



Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Physically strong men are more militant: A test across four countries

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ARTICLE INFO

Article history:

Initial receipt 12 April 2016

10 November 2016

Final revision received 10 November 2016

Available online xxxx

ABSTRACT

There is substantial evidence from archaeology, anthropology, primatology, and psychology indicating that humans have a long evolutionary history of war. Natural selection, therefore, should have designed mental adaptations for making decisions about war. These adaptations evolved in past environments, and so they may respond to variables that were ancestrally relevant but not relevant in modern war. For example, ancestrally in small-scale combat, a skilled fighter would be more likely to survive a war and bring his side to victory. This ancestral regularity would have left its mark on modern men's intergroup psychology: more formidable men should still be more supportive of war. We test this hypothesis in four countries: Argentina, Denmark, Israel, and Romania. In three, physically strong men (but not strong women) were significantly more supportive of military action. These findings support the hypothesis that modern warfare is influenced by a psychology designed for ancestral war.

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1. Introduction

By coordinating their actions, animals can greatly increase their effectiveness. However, this coordination has sizeable evolutionary barriers to its evolution; e.g., free riders can parasitize others' investment in collective actions (Delton, Cosmides, Guemo, Robertson, & Tooby, 2012; Delton & Sell, 2014; Ostrom, 2010). Nonetheless, coordinated actions do evolve in many species, either via kin selection (e.g. social insects, Hamilton, 1964) or through other means still being mapped by evolutionary psychologists and behavioral ecologists (Boyd, Gintis, & Bowles, 2010; Cosmides & Tooby, 1992; Delton et al., 2012; Ostrom, 2010; Panchanathan & Boyd, 2004). We know that these evolutionary barriers have been overcome, however, because animals evidence these behaviors; e.g., collective hunting is common in some mammals (e.g. Creel & Creel, 1995) and is understood as a collective action problem with scavengers as the defectors (see Packer & Ruttan, 1988).

Given the widespread importance of aggression in the animal kingdom (Huntingford & Turner, 1987), there would have been a selective advantage to organisms that coordinated their aggression toward a common opponent, because such coordination would enhance an

individual's own formidability. Provided that evolutionary barriers such as free-riding were overcome, engaging in coalitional aggression would be selected for in species where aggression was common.

Convergent evidence now shows that these preconditions have been met for our own species, and that we come from a long evolutionary history of war (Gat, 2015; LeBlanc & Register, 2003; Pinker, 2011; van der Dennen, 1995). Such evidence comes from multiple sources, including: evidence of coalitional killing among chimpanzees (Wrangham & Glowacki, 2012), ethnographic surveys of modern societies showing that war is prevalent in virtually all known cultures (Otterbein & Otterbein, 1965; Otterbein, 1968, 2004), archeological evidence of slaughter and weapon hoarding (Keeley, 1996, 1997), and psychological evidence of coalitional thinking (Tooby & Cosmides, 2010; Van Vugt, De Cremer, & Janssen, 2007).

1.1. Warfare in chimpanzees

The closest living relatives of our species are the bonobos and chimpanzees. Chimpanzees live in patrilocal groups who compete against rival groups for access to territory and feeding grounds. Aggression is common among chimpanzees and particularly among chimpanzee males (Wrangham, Wilson & Muller, 2006). And like human males (Sell, Hone, & Pound, 2012), male chimpanzees show evidence of combat design (e.g. males are larger than females, have larger teeth, mature

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later, and die earlier). Unlike gorillas, bonobos, and orangutans, chimpanzees are known to engage in coalitional aggression with their male allies. These groups patrol their territory and capitalize on temporary asymmetries in group size to eliminate outgroup members.

The mechanisms that give rise to inter-group aggression in chimpanzees appear to have been designed by natural selection to expand territory and get access to food and mates. In short, the propensity for war is part of chimpanzees' evolved nature. We know this because group aggression in chimpanzees bears the hallmark of natural selection: complex functional design (Williams, 1966). Features of chimpanzee aggression that illustrate this design include:

