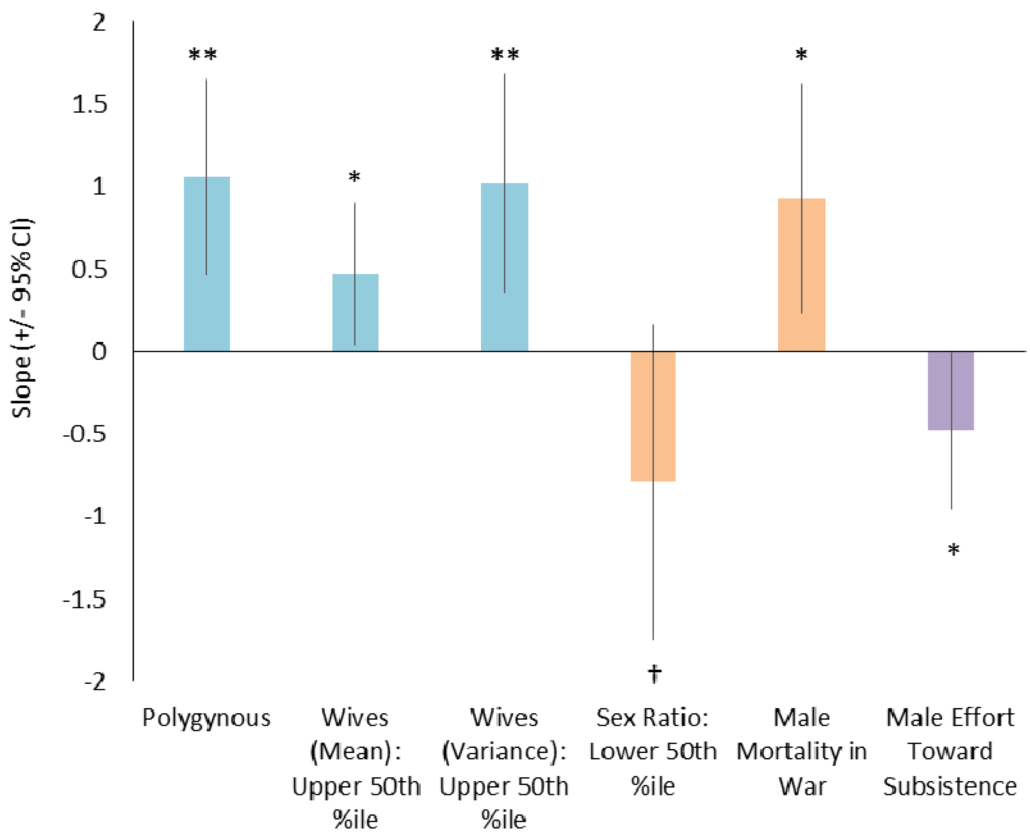

Figure 1. Estimates for the effects of various factors that influence the strength of sexual selection on a composite measure of behavior and beliefs related to male aggression. All estimates are from the multivariate linear regression models. (Note: † *p*<0.10, * *p*<0.05, and ** *p*<0.01.)

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Discussion

We investigated the relationship between behaviour and beliefs related to male aggression and factors that should affect the intensity of sexual selection in a sample of 78 societies. Two results were relatively straightforward. First, levels of aggression were higher in societies where polygyny is allowed, and where it leads to the most intense competition, as measured by mean and variance in number of wives. This is consistent with theory (Emlen and Oring 1977, Shuster 2009), and with empirical findings such as the decrease in the intensity of sexual selection in Mormon populations after polygyny was outlawed (Moorad, Promislow et al. 2011). Second, levels of male aggression were lower when males expended effort toward subsistence, which is consistent with less expenditure toward finding mates, and the empirical finding that monogamous unions are more stable with subsistence complementarity (Quinlan 2008).

