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Ritual fights and male reproductive success in a human population

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Abstract

Ritual fights are widespread across human populations. However, the evolutionary advantage associated with this behaviour is unclear because these fights rarely provide direct benefits such as territory, resources or mates. Here, the reproductive success of men competing in a traditional ritual fight, Sereer wrestling, was investigated for the first time. Involvement in wrestling had a significant positive effect on men's number of offspring and a marginally significant effect on polygyny, controlling for age, body condition and socio-economic status. These positive effects suggest that being involved in wrestling competition provides prestige, facilitating access to mates and thereby increasing fecundity. However, when women were interviewed on their preference concerning qualities of potential mates, the quality 'being involved in wrestling competition' was poorly ranked. This discrepancy may arise either from deceptive reports or from discordance between parents and daughters in the choice of a husband.

Introduction

Ritual fights in human populations are widespread throughout the world, for example, male stick-duelling (sagine) in the Surma people of Southern Ethiopia (Abbink, 1999), Engolo fights in Angola (Desch-Obi, 2008), chest pounding in the Yanomamö people in Venezuela (Chagnon, 1997), or Judo in Japan (Carr, 1993). Their evolutionary significance remains unclear. Ritual fights are often costly in time and energy, and in many cases, males involved in such violent interactions have no direct gains, such as territory, resources or mates.

Similarly, in the Ache populations in Paraguay, there is apparently no direct benefit of being a good hunter. Indeed, the men belonging to the class of hunters take risks to capture prey, but all the food obtained is fairly divided among people of the village. However, Kaplan & Hill (1985) showed that hunting ability in the Ache males is associated with an increased number of offspring raised to adulthood through increased chances of survival of their children and a higher access to female partners, including illegitimate mating. This effect seems to be due to the prestige attributed to good hunters. The higher reproductive success observed in such categories could reflect a 'prestige' effect, but it could also be the result of better health and body condition. The strongest/healthiest men may have a greater probability to become prestigious hunters, and their greater reproductive success could be due to their better health/body condition rather than their reputation as hunters.

Another example is found among the Yanonamö populations from Venezuela. In this population, intergroup homicides are frequent. These homicides do not correspond to competition for resources but are instead attributed to revenge. Chagnon (1988) highlighted that the *Unokaï*, i.e. people who have committed a killing at least once in their life, have greater reproductive success, as measured by their number of wives or children. Homicide may thus allow the *Unokai* to acquire great prestige or reputation, leading to greater mating success (increased number or fertility of their mates). More generally, Irons (1979) suggested that competition for cultural success (or prestige) evolved because of its relationship with reproductive success.

In this study, we focused on the reproductive success of men who participate in ritual fights in a rural population in Senegal composed primarily of Sereer people. Sereer wrestling is a traditional fight with rules

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similar as those of Greco-Roman wrestling. Wrestling contests are regularly organized in the villages, and wrestlers from neighbouring villages come to participate. These competitions represent festive occasions: village inhabitants (men, women and children) attend the fights and encourage their champions. The competition takes place during the night (from about 10 PM to 2 AM) and lasts several days (normally 4 days, from Thursday to Sunday). The first evenings are dedicated to the youngest and most inexperienced wrestlers, and the level of wrestling increases throughout the days. Usually, on Sunday evenings, the best champions compete, and the spectators are more numerous. Wrestlers reaching the final fights can win money, from 1000 to 150 000 CFA francs (African Financial Community francs) (as a reference, the local prices are 50 000 CFA francs for a sheep and 300 000 CFA francs for 1 ha of land). Alternatively, they can win fabric for clothes or an animal (e.g. a cow). However, material gain is a recent occurrence (< 10 years old). Previously, wrestlers would gain only a flag representing their victory. Wrestling is an important part in the games played by the children in the villages. Males who decide to become wrestling competitors start seriously training at the age of 16–17 years by practicing and exercising their muscles. The decision to become a wrestler depends not just on physical prowess, but also on social and familial context. For example, boys whose fathers used to be wrestlers are more likely to become wrestlers themselves. Boys who have low scores at school are also more motivated to practice wrestling. Only a small proportion of men are involved in wrestling competitions (< 10%, as we roughly estimated).