- i) coalitional aggressors are composed almost entirely of the sex that benefits the most from increased mating opportunities (i.e. males, Wilson et al., 2014)
- ii) coalitional aggressors frequently exempt adult females from aggression and may focus instead on males and infants (Wrangham & Glowacki, 2012; Wilson et al., 2014; though see Pradhan & Pandit, 2014)
- iii) lethal aggression is timed to periods of asymmetric fighting ability such as when one group greatly outnumbers another (Wilson et al., 2014), the result being that attackers are rarely seriously injured (Watts, Muller, Amsler, Mbabazi, & Mitani, 2006)
- iv) the aggression is often preceded by coordinated forays and patrols, often into enemy territory
- v) individual chimpanzee males who would benefit most from increased territory are often the ones who instigate these patrols for their group (e.g. those males who are more likely to mate with parous females patrol more frequently, Watts & Mitani, 2001)
- vi) chimpanzee males who are superior fighters, and thus are less likely to be injured during aggressive encounters, are more likely to patrol, e.g. males who were good hunters patrolled more (Watts & Mitani, 2001), and males who are higher in rank travelled further when they visited the periphery of their territory where coalitional aggression was more likely to take place (Wilson, Kahlenberg, Wells, & Wrangham, 2012).

While our understanding of chimpanzee cognition is limited, these findings suggest that chimpanzee minds (at least those of males) have been designed by natural selection to coordinate lethal aggressive action and exploit asymmetries in power so as to target and eliminate enemy males and infants. The preconditions that resulted in this selective regime were most likely present among human ancestors as well, e.g. patrilocality,¹ fission-fusion grouping, territoriality, cognitive mechanisms allowing cooperation and collective actions, male design for aggression, and polygyny (Wrangham & Glowacki, 2012; Tooby & DeVore, 1987; see also Zefferman & Mathew, 2015).

1.2. Universality of warfare

How widespread is war among humans? While different definitions of "war" will return different answers, coalitional aggression in the form of feuding or raiding has been found in almost all known cultures (Pinker, 2011; Wrangham & Glowacki, 2012), and among humans' earliest civilizations for which we have data (Gat, 2015; Keeley, 1996, 1997; LeBlanc & Register, 2003; Otterbein, 2004; van der Dennen, 1995). Furthermore, coalitional aggression appears more common in populations whose lifestyles resemble our ancestors', e.g. both patrilocality and polygyny predict coalitional aggression (Otterbein, 1968; Otterbein & Otterbein, 1965), and aggression is far more

prevalent among foragers than among modern nation-states (Eisner, 2003; Pinker, 2011).

There are, of course, human civilizations that have forgone war for many generations, e.g., the Jains, the Amish, the Lapps. These exceptions are exceedingly rare, however, and tend to exist as subpopulations protected by larger nation-states. The bulk of the evidence indicates that human societies have engaged in group aggression throughout recorded history and before (Pinker, 2011).

There is also more direct evidence that human psychology, and in particular male psychology, has been shaped by this inter-group conflict. For example, in public goods games males contributed more to their own coalition when they were put in a context of inter-group competition. When women (sampled from the same population) were put in inter-group competition it had little effect on their contributions to their own group (Van Vugt et al., 2007). Human prejudice and discrimination aimed at outgroup members is also consistent with the view that the human mind (particularly the male mind) was designed for coalitional aggression (see McDonald, Navarrete, & Van Vugt, 2012). Perhaps most convincingly, an analysis of the structure of human moral systems shows that they function to regulate coalitional living generally and group conflict in particular (Tooby & Cosmides, 2010).

We conclude that a selective regime has been in place favoring designs in men that navigate the costs and benefits of war in ways that increased their reproduction in past environments. In other words, modern men should be designed for ancestral-style warfare (Tooby & Cosmides, 1988). Therefore, men who would have been more likely to survive and benefit from war ancestrally should be more supportive of war now. Because modern warfare differs from ancestral warfare, the variables that predict whether a man would have survived and benefited from war may no longer be predictive in a modern industrial society. For example, ancestral weapons were powered by the upper body (Brues, 1959) whereas casualties caused by hand-to-hand combat are extremely rare in modern war (e.g. one study of casualties in Iraq showed 56% of the dead were killed by gunshots, 27% died to car bombs or other explosives, 13% to airstrikes, 2% to accidents, and only 2% expired from unknown causes which may have included deaths caused by knives, bayonets, or unarmed combat; Burnham, Doocy, Dzeng, Lafta, & Roberts, 2006).