The sex ratio results are less straightforward. Excess females were associated with higher levels of male aggression. The operational sex ratio (OSR) (Emlen and Oring 1977), the balance of males to females in the mating pool, was the target but we may have failed to capture it in our first measure. For the vast majority of SCCS societies, the information on sex ratio is based on the entire society rather than the breeding population. For this reason, our second measure, male mortality at war, may provide a better measure because most males in battle are of reproductive age (Quinlan and Quinlan 2007). Each having a similar relationship with levels of aggression supports the efficacy of the measures. This runs 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, Kvarnemo and Ahnesjo 1996), but supports the suggestion that, under certain conditions, the converse may be true (Kokko and Monaghan 2001, Kokko and Rankin 2006, Kokko and Jennions 2008, Kokko, Klug et al. 2012).

A recent review of sex ratio and male violence supports the notion of a complex relationship between OSR and mating strategies (Schacht, Rauch et al. 2014), as does a field study of eight Guyanese communities (Schacht and Borgerhoff Mulder 2015).

There are a number of potential alternative explanations that we were able to rule out by using multivariate methods. First, it could be that warfare, societal complexity, or some combination of the two confounds the relationships of interest (Ember 1974). For example, the positive association between levels of male aggression and male mortality in warfare could be explained by the presence of warfare without the need to invoke sexual selection. Similarly, it has been suggested that aggressive beliefs and behaviours may serve to socialize boys in societies where war is part of life (Chick and Loy 2001). It could also be that simpler societies may be more likely to allow polygyny and value aggression without necessitating a causal link between the two. Second, shared cultural histories and similar environments can lead to spurious cross-cultural correlation. Our results stood up to statistical control for all of these factors.

The results, thus, provide strong support for the hypothesis that intrasexual selection explains the distribution of behaviour and beliefs related to male aggression in human societies. We acknowledge that our comparative approach, in seeking a large enough sample to conduct multivariate approach, used data that overlooks intra-societal variation. For complementarity, future analyses should compare a smaller subset of societies using richer behavioural and ethnographic data (Apicella and Barrett 2016).

Data Availability

The data used in the analysis are included in Table S4 in the SEM.

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Author Contributions

GK formulated the research question; TLC & GK contributed equally to the analyses and writing.

Conflicts of Interest

The authors have no conflicts of interest to declare.

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Electronic Supplementary Material

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

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Table S1. Summary of dependent variables.

Table S2. Summary of independent variables.

Table S3. Full details of the bivariate and multivariate linear regression models used for inference.

Table S4. Raw data.

Appendix S1. Supplementary References.

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Table S1. Summary of dependent variables.

Variable	Coding	SCCS Variable	SCCS Coding	Source
Frequent Interpersonal Violence	0 Absent 1 Present	Moderate or frequent interpersonal violence (v666)	1 Absent 2 Present	Sanday 1981
Warriors Have Prestige	0 None or some 1 Great deal	Prestige of warriors (v903)	1 Great deal 2 Some 3 None	Otterbein 1970
Wives Taken From Hostile Groups	0 No female captives 2 Women taken	Wives taken from hostile groups (v870)	0 No female captives 1 Taken but not married 2 Taken as wives or concubines	White 1988
Male Scarification	0 Scarification absent 1 Scarification present	Scarification, including piercings and tattoos (v1694)	1 No scarification 2 Ear, nose piercing 3 Tatooing and cicatrisation 4 Scarification includes removal of skin	Ludvico and Kurland 1995

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Table S2. Summary of independent variables.