This study aimed at testing whether competitive wrestling could bring a reproductive advantage to men, controlling for body condition and socio-economic status.

First, we recorded the number of children and grandchildren of wrestlers and nonwrestlers in Sereer villages. As wrestling competitions can now provide economic gains to the wrestlers, we controlled for a potentially confounding effect of socio-economic level. Economic status has been shown to have a great influence on male reproductive success in both traditional (Cronk, 1991) and industrialized societies (Nettle & Pollet, 2008). We also controlled for the potentially confounding effect of body condition. Wrestlers may have a better intrinsic body condition, whereas men with a weaker body condition may be unable to practice this sport. To further characterize the wrestlers' reproductive success, the number of wives was also investigated. We tested whether the prestige acquired through wrestling allows a greater access to sexual partners. Finally, the women's preferences concerning different men's qualities, such as kindness, strength, wealth or involvement in wrestling competition, were investigated by interviewing women about the qualities they find important when choosing a husband.

Materials and methods

Population studied

A survey was performed in the traditional villages surrounding the small town of Sokone (13°52'N, 16°22'W), located in the Sine Saloum area of Senegal on the West coast of Africa. The most common ethnic groups in this area are the Sereer, the Wolof and the Peuhl. The subsistence mode is mainly agriculture, especially cash crops like peanuts and cashew nuts, but also subsistence crops like millet. The inheritance mode is patrilineal, and the residence is patrilocal. Polygynous marriages are common, with a maximum of four wives, as determined by the Islamic religion to which most people belong.

The protocols used to recruit families and collect data have received the agreement of both the French National Committee of Information and Liberty (CNIL) and the ethical committee of the Senegalese National Research Council for Health. Informed consent was obtained from all subjects. Participants were not paid, but gifts like clothes, books, soaps, school and farming equipments were given to the head of the village in charge of the distribution among the villagers.

Components of men's reproductive success

In each study village, we interviewed several informers who indicated us the men currently involved in wrestling competition, and the men who had been wrestling champions in the past. We included all in our study. The control sample was randomly selected among men in the same age range. Forty-one current or former wrestlers and 55 nonwrestling men aged 15–88 were interviewed in these villages. Their age and the number of wives, children and grandchildren alive were recorded. Socio-economic status was estimated by recording land and cattle possessions. We calculated the price in CFA francs for 1 ha of land and for cattle animals (cows, donkeys, sheep and goats) by averaging the prices given by five local informers. Body height and weight were measured and used to compute the body mass index (BMI). The circumferences of both arms were also measured, and the average arm circumference was computed (mid-arm circumference or MAC). The MAC and BMI were used as estimates of men's body condition. These are both important components of body condition in this traditional society because they may reflect access to resources and resistance to parasites (Visweswara & Singh, 1970). Because they were highly correlated (Pearson correlation coefficient: $\rho = 0.87$; $P < 0.0001$), only the MAC was used to estimate body condition in the models reported here. However, using BMI instead did not significantly change the results.

Statistical analyses of men's reproductive success

All statistical analyses were performed with the software R 2.5.1 (http://www.r-project.org). Logistic regressions were computed to analyse the probability of ever reproducing (among all men, $N = 96$), or the probability of being polygynous (among married men, $N = 52$). General linear models (GLM) assuming a Poisson error distribution were computed to analyse the number of children among men who had at least one ($N = 48$ fathers), and the number of grandchildren among men who had at least one ($N = 20$ grandfathers). The Quasi-poisson correction was used in both cases to take into account the slight over-dispersion of residuals. The effects of the variables WRESTLER (wrestler vs. nonwrestler), AGE, MAC and SES (socio-economic status) were tested in all models. Additionally, the effect of the number of wives was tested in the analysis of the number of children. The significance of a model term was tested by computing the variation of deviance between the model with and without the term. This variation follows a chi-squared distribution (in logistic regressions) or an F-distribution (in GLMs with Poisson error structure and correction for over-dispersion).