1.3. Fighting ability and warfare

If natural selection designed mental adaptations to navigate the selection pressures inherent in ancestral warfare, then such mechanisms should regulate an individual's support for war as a function of variables that – ancestrally – predicted the reproductive consequences of advocating for war in that individual and their kin. In the small-scale, technologically-sparse world of ancestral warfare, men with superior fighting ability would have been more likely to survive a war, to lead his side to victory, and to receive a sizeable portion of the spoils of war (Chagnon, 1988; Escasa, Gray, & Patton, 2010; Van Vugt et al., 2007). Therefore, men who are better physical fighters today should still favor war as a tactic in resolving group disputes more so than men who are poor fighters (prediction #1). Furthermore, because war has been (and still is) almost exclusively a male activity the relationship between fighting ability and preference for coalitional aggression should be limited to men (prediction #2). Previous research has confirmed these predictions on two samples of US subjects (Sell, Tooby & Cosmides, 2009; see also Sell et al., 2012). In this paper, we report additional tests of these predictions on men and women from Argentina, Denmark, Israel, and Romania.

2. Methods

We tested the hypothesis that fighting ability in men (but not women) tracks support for military action in four countries.

¹ Though the degree of patrilocality in modern foragers is arguably less than once thought and certainly less than chimpanzees (see Hill et al., 2011). Interestingly, in Hill et al.'s sample of 32 foraging societies, brothers were particularly likely to coreside.

2.1. Subjects

Argentinean subjects were students at the University of Buenos Aires who were paid for their participation. Israeli subjects were students at Ben Gurion University and the Interdisciplinary Center (IDC) Herzliya, and were either paid or given course credit for their participation. Romanian subjects were students from the West University of Timisoara, who participated for partial fulfillment of their course credit. Danish subjects came from a large nationally representative sample contacted via a survey agency. Subjects were drawn from YouGov Zagera's standing web panel based on quota sampling such that the sample was nationally representative on sex, age, and geographical location. The response rate was 34%. Experimenters aimed to recruit at least 80 male and 80 female subjects, but recruited more when convenient. Data collection on each sample was completed and closed before data analysis began on that sample.

Table 1 presents descriptive statistics for all four samples.

2.2. Measures

2.2.1. Fighting ability

Fighting ability is difficult to measure in an ethical manner. Previous research and theorizing, however, suggests that upper body strength is a good approximation of fighting ability. This is for many reasons. Among them, archeological evidence shows that upper body strength powered all ancestral weapons (Brues, 1959). There is also greater sexual dimorphism in upper body strength than lower body strength or body size generally (Lassek & Gaulin, 2009). Furthermore, when subjects estimate others' fighting ability, they produce ratings that more closely track upper body strength than lower body strength, even when estimating fighting ability from the face (Sell et al., 2009) or voice (Sell et al., 2010; Sell, 2012). Finally, there are theoretical reasons to believe that fighting ability in men is linked to individual aggression and anger, and it is upper body strength, relative to lower body strength and body size, that is the more powerful predictor of an individual man's anger and aggression (Sell, Tooby & Cosmides, 2009; Sell, Eisner, & Ribeaud, 2016).

Research has shown that flexed biceps circumference is the single most accurate morphological measure of upper body strength in adult males (see Sell et al., 2009, supplemental information). Therefore, upper body strength was operationalized as the circumference of the flexed biceps of the dominant arm (see Petersen, Sznycer, Sell, Tooby, & Cosmides, 2013). Argentinean, Israeli, and Romanian subjects were measured by the experimenters. The Danish subjects (who provided data via an online survey) were instructed on how to self-measure their flexed biceps circumference or recruit someone to measure their arm for them. Of 1537 Danes who responded to the questionnaire, 803 returned strength measurements (421 males and 372 females).

2.2.2. Support for warfare

Support for warfare among Argentinean and Danish subjects was measured with four-item scales designed for each country as part of a previous project (see Petersen et al., 2013). Israeli subjects were given a 10-item scale based primarily on the Israeli-Palestinian conflict. Romanian subjects were given a scale originally designed for US subjects (see Sell, Tooby & Cosmides, 2009) with items that referred to the US removed. This resulted in a scale with nine items. All scales are reported in supplemental online materials. Sample items include:

“Argentina must amass enough military power and (re)take the Falkland Islands by force” (Argentina), “It was wrong of Denmark to go along with the war in Iraq” (Denmark), “The only way Israel can solve the conflict with the Palestinians is by using force” (Israel), and “When it comes to international conflicts, violence never solves anything” (Romania). Subjects reported their agreement with these statements from 1 (strongly disagree) to 7 (strongly agree).

2.3. Data screening

Data was screened for any subjects who were more than 3 standard deviations above or below the mean on measures of physical strength. Treatment of these outliers is detailed below.