Variable	Coding	SCCS Variable	SCCS Coding	Source
Polygyny	0 Non-polygynous 1 Polygynous	Polygamy (v79)	1 Polyandry 2 Monogamy 3 Polygyny (<20%) 4 Polygyny (>20%)	Murdock and Wilson 1972
Wives (Mean): Upper 50th %ile	0 Lower 50th percentile 1 Upper 50th percentile	# of Wives (mean) (v2176a)	n/a	White 1988
Wives (Median): Upper 50th %ile	0 Lower 50th percentile 1 Upper 50th percentile	# of Wives (variance) (v2176b)	n/a[1]	White 1988
Sex Ratio: Lower 50th %ile	0 Upper 50th percentile 1 Lower 50th percentile	Sex Ratio (v1689)	# males / # females x 1000	Ember and Ember 1992
Male War Mortality[1]	0 None or negligible 1 Higher male mortality	None	n/a	n/a
Males Expend Subsistence Effort	0 Women more 1 Equal or men more	Relative time and effort expended on subsistence activities (v586)	1 Men clearly more 2 Men and women roughly equal 3 Women clearly more	Whyte 1978
Frequent Warfare	0 Absent or occasional 1 Frequent or endemic	Warfare (v679)	1 Absent or occasional or periodic 2 Frequent or endemic	Murdock 1962-71
Political Complexity	0 no state 1 states	Jurisdictional hierarchy beyond the local community (v237)	1 No political authority beyond comm. 2 One level (e.g., petty chiefdoms) 3 Two levels (e.g., larger chiefdoms) 4 Three levels (e.g., states) 5 Four levels (e.g., large states)	
Region	9 Dummy Variables (No observations included in study from 10th region)	V1858	10 Dummy Variables	Burton 1999

[1] Unpublished data on male war mortality provided by Carol Ember. The original was an interval variable ranging from 0 (lowest) to 6 (highest). We recoded it as 0=none or negligible (0 from original) and 1=higher male mortality (1-6 from original). These data were also used by Quinlan and Quinlan (2007).

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Table S3. Full details of the bivariate and multivariate linear regression models used for inference.

	Variables	Bivariate			Multivariate		
		β	p		β	p	
Polygyny	Constant	-1.67	<0.001	n=78	-2.67	<0.001	n=74
	Polygynous	0.95	0.015	R^2=0.076	1.06	0.001	R^2=0.519
	Complexity				-0.04	0.910	
	Warfare				1.46	<0.001	
	Mesoamerica and Andes				-1.19	0.037	
	Constant	-1.26	<0.001	n=69	-2.00	<0.001	n=65
	Wives (Mean): Top 50th ile	0.60	0.030	R^2=0.069	0.47	0.032	R^2=0.479
	Complexity				-0.44	0.261	
	Warfare				1.43	<0.001	
	Mesoamerica and Andes				-1.23	0.044	
	Constant	-1.43	<0.001	n=25	-2.26	<0.001	n=24
	Wives (Variance): Top 50th %ile	1.46	0.001	R^2=0.409	1.02	0.004	R^2=0.818
	Complexity				0.67	0.155	
	Warfare				1.45	0.001	
	SE Asia and Insular Pacific				1.40	0.033	
Sex Ratio	Constant	-0.71	0.107	n=24	-0.91	0.080	n=22
	Sex Ratio: Top 50th ile	-0.63	0.236	R^2=0.063	-0.79	0.099	R^2=0.442
	Complexity				-1.17	0.109	
	Warfare				0.99	0.046	
	Constant	-1.74	<0.001	n=42	-1.85	<0.001	n=40
	Male War Mortality	1.39	<0.001	R^2=0.375	0.93	0.011	R^2=0.510
	Complexity				0.23	0.776	
	Warfare				0.76	0.036	
Other	Constant	-0.05	0.879	n=34	-1.16	<0.001	n=32
	Male Effort Toward Subsistence	-0.90	0.025	R^2=0.147	-0.48	0.046	R^2=0.739
	Complexity				-0.68	0.104	
	Warfare				1.48	<0.001	
	SE Asia and Insular Pacific				-1.51	<0.001	
	NW Coast of America				1.24	<0.001	
	Mesoamerica and Andes				-1.16	0.008	

Table S4. Raw data.