Women's preference assessment

Seventy women of reproductive age (at least 14 years old) were also interviewed about their preferred qualities for a husband. Seven cards representing different qualities of a man were drawn by a Sereer woman. The qualities represented were the following: 'a man who is rich'; 'a man who is a good wrestler'; 'a man who is kind with his children'; 'a man who is kind with his wife'; 'a man who is courageous, hard-worker'; 'a man who is generous'; and 'a man who is educated'. These cards were presented in random order to the women interviewed. Women were asked to rank the cards according to how important they considered each quality when evaluating a potential husband. The order chosen by the women was recorded, as well as their age. The average rank for each card, as assessed by the 70 women, was computed. In addition, a nonparametric test of the correlation between the woman's age and rank of the card 'a man who is a good wrestler' was performed (Spearman's rank test).

Results

Descriptive statistics

Table 1 presents the average age, MAC and SES in the study samples. On average, wrestlers had a higher MAC than nonwrestlers (Wilcoxon test, $W = 1637$, $P < 0.0001$). However, no significant difference in SES was detected between wresters and nonwrestlers (Wilcoxon test, $W = 1115.5$, $P = 0.91$).

Table 1 Descriptive statistics [mean and standard deviation of the age, mid-arm circumference (MAC) and socio-economic status (SES)].

	Sample size	Age	MAC	SES (10^6 CFA)
Total sample	96	36.06 ± 16.4	26.94 ± 2.49	3.33 ± 3.3
Wrestlers	41	39.67 ± 14.6	27.98 ± 2.21	3.35 ± 3.8
Nonwrestlers	55	31.22 ± 17.7	26.15 ± 2.41	3.33 ± 2.8
Fathers (Sample 1)	48	48.10 ± 13.21	26.34 ± 2.65	3.13 ± 2.5
Nonfathers	48	24.02 ± 8.71	27.55 ± 2.18	3.54 ± 3.8
Grandfathers (Sample 2)	20	57.85 ± 12.31	26.17 ± 2.54	3.23 ± 2.4
Nongrandfathers	76	30.33 ± 12.01	27.14 ± 2.46	3.36 ± 3.4
Married men (Sample 3)	52	47.54 ± 13.69	26.42 ± 2.67	3.15 ± 2.5
Unmarried men	44	22.5 ± 5.28	27.54 ± 2.15	3.56 ± 3.92

Probability of ever reproducing

In the total sample, the probability of ever reproducing was significantly higher among wrestlers than nonwrestlers (logistic regression with the variable WRESTLER alone: $\chi^2_1 = 12.6$, $P < 0.001$). Younger men were obviously less likely to have already reproduced (logistic regression with the variable AGE alone: $\chi^2_1 = 76.1$, $P < 0.001$). MAC had a significant positive effect on the probability of ever reproducing (logistic regression with the variable MAC alone: $\chi^2_1 = 5.26$; $P = 0.02$), indicating that men with a larger MAC were more likely to ever reproduce. SES had no effect on this probability (logistic regression with the variable SES alone: $\chi^2_1 = 0.063$; $P = 0.80$). When controlling for AGE and MAC (respectively $\chi^2_1 = 62.8$; $P < 0.001$ and $\chi^2_1 = 0.008$; $P = 0.93$), the difference between wrestlers and nonwrestlers on the probability of ever reproducing was no longer significant ($\chi^2_1 = 1.41$; $P = 0.23$).

Number of children

The number of children alive was analysed among the men who reproduced at least once (sample 1, see Table 1). As shown in Fig. 1, wrestlers had, on average, more children than other men ($F_{1,47} = 8.3211$; $P = 0.006$; 14.04% of deviance explained).