2.3.1. Argentina

We identified a single outlier whose z-scored biceps circumference was 4.34 SD above the mean; specifically, 46.3 cm. This measure was taken by experimenters and is well within the range of plausible measures for male flexed biceps circumference. To minimize the impact of this extreme score, the flexed biceps circumferences of Argentinian subjects (both male and female) were given a square-root transformation. This transformation did not change the significance of any reported test, and worked against our hypothesis (i.e. it decreased the correlation between strength and support for war in males).

Three subjects from Argentina left the support for war questions blank and were removed.

2.3.2. Denmark

Unlike Argentinean subjects who were measured by experimenters, the Danish subjects were asked to measure their own biceps or recruit someone to help measure them after reading instructions on how to do this. This meant that outliers could be errors in measurement or reporting. For example, there were three subjects who reported inhumanly low biceps circumferences, e.g. less than 8 cm; these data were removed from analyses. Additionally, two subjects reported biceps circumferences that were inhumanly large: e.g. 250 and 295 cm. These subjects were excluded because they were almost certainly data entry errors on behalf of the subjects.

With those outliers removed, there remained 798 subjects. These subjects had their z-scores recomputed because the data entry errors had increased the variance substantially. The new distribution showed 8 subjects with z-scored biceps circumferences that were greater than 3SD or lower than -3SD. Because these subjects were not measured by experimenters, these outliers were removed from analysis. Leaving them in the analysis did not change the significance of any reported test.

Furthermore, subjects from Denmark were allowed to answer “I don't know” for any of the four questions in the support for war scale. Because five subjects answered “I don't know” to all four questions, they were also removed from analyses.