Society	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Ashanti	1	1	1	0	0.060583627	1	1	1				1	0	Subsaharan Africa
Azande	1	1	1	1	0.581053665	1	1		0	1		1	0	Subsaharan Africa
Fon	1	1	1	1	0.581053665	1						1	1	Subsaharan Africa
Ganda	1	1	1	0	0.060583627	1	1			1		1	1	Subsaharan Africa
Kikuyu	1	1	1	0	0.060583627	1				1	1	1	0	Subsaharan Africa
Kung Bushmen	0	0	0	1	-2.37895523	1	1	0		0		0	0	Subsaharan Africa
Masai	1	1	1	1	0.581053665	1	1	1				1	0	Subsaharan Africa
Mbuti	0	0	0	1	-2.37895523	1	1	0			1	0	0	Subsaharan Africa
Mende	1	1	1	1	0.581053665	1	1	1	0			1	0	Subsaharan Africa
Nama Hottentot	1	1	0	1	-0.273323343	1	1			1	1	1	0	Subsaharan Africa
Nyakyusa	1	1	0	0	-0.79379338	1	1			0		1	0	Subsaharan Africa
Otoro Nuba	0	1	1	1	-0.536383469	1	1	1				1	0	Subsaharan Africa
Pastoral Fulani	0	0	1	0	-2.04504826	1	1	1			1		0	Subsaharan Africa
Thonga	1	1	1	1	0.581053665	1	1				0	1	0	Subsaharan Africa
Tiv	1	0	1	1	-0.407141089	1	1	1				1	0	Subsaharan Africa
Wolof	1	0	1	0	-0.927611126	1	1			0	0	0	0	Subsaharan Africa
Amhara	0	1	0	1	-1.390760477	0	0				1	1	1	Middle Old World
Egyptians	1	0	0	0	-1.781988134	1	0	0	0		1	0	1	Middle Old World
Kurd	1	1	0	1	-0.273323343	1	0				1	1	0	Middle Old World
Lepcha	0	0	0	0	-2.899425267	1	1	0		0		0	0	Middle Old World
Lolo	1	1	1	0	0.060583627	1	0			1	1	1	0	Middle Old World
Riffians	1	1	0	1	-0.273323343	1	1	0				1	0	Middle Old World
RwalaBedouin	1	1	0	1	-0.273323343	1				1		1	0	Middle Old World
Santal	0	0	0	1	-2.37895523	1	0		1	0			0	Middle Old World
Teda	1	1	1	1	0.581053665	1	1	1				1	0	Middle Old World
Tuareg	0	1	1	0	-1.056853506	0	0			1	1	1	0	Middle Old World
Vedda	0	0	0	0	-2.899425267	0	0			0		0	0	Middle Old World
Balinese	0	0	0	0	-2.899425267	0	1		0			0	1	SE Asia and Insular Pacific
Iban	0	1	0	1	-1.390760477	0	0			0	1	1	0	SE Asia and Insular Pacific
Ifugao	1	1	0	1	-0.273323343	1	0			1		1	0	SE Asia and Insular Pacific
Maori	1	1	1	1	0.581053665	1	0	0		1		1	0	SE Asia and Insular Pacific
Marquesans	1	0	0	1	-1.261518096	0	0		1	1	1	1	0	SE Asia and Insular Pacific
Siamese	0	0	0	1	-2.37895523	1	0		1			0	1	SE Asia and Insular Pacific
Trukese	0	0	0	1	-2.37895523	1	0		1		1	1	0	SE Asia and Insular Pacific
Western Samoans	1	0	1	1	-0.407141089	1	0			1		1	0	SE Asia and Insular Pacific
Yapese	1	0	1	1	-0.407141089	1	1		1			1	0	SE Asia and Insular Pacific
Aranda	1	1	1	1	0.581053665	1	1	1			0	1	0	Sahul
Kwoma	1	1	0	1	-0.273323343	1	1	1	1	1	1	1	0	Sahul
Manus	1	0	0	0	-1.781988134	1	0		1	0		0	0	Sahul
Mbau Fijians	1	0	1	1	-0.407141089	1	0					1	0	Sahul
Orokaiva	1	1	1	0	0.060583627	1	1					1	0	Sahul
Tikopia	1	0	0	1	-1.261518096	1	0		1	0		0	0	Sahul
Tiwi	1	1	1	1	0.581053665	1	1		0	1		0	0	Sahul
Trobrianders	1	1	0	0	-0.79379338	1	1			0		0	0	Sahul
Ainu	1	0	1	0	-0.927611126	1	0		0			1	0	N Eurasia and Circumpolar
Aleut	1	1	1	1	0.581053665	1			0	1	1	1	0	N Eurasia and Circumpolar
Copper Eskimo	0	0	0	0	-2.899425267	1	1		1	0		0	0	N Eurasia and Circumpolar
Gheg Albanians	1	1	0	1	-0.273323343	1	1			1		1	0	N Eurasia and Circumpolar
Gilyak	1	0	1	0	-0.927611126	1	0	0			1	1	0	N Eurasia and Circumpolar
Lapps	0	0	0	0	-2.899425267	0	0			0		0	0	N Eurasia and Circumpolar
Yukaghir	1	0	1	0	-0.927611126	0	0		1				0	N Eurasia and Circumpolar