Because AGE, MAC and SES could be important components of this increased reproductive success effect, we controlled for their potentially confounding effect and the effect of all possible two-way interactions. The minimum model obtained after simplification of nonsignificant variables contained MAC, SES and WRESTLER. The Quasipoisson correction was used to take into account the slight over-dispersion of residuals (the deviance of residuals was 65.08 for 44 degrees of freedom). Using this model, we showed that men with a higher MAC had significantly more children ($F_{1,47} = 6.84$; $P = 0.01$, 10.41% of deviance explained) as did men with higher

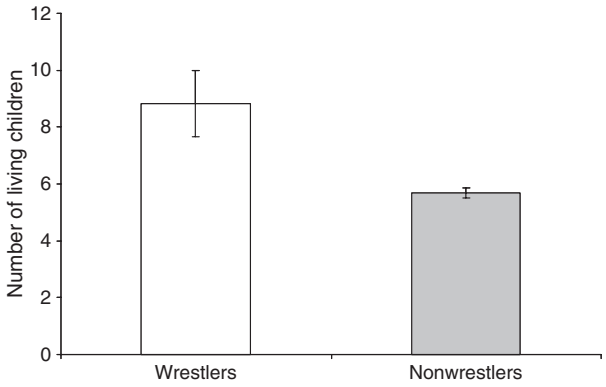

Fig. 1 Number of living children among men who reproduced at least once, depending on whether they are wrestlers. Error bars correspond to the standard error of the mean.

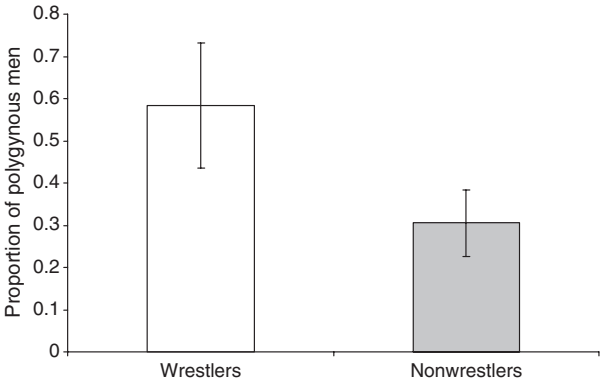

Fig. 2 Proportion of polygynous men among married men, depending on whether they are wrestlers. Error bars correspond to the standard error of the mean.

SES, which was marginally significant ($F_{1,47} = 3.35$; $P = 0.07$, 5.09% of deviance explained). The effect of WRESTLER remained significant when controlling for MAC and SES. Wrestlers still had more children than nonwrestlers ($F_{1,47} = 8.24$; $P = 0.006$, 12.52% of deviance explained). The interactions between WRESTLER and MAC and between WRESTLER and SES had no significant effect (respectively $F_{1,44} = 0.46$, $P = 0.50$ and $F_{1,44} = 0.85$, $P = 0.36$).

When adding the number of wives to this model, neither the effect of the variable WRESTLER ($F_{1,47} = 3.04$; $P = 0.09$) nor the effect of SES ($F_{1,47} = 0.88$; $P = 0.35$) were significant. The minimum model obtained then contained the number of wives and the MAC: men with more wives and those in better body condition had more children (respectively $F_{1,47} = 12.67$; $P < 0.001$ and $F_{1,47} = 4.22$; $P = 0.04$).

Number of grandchildren

Neither MAC nor SES had a significant effect on the probability to have at least one grandchild (respectively $\chi^2_1 = 0.19$; $P = 0.66$ and $\chi^2_1 = 1.61$; $P = 0.20$). Being a wrestler or not had no effect on the probability to have at least one grandchild ($\chi^2_1 = 2.59$; $P = 0.10$), controlling for AGE ($\chi^2_1 = 52.48$; $P < 0.0001$).