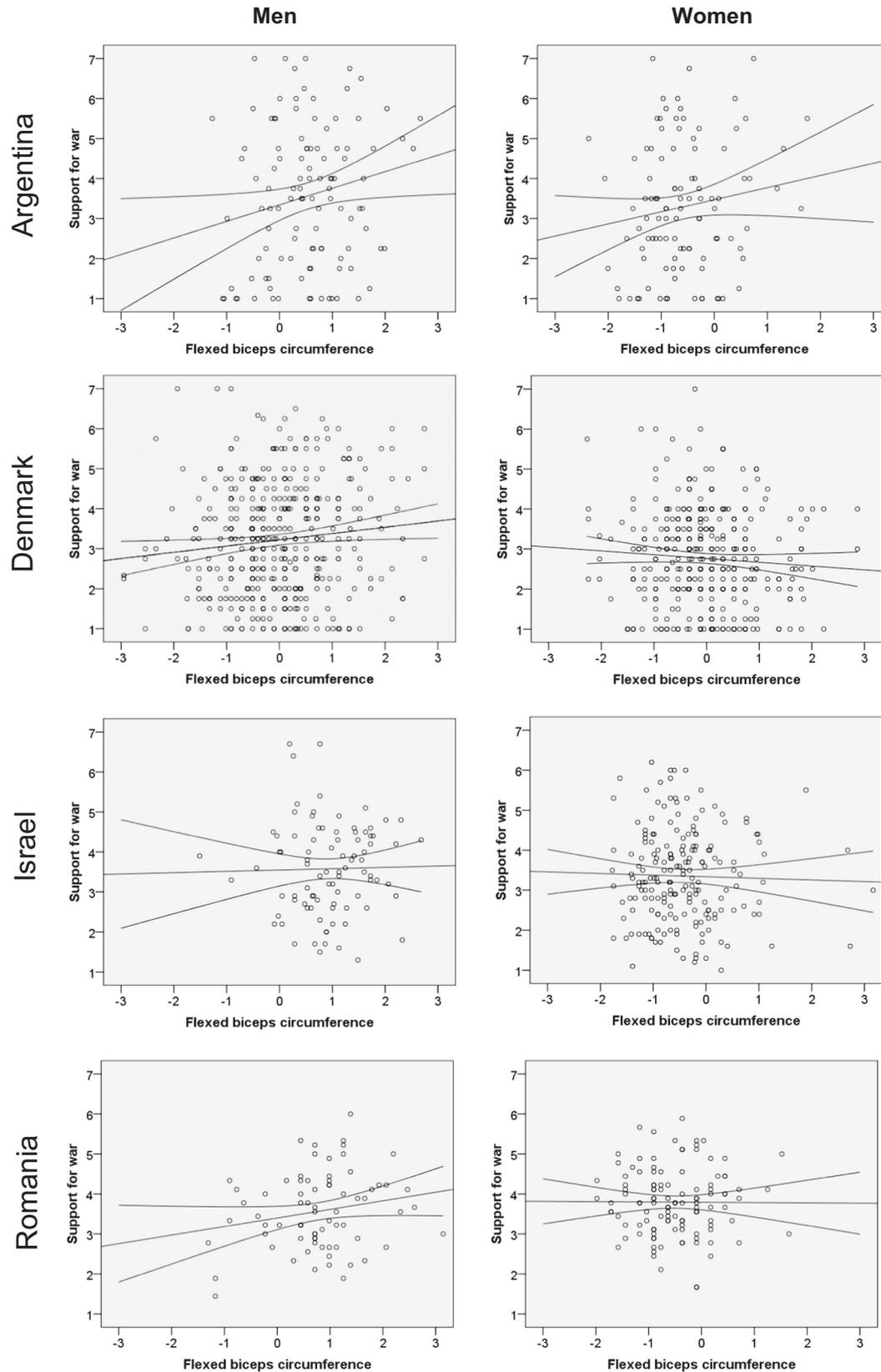
2.3.3. Israel

There was one Israeli subject who had an extreme score on biceps circumference (i.e., z-score of 3.16). Because this measurement was taken by experimenters, and the score is not very extreme, it is unlikely that it was a measurement error. This outlier was included in analyses; removing him did not change the significance of any test.

Table 1

Descriptive statistics and measures.

	Argentina	Denmark	Israel	Romania
Sample size	215 (104 female)	785 (364 female)	281 (193 female)	191 (117 female)
Mean age	20.9, SD = 2.9	49.0, SD = 13.7	23.3, SD = 2.2	21.0, SD = 3.6
Support for warfare measure	4 self-report items ($\alpha = 0.86$)	4 self-report items ($\alpha = 0.71$)	10 self-report items ($\alpha = 0.85$)	9 self-report items ($\alpha = 0.64$)



Note: Scatterplots show flexed biceps circumference regressed on support for war; regression lines and 95% confidence intervals are displayed for both sexes separately.

Fig. 1. Strength and support for war across four countries. Note: Scatterplots show flexed biceps circumference regressed on support for war; regression lines and 95% confidence intervals are displayed for both sexes separately.

2.3.4. Romanian

There were no outliers in the Romanian samples.

3. Results

Results are discussed by hypothesis and summarized in Fig. 1.

Hypothesis #1. Are physically strong men more supportive of warfare?

Yes. In three of the four countries, the flexed biceps circumference of men positively predicted their support for warfare (Argentina: $r = 0.20$, $p = 0.016$; Denmark: $r = 0.11$, $p = 0.012$; Israel: $r = 0.02$, $p = 0.42$; Romania: $r = 0.20$, $p = 0.04$, all one-tailed). See supplemental online materials for more analyses on this hypothesis.

Hypothesis #2a. Is this relationship specific to men?

Yes. Women's physical strength was never a significant predictor of their support for warfare (Argentina: $r = 0.15$, $p = 0.14$; Denmark: $r = -0.07$, $p = 0.19$; Israel: $r = -0.03$, $p = 0.72$; Romania: $r = -0.01$, $p = 0.94$, all two-tailed).

Hypothesis #2b. Was the correlation in men significantly higher than that of women?

Somewhat. A Fisher's r -to- z transformation test for differences between correlations revealed that the correlation between strength and support for war was significantly higher among men than among women in the large Danish sample ($z = 2.5$, $p = 0.007$), and marginally significant in the Romanian sample ($z = 1.4$, $p = 0.08$); though analyses with a more comprehensive measure of upper body strength did reveal a fully significant effect in Romania (see supplemental online materials). The correlations did not differ significantly for subjects in Argentina ($z = 0.42$, $p = 0.34$) or Israel ($z = 0.38$, $p = 0.35$, all one-tailed).

3.1. Additional analyses and controls

The Danish sample was different from the Argentine, Israeli, and Romanian samples in several respects. The Danish sample was a nationally representative sample, so many older subjects participated (see Table 1). Furthermore, the biceps circumference was reported by the subjects themselves without independent verification by experimenters. This introduces a number of potential confounds that are addressed here.

3.1.1. Does age confound the relationship between strength and support for war among Danish subjects?

No. We ran two regression analyses (one for each sex) testing the ability of flexed biceps circumference and age to predict support for war. For men, biceps circumference remained a small but significant predictor: Beta = 0.13, $p = 0.004$ (one-tailed), while age was not predictive: Beta = 0.04, $p = 0.62$. For women, biceps circumference was again not predictive: Beta = -0.04, $p = 0.40$, while age was a weak but significant predictor, Beta = -0.13, $p = 0.01$ (two-tailed) such that older women tended to be less supportive of military action. See supplemental online materials for many additional controls.