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Yurak Samoyed	0	0	0	0	-2.899425267	1	0			1	1		0	N Eurasia and Circumpolar
Ingalik	1	0	1	1	-0.407141089	1	0			1		1	0	NW Coast of N America
Kaska	1	0	1	1	-0.407141089	1	0		1	0	1	0	0	NW Coast of N America
Chiricahua	1	1	0	1	-0.273323343	1	1					1	0	NW Coast of N America
Society	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**
GrosVentre	0	1	1	1	-0.536383469	1	1					1	0	NW Coast of N America
Havasupai	0	0	1	1	-1.524578222	1	1		1	0		0	0	NW Coast of N America
Montagnais	1	0	0	1	-1.261518096	1				0	1	0	0	NW Coast of N America
Paiute (North.)	1	0	0	1	-1.261518096	1	1	0			0	0	0	NW Coast of N America
Pomo (Eastern)	1	0	0	1	-1.261518096	1	0			1	1	0	0	NW Coast of N America
Yokuts (Lake)	0	0	0	0	-2.899425267	1	1					0	0	NW Coast of N America
Yurok	0	0	0	1	-2.37895523	1	0		0	1		0	0	NW Coast of N America
Abipon	1	1	0	1	-0.273323343	1	1			1	0	1	0	Eastern Americas
Aweikoma	1	0	0	0	-1.781988134	1	1	0	1			1	0	Eastern Americas
Comanche	1	1	1	1	0.581053665	1		1			0	1	0	Eastern Americas
Creek	1	1	0	1	-0.273323343	1		0		1	0	1	0	Eastern Americas
Haitians	0	1	0	1	-1.390760477	1		0				0	1	Eastern Americas
Hidatsa	1	0	1	1	-0.407141089	1	1	1			1	1	0	Eastern Americas
Huron	1	1	0	1	-0.273323343	0	0			1		1	0	Eastern Americas
Jivaro	1	1	1	0	0.060583627	1	1		1		1	1	0	Eastern Americas
Mundurucu	1	1	1	1	0.581053665	1	1					0	0	Eastern Americas
Natchez	0	0	1	1	-1.524578222	1				1		1	0	Eastern Americas
Omaha	1	1	1	1	0.581053665	1	1	1		1	1	1	0	Eastern Americas
Trumai	0	0	0	1	-2.37895523	1	1	0	1		1	0	0	Eastern Americas
Tupinamba	1	1	1	1	0.581053665	1	1	1		1	0	1	0	Eastern Americas
Yanomamo	1	1	1	1	0.581053665	1	1		1	1	1	1	0	Eastern Americas
Goajiro	1	0	0	1	-1.261518096	1	1				1	1	0	Mesoamerica and Andes
Papago	0	1	0	1	-1.390760477	1	1			0	1	1	0	Mesoamerica and Andes

Column Headings:

A. Frequent Interpersonal Violence
B. Warriors Have Prestige
C. Wives Taken From Hostile Groups
D. Male Scarification
E. Beliefs and Behaviour Related to Male Aggression (1^{st} PCA of A-D)
F. Polygyny
G. Wives (Mean): Upper 50th %ile
H. Wives (Median): Upper 50th %ile
I. Sex Ratio: Upper 50th %ile
J. Male War Mortality
K. Males Expend Subsistence Effort
L. Frequent Warfare
M. Political Complexity
N. Region

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Appendix S1: Supplementary References

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