The factors influencing the number of grandchildren alive were then investigated among men who had least one grandchild (sample 2, Table 1). The Quasipoisson correction was used to take into account the over-dispersion of residuals (the deviance of residuals was 37.397 for 15 degree of freedom). Neither AGE nor SES had a significant effect on the number of grandchildren (respectively $F_{1,19} = 3.60$; $P = 0.07$ and $F_{1,19} = 0.03$; $P = 0.86$). Men in better body condition had more grandchildren ($F_{1,19} = 0.39$; $P = 0.03$). No effect of being a wrestler was detected on the number of grandchildren ($F_{1,19} = 3.01$; $P = 0.10$), controlling for MAC ($F_{1,19} = 6.76$; $P = 0.02$).

Probability of being polygynous

The factors influencing the probability of having more than one wife were investigated among married men (sample 3, see Table 1). As shown on Fig. 2, wrestlers were more likely to have more than one wife. AGE and MAC had no significant effect on the probability of being polygynous (respectively $\chi^2_1 = 0.16$; $P = 0.69$ and $\chi^2_1 = -0.01$; $P = 0.9$). Wealthier men were more likely to become polygynous ($\chi^2_1 = 4.70$; $P = 0.03$). However, the WRESTLER variable was not significant ($\chi^2_1 = 2.63$; $P = 0.10$, 3.85% of deviance explained), when controlling for SES ($\chi^2_1 = 5.15$; $P = 0.02$, 7.55% of deviance explained).

Women's preferences

The experiment regarding women's choice aimed at investigating whether wrestlers were judged as more attractive when compared to men having other qualities. Table 2 presents the mean rank for each of the cards presented to the women. The highest rank was obtained for the card that represented 'A man who is kind with his

Table 2 Ranking of seven husband's qualities by 70 women.

Quality	Mean rank (out of 7)
A man who is kind with his wife	2.46
A man who is kind with his children	3.07
A man who is courageous, hard-worker	3.16
A man who is generous	3.86
A man who is educated	3.87
A man who is a good wrestler	5.70
A man who is rich	5.86

wife' and the lowest for the card representing 'A man who is rich'. The fact that a man is a wrestler did not seem to be a characteristic considered as important by the women (mean rank of the card 'A man who is a good wrestler' = 5.7 out of 7) whatever of the woman's age (Spearman correlation test between the rank of this card and the age of the women interviewed, $\rho = -0.13$; $P = 0.28$).

Discussion

Components of men's reproductive success

Our results suggest that wealthier men are more likely to be polygynous and have more children. The importance of socio-economic status for the access to mates has already been observed in many traditional (Hill, 1984) and industrialized (Fieder & Huber, 2007; Nettle & Pollet, 2008) societies. However, this study is the first to show that wrestlers have significantly more children than other men. This result suggests that there is a positive effect of being involved in wrestling competition on male fitness. Body condition, as estimated by the MAC, also had a positive influence on men's reproductive success. However, the effect of being a wrestler on offspring count is still significant when controlling for body condition (MAC) and SES. Therefore, wrestlers not only have a better body condition on average (as estimated by a higher MAC), they also obtain an additional fitness benefit, possibly due to the prestige acquired through wrestling practice. The positive effect of prestige on men's reproductive success had already been highlighted in Ache hunters (Kaplan & Hill, 1985) and Yanomamö *Unokaï* (Chagnon, 1988), but the precise contributions of body condition and SES to this effect remained unclear. Concerning Sereer wrestling, we demonstrated an additional prestige effect facilitating access to mates besides the positive effects of body condition (estimated by MAC) and SES.

In this Sereer population, the number of wives seems to be the major factor that leads to an increase in the number of children, suggesting that the 'prestige' may provide a greater access to reproductive partners. We confirmed that this increase in the number of children in wrestlers was mainly due to an increase in the number of wives by a confirmatory path analysis (Shipley, 2009). We compared a causal scheme where the variable WRESTLER had only a direct influence on the number of offspring (model 1) and a causal scheme where the variable WRESTLER had only a direct influence on the number of wives, which obviously influenced the number of offspring (model 2). In both models, SES and MAC both had an influence on both the number of offspring and the number of wives. Model 1 has a lower probability ($\chi^2_{12} = 22.75$; $P = 0.03$) than model 2 ($\chi^2_8 = 6.49$; $P = 0.59$), suggesting that the number of wives was the major, if not only, path for wrestlers to increase their reproductive success. The effect of prestige on access to mating partners is also found for sports in industrialized societies. In a population of French students, athletes reported having more sexual partners than men who did not practice any sports (Faurie *et al.*, 2004). This study suggests that involvement in sports, like involvement in ritual fights, is under sexual selection.