3.1.2. Did self-measurement render Danish subjects' biceps circumference measurements inaccurate?

Danish subjects were instructed visually and verbally on how to measure their biceps. They were encouraged to get help from a family member or roommate if possible. Subjects reported whether they did the measurements themselves or had help from another. This enables us to test the robustness of the effects by looking specifically at subjects who presumably had the more accurate biceps circumference measurements (i.e. those who received help with the measurement). We split our data set between those subjects who measured their own biceps (308 females and 315 males) and those who received help with the

measurements (62 females and 108 males) and reran the correlation analyses.

Correlations between support for war and biceps circumference for males replicated in both sub-samples; those who measured themselves ($r = 0.12$, $p = 0.017$, one-tailed) and those who were measured by others ($r = 0.15$, $p = 0.06$, one-tailed). Correlations for females remained non-significant for those who measured themselves: $r = -0.07$, $p = 0.26$ and those who were measured by others: $r = -0.11$, $p = 0.41$, two-tailed.

Danish subjects were also asked how confident they were in their measurements of their own biceps. Answers were given from 1 (very uncertain) to 7 (very certain). There is no reason to believe there is a linear relationship between this uncertainty and the subjects' biceps circumference (i.e. subjects who were uncertain could have erred to make their biceps larger or smaller). Therefore, regression analyses to control for this difference would be inconclusive. Instead, we truncated the sample to only those subjects who reported being very certain that their measurement was accurate (i.e. those subjects who reported 7 on the 7-point scale). Among this smaller sample (139 females and 168 males), the correlation between support for war and biceps circumference was still significant for men, $r = 0.14$, $p = 0.033$, (one-tailed).² The correlation for women remained nonsignificant and slightly negative, $r = -0.12$, $p = 0.14$ (two-tailed).

Taken together, this evidence suggests that the self-measured biceps circumference of Danish subjects was accurate enough to reveal a real relationship between physical strength and support for war among men. Additional analyses on the Danish sample shows that the effect was robust to basic control variables as well, e.g. body size, socioeconomic status, exercise. See the supplemental online materials for details.

4. Discussion

A substantial body of evidence indicates that humans have a long evolutionary history of war. This is a profound discovery, because it informs us of a potent selection pressure that was active on our lineage. A selection pressure of this magnitude can be expected to have greatly impacted the evolved human psychology. In short, men should be designed for war (McDonald et al., 2012; Tooby & Cosmides, 2010; Van Vugt et al., 2007; see also Sugiyama, 2014).

If so, we can generate testable hypotheses about how the male mind responds to intergroup aggression, and predict some of the variables that explain individual differences in proneness to such aggression. One such hypothesis is that physically stronger men, who, ancestrally, would have incurred lower costs and derived higher benefits from war, would today be more likely to support war. This hypothesis was confirmed across three of the four tested countries, and replicates what was previously found in two samples of US college students (Sell, Tooby & Cosmides, 2009) and a sample of Hollywood actors (Sell et al., 2012). Specifically, measures of upper body strength predicted support for warfare in men but not women.

No correlation was found between strength and support for war among Israeli men. There are a number of potential explanations for this null effect. One, it may simply be a Type II error, as our Israeli sample was made up mostly of women (there were only 88 males compared to 193 females). This explanation is not likely though, as the effect was not even approaching significance. Another possibility is that Israeli men are much more likely to have military experience than men in our other samples, and so their internal sense of their own fighting ability may have been set by martial skills that were not assessed in our study and not known to other subject populations (e.g. accuracy of

² Selecting only subjects who rated their confidence as 6 or 7 (out of 7) increased the sample size to 278 males and the correlation remained significant at 0.10, $p = 0.043$, one-tailed. Doing a median split on confidence produced exactly the same results because a score of 6 was the median.

firearm shooting may contribute to a man's sense of fighting ability, and would be known among Israelis but not, for example, the typical Romanian student). It is also possible that the Israeli-Palestinian conflict is different than the kinds of military actions measured in other populations. For example, the survival of Israel is threatened by its enemies, while the same cannot be meaningfully said of Argentina or Denmark. Men may respond differently to wars of survival (or defensive wars generally) than to offensive or optional wars. Unfortunately, the current data set does not allow for testing between these alternatives.

Excepting the Israeli data, the correlation between upper body strength and support for war (among men) has now been found in two samples of US college students, Hollywood actors, students in Argentina and Romania, and in a nationally representative sample of Danes. This indicates a robust effect. However, despite this, the effect sizes for all samples were small. This may be because the measures of fighting ability were inexact. For example, the effect was larger in a US sample in which upper body strength was measured via weight-lifting machines (i.e. $r = 0.28$; see Sell, Tooby & Cosmides, 2009). Our measures of support for war were also abstract and may not be ideally suited for evoking ancestral predilections for war; e.g., some subjects may not identify with the country they reside in, or may have loyalties to political parties whose stances on war they feel obligated to support. Additionally, war adaptations in men may include circuits designed to benefit warriors even if the individual is not likely to fight (gratitude for warriors is common to human nature and often instantiated in cultural rituals, Pinker, 2011). These circuits may lead weaker men who are at particular risk from enemies to value warriors who protect them, dulling the correlation between fighting ability and support for war; this explanation would predict that weaker males are more likely to support defensive wars, which could explain the lack of effect in Israel. Finally, the theory predicts that these effect sizes should be small, because fighting ability (even comprehensively measured) is only one predictor of the likely costs and benefits of ancestral wars. Coalitional support, the strength of one's allies and family, the resources to be acquired in victory, the opportunity costs of war, the benefits of reconciliation, and many other factors likely calibrate an individual's willingness to engage in coalitional aggression. That said, the theory predicts that more ecologically valid stimuli and more comprehensive measures of fighting ability will magnify the effects found here, and if they fail to do so the hypothesis should be rejected.

Acknowledgements

We would like to thank Roni Porat, Shaul Shalvi, and Eran Halperin for help with collecting the Israeli data. We would also like to thank Joshua Kertzer, Elsa Ermer, and Andy Delton for advice and recommendations, and three anonymous reviewers for their constructive comments.

Appendix A. Supplementary analyses

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.evolhumbehav.2016.11.002>.