The number of grandchildren is a better measure of reproductive success because it takes into account offspring survival and their capacity to reproduce. However, no significant effect of involvement in wrestling on the number of grandchildren was detected in this rather small, and on average young, sample.

Wrestling as part of a reproductive strategy

Despite the fitness benefits revealed by this study, the proportion of wrestlers in the male population was quite low. This could be explained by the high costs and risks involved, in terms of time, finance and health. Participating in wrestling competitions implies extensive training. Wrestlers reported training more than 2 h per day (running, bodybuilding, wrestling, etc.). There can also be various social costs (e.g. the social cost of defeat). Those costs are probably similar to the costs involved in sport competition in Western societies. Additional costs are likely to exist in this specific population. Firstly, wrestling requires an important commitment in magic ceremonies. Moreover, wrestlers have to follow a specific diet, very rich in protein (eggs, milk, meat and fish), which is quite different from the local diet, and much more expensive. Finally, the risk of injury is very serious, because this population has little access to medical care.

The difference in number of children between wrestlers and other men can be interpreted as a difference in reproductive strategies, i.e. a differential allocation regarding the trade-off between (i) investment in mating, i.e. maximizing the number of reproductive events and (ii) investment in parenting, i.e. maximizing offspring survival (Trivers, 1972; Marlowe, 2000). This trade-off is mediated by testosterone levels, which are on average higher in individuals favouring mating as compared to individuals favouring parenting, and are also higher in individuals involved in aggressive behaviour and risky behaviour (Archer, 2006). We can hypothesize that wrestlers have higher levels of testosterone and invest relatively more in mating. The co-existence of wrestlers and nonwrestlers in this population may correspond to different ways of dealing with the mating vs. parenting trade-off.

Women's self-reported preferences and actual mating

Results of the women's interviews on their preferences for male qualities showed that wrestling ability and wealth are ranked as unimportant criteria for choice of husbands. Reported preferences thus appear to be

inconsistent with actual choices. This discrepancy may be due to a cultural bias. Some women explained to us that declaring a preference for wealthy men is socially poorly regarded. Additionally, women's preferences may have little influence on marriage. The decision may be exclusively made by the man, the man's family or the bride's family. The parents' choices could differ from the women's preferences. Indeed the interests, in terms of fitness, may differ between parents and daughters. As highlighted by Trivers (1974), the selection acting on parental and offspring fitness may lead to familial conflicts. For example, marriage of a woman to a wealthy man may bring resources to the woman's family, leading to an increase in parental inclusive fitness, even if the fitness of this woman is decreased by this marriage choice. It is thus possible that the quality ranked first by women, 'a man who is kind with his wife', has a lower importance for the parents, who would value resources. Our results suggest that the results of studies based on hypothetical mate choice preferences should be interpreted cautiously, since there seems to be a discrepancy between self-reported preferences and actual mating.

Another possible explanation of this discrepancy between female preferences and mating success may be that selection is not acting through female choices, but rather through male–male competition: the prestige acquired by wrestlers may dissuade other men from competing for the same female.

Conclusions

We have highlighted that a human behaviour, such as ritual fighting, that first appears to bring no direct fitness benefit and is costly in terms of health, may have been positively selected through sexual selection. Like the peacock's tail (Darwin, 1871), some costly traits are maintained through sexual selection in humans and other animals. Such phenomena highlight the importance of precise measures of reproductive success. The practice of sports or ritual fights in humans could represent a signal of quality used by females (or their parents) when choosing their mating partners. The biological or social pathway responsible for women's mating patterns and choices remain to be explained.

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