References

- Boyd, R., Gintis, H., & Bowles, S. (2010). Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science*, 328(5978), 617–620.
- Brues, A. (1959). The spearman and the archer—An essay on selection in body build. *American Anthropologist*, 61(3), 457–469.
- Burnham, G., Doocy, S., Dzung, E., Lafa, R., & Roberts, L. (2006). *The human cost of the war in Iraq: A mortality study, 2002–2006*. Center for International Studies, Massachusetts Institute of Technology.
- Chagnon, N. A. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science*, 239(4843), 985–992.
- Cosmides, L., & Tooby, J. (1992). Cognitive adaptations for social exchange. *The Adapted Mind*, 163–228.
- Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, 50(5), 1325–1339.
- Delton, A. W., & Sell, A. (2014). The co-evolution of concepts and motivation. *Current Directions in Psychological Science*, 23(2), 115–120.
- Delton, A. W., Cosmides, L., Guemo, M., Robertson, T. E., & Tooby, J. (2012). The psychosemantics of free riding: Dissecting the architecture of a moral concept. *Journal of Personality and Social Psychology*, 102(6), 1252.
- Eisner, M. (2003). Long-term historical trends in violent crime. *Crime and Justice*, 83–142.
- Escasa, M., Gray, P. B., & Patton, J. Q. (2010). Male traits associated with attractiveness in Conambo, Ecuador. *Evolution and Human Behavior*, 31(3), 193–200.
- Gat, A. (2015). Proving communal warfare among hunter-gatherers: The quasi-Rousseauian error. *Evolutionary Anthropology*, 24, 111–126.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17–52.
- Hill, K. R., Walker, R. S., Božičević, M., Eder, J., Headland, T., Hewlett, B., ... Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, 331(6022), 1286–1289.
- Huntingford, F. A., & Turner, A. K. (1987). *Animal conflict*. London: Chapman.
- Keeley, L. H. (1996). *War before civilization*. Oxford University Press.
- Keeley, L. H. (1997). Frontier warfare in the early Neolithic. *Troubled Times: Violence and Warfare in the Past*, 4, 303.
- Lassek, W. D., & Gaulin, S. (2009). Costs and benefits of fat-free muscle mass in men: Relationship to mating success, dietary requirements, and natural immunity. *Evolution and Human Behavior*, 30, 322–328.
- LeBlanc, S. A., & Register, K. E. (2003). *Constant battles: The myth of the peaceful, noble savage*. Macmillan.
- McDonald, M. M., Navarrete, C. D., & Van Vugt, M. (2012). Evolution and the psychology of intergroup conflict: The male warrior hypothesis. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 367(1589), 670–679.
- Ostrom, E. (2010). Collective action and the evolution of social norms. *Journal of Economic Perspectives*, 14(3), 137–158.
- Otterbein, K. F. (1968). Internal war: A cross-cultural study. *American Anthropologist*, 70(2), 277–289.
- Otterbein, K. F. (2004). *How war began*. Texas A&M University Press.
- Otterbein, K. F., & Otterbein, C. S. (1965). An eye for an eye, a tooth for a tooth: A cross-cultural study of feuding. *American Anthropologist*, 67(6), 1470–1482.
- Packer, C., & Rutman, L. (1988). The evolution of cooperative hunting. *American Naturalist*, 132(2), 159–198.
- Panchanathan, K., & Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature*, 432(7016), 499–502.
- Petersen, M. B., Sznycer, D., Sell, A., Tooby, J., & Cosmides, L. (2013). The ancestral logic of politics: Upper body strength regulates men's assertion of self-interest over income redistribution. *Psychological Science*, 24(7), 1098–1103.
- Pinker, S. (2011). *The better angels of our nature: Why violence has declined*. Penguin.
- Pradhan, G. R., & Pandit, S. A. (2014). Why do chimpanzee males attack the females of neighboring communities? *American Journal of Physical Anthropology*, 155(3), 430–435.
- Sell, A. (2012). Evolved cognitive adaptations. In J. Vonk, & T. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology*. Oxford University Press.
- Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., & Gurven, M. (2009a). Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proceedings of the Royal Society*, 276, 575–584.
- Sell, A., Tooby, J., & Cosmides, L. (2009b). Formidability and the logic of human anger. *Proceedings of the National Academy of Science*, 106(35), 15073–15078.
- Sell, A., Bryant, G., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., ... Gurven, M. (2010). Adaptations in humans for assessing physical strength and fighting ability from the voice. *Proceedings of the Royal Society*, 277, 3509–3518.
- Sell, A., Hone, L., & Pound, N. (2012). The importance of physical strength to human males. *Human Nature*, 23, 30–44.
- Sell, A., Eisner, M., & Ribeaud, D. (2016). Bargaining power and adolescent aggression: The role of fighting ability, coalitional strength, and mate value. *Evolution and Human Behavior*, 37(2), 105–116.
- Sugiyama, M. S. (2014). Fitness costs of warfare for women. *Human Nature*, 25(4), 476–495.
- Tooby, J., & Cosmides, L. (1988). The evolution of war and its cognitive foundations. *Institute for Evolutionary Studies Technical Report*, 88(1), 1–15.
- Tooby, J., & Cosmides, L. (2010). Groups in mind: The coalitional roots of war and morality. *Human Morality and Sociality: Evolutionary and Comparative Perspectives*, 91–234.
- Tooby, J., & DeVore, I. (1987). In W. G. Kinzey (Ed.), *The reconstruction of hominid behavioral evolution through strategic modeling. The evolution of human behavior: primate models* (pp. 183–237).
- van der Dennen, J. M. G. (1995). *The origin of war: The evolution of a male-coalitional reproductive strategy, vols. 1 & 2*. Origin Press.
- Van Vugt, M., De Cremer, D., & Janssen, D. P. (2007). Gender differences in cooperation and competition in the Male-Warrior hypothesis. *Psychological Science*, 18(1), 19–23.
- Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, 138(3), 299–327.
- Watts, D., Muller, M., Amsler, S., Mbabazi, G., & Mitani, J. (2006). Lethal intergroup aggression by chimpanzees in the Kibale National Park, Uganda. *American Journal of Primatology*, 68, 161–180.
- Williams, G. C. (1966). *Adaptation and natural selection*. Princeton University Press.
- Wilson, M. L., Kahlenberg, S. M., Wells, M., & Wrangham, R. W. (2012). Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour*, 83, 277–291.
- Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., ... Lloyd, J. N. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature*, 513(7518), 414–417.

Wrangham, R. W., & Glowacki, L. (2012). Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers. *Human Nature, 23*(1), 5–29.

Wrangham, R. W., Wilson, M. L., & Muller, M. N. (2006). Comparative rates of violence in chimpanzees and humans. *Primates, 47*(1), 14–26.

Zefferman, M. R., & Mathew, S. (2015). An evolutionary theory of large-scale human warfare: Group-structured cultural selection. *Evolutionary Anthropology: Issues, News, and Reviews, 24*(2), 50–61.