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Digit ratio and hand grip strength are associated with male competition outcomes: A study among traditional populations of the Yali and Hadza

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Abstract

Objectives: Indirect measures of physiological features, such as digit ratio and hand grip strength (HGS), are associated with the outcome of male competition activities. However, most of the studies were conducted in developed and industrialized societies. We tested the hypothesis that both digit ratio and HGS are associated with performance in male-specific activities in two traditional preindustrial societies: Yali and Hadza.

Methods: To measure masculine behavioral traits, we determined warriorship status (Yali; n = 49) and assessed hunting skills (Yali n = 47 and Hadza n = 49). We also assessed the digit ratio and HGS of each male. We conducted our analyses using the Bayesian approach.

Results: Bayesian regression models indicated that greater hand grip strength is associated with better hunting outcomes among Hadza males. We did not find a similar link for the Yali. We found anecdotal evidence for the link between left hand digit ratio and the number of birds hunted by Hadza. We found no evidence for the link between digit ratio and performance in male-male competition.

Conclusions: Our results suggest that male-male competition outcomes are determined by upper body strength, but only in the Hadza population. We also found limited support for the hypothesis that digit ratio is associated with hunting success among the Hadza. We found no support for the hypothesis concerning the digit ratio or HGS among the Yali. Our research provides partial support for the evolutionary hypotheses based on studies conducted in industrialized populations.

1 | INTRODUCTION

Human male-male competition is considered to be a selective pressure that shapes masculine physiological as well as behavioral characteristics (Andersson, 1994; Darwin, 1872; Miller, 2013). It has been shown that indirect measures of physiological features, such as digit ratio (Manning, Scutt, Wilson, & Lewis-Jones, 1998) and hand grip strength (HGS; Rantanen et al., 1999) are associated with behavioral traits connected to male performance in intrasex competition (eg, Manning & Taylor, 2001; Wind, Takken, Helders, & Engelbert, 2010). However, most of these studies used sports performance results as an indicator of performance in male-male competition activities (ie, Bennett, Manning, Cook, & Kilduff, 2010; Hansen, Bangsbo, Twisk, & Klausen, 1999; Hönekopp & Schuster, 2010; Kilduff, Cook, & Manning, 2011; Longman, Stock, & Wells, 2011; Longman, Wells, & Stock, 2015; Manning & Taylor, 2001; Watts, Joubert, Lish, Mast, & Wilkins, 2003).

Second-to-fourth digit ratio (2D:4D) had been suggested to be a biomarker of hormonal masculinization via prenatal exposure to sex hormones: the lower the ratio, the higher the masculinization. It was believed that it negatively correlated with testosterone and positively correlated with estrogen (Manning et al., 1998). Recent meta-analyses, however, did not support this hypothesis, questioning digit ratio as an indicator of prenatal androgen activity (Hönekopp, 2013; Voracek, 2014). Digit ratio is sexually dimorphic and is stable across the life-span (McIntyre, Ellison, Lieberman, Demerath, & Towne, 2005). It is important to acknowledge that there is an ongoing debate on whether digit ratio actually indicates prenatal exposure to sex hormones or if it is simply the by-product of an allometric shift of digit ratio with digit length (Forstmeier, 2011; Kratochvíl & Flegr, 2009; Lolli et al., 2017; Manning & Fink, 2018).

It has been hypothesized that sports performance, associated with 2D:4D, may serve as a proxy for performance in male-male physical competition (Manning & Taylor, 2001). Data suggest that males with a lower digit ratio (more masculine) tend to have physical advantages, that is, higher body mass (Klimek, Galbarczyk, Nenko, Alvarado, & Jasienska, 2014), higher maximal oxygen uptake (Hill, Simpson, Manning, & Kilduff, 2012), and greater upper body strength (as indicated by HGS; (Kociuba, Chakraborty, Ignasiak, & Kozieł, 2019; Zhao, Li, Yu, & Zheng, 2012). Moreover, it has been demonstrated that 2D:4D correlates with situational aggression (Kilduff, Hopp, Cook, Crewther, & Manning, 2013), risk-taking behavior (Stenstrom, Saad, Nepomuceno, & Mendenhall, 2011), and sensation seeking (Fink, Neave, Laughton, & Manning, 2006). Also, digit ratio negatively correlates with athletic prowess (Hönekopp & Schuster, 2010) and general performance in a wide array of disciplines, including football (Manning & Taylor, 2001), rugby (Bennett et al., 2010), basketball (Klapprodt, Fitzgerald, Short, Manning, & Tomkinson, 2018), rowing (Longman et al., 2011), softball, water polo (Lombardo, Otieno, & Heiss, 2018), and even surfing (Kilduff et al., 2011). Although digit ratio has been confirmed to be related to athletes' endurance (Longman et al., 2015), it remains unclear whether this relationship exists in a more evolutionarily relevant male-male competition activity (eg, hunting).

HGS is a biomarker of overall physical health, nutritional status, and levels of circulating testosterone (Chin et al., 2012; Norman, Stobäus, Gonzalez, Schulzke, & Pirlich, 2011). Unlike digit ratio, HGS is not stable across the lifespan; it increases into the 30s and declines in late adulthood (Kallman, Plato, & Tobin, 1990). HGS correlates with male physical aggression (Archer & Thanzami, 2007; Gallup, White, & Gallup, 2007; Muñoz-Reyes, Gil-Burmann, Fink, & Turiegano, 2012), promiscuity (Gallup et al., 2007), sensation-seeking (Fink, Hamdaoui, Wenig, & Neave, 2010), and socially-dominant behaviors (Gallup, O'Brien, White, & Wilson, 2010). Men with weaker HGS tend to report lower health-related quality of life (Sayer et al., 2006), and weaker HGS is associated with disabilities and mortality (Norman et al., 2011). Additionally, HGS was considered to be a marker of reproductive success in traditional societies (Atkinson et al., 2012). In summary, as a secondary sexual male characteristic, HGS is also suggested to be an indicator of physical male-male competitiveness (Sell, Hone, & Pound, 2012).

Both digit ratio and HGS have been connected with male-male competition activities in rich, developed, industrialized, and modern countries. However, there is a lack of studies exploring this link in traditional societies, where a similar relationship should be apparent among males taking part in more evolutionarily relevant male competition. It has been shown that successful warriors get personal rewards from raiding (Chagnon, 1988). Through waging wars, males acquire social status, wealth, and most importantly, they increase their reproductive success (for a review see Glowacki & Wrangham, 2013). Similarly, it has been theorized that hunting has been crucial throughout human evolution (Hawkes & Bliege Bird, 2002); by showing off hunting skills, men earn respect among other men and increase their mating value. Empirical data confirmed that good hunters have higher reproductive success (Gurven & Von Rueden, 2006; Smith, 2004).

In the present study, we tested whether measures of prenatal masculinization (2D:4D) and HGS are associated with warriorship status and hunting performance among Yali males of New Guinea and hunting performance among Hadza males of northern Tanzania. Both digit ratio and HGS were linked to performance in male-male competition, yet there is a lack of evidence that these measures are associated with performance in male activities that have been crucial for human evolution.

To our knowledge, only one study to date has explored the link between HGS and hunting in traditional societies. Apicella (2014) conducted a study among the Hadza, using HGS as an upper body strength indicator, and showed that men with greater upper body strength tend to be perceived as better hunters (no actual hunting performance was tested). We are not aware of any direct data exploring the link between warriorship status and digit ratio or HGS.

Conducting studies in traditional societies, especially those remote and distinct to each other, is necessary to rule out the probability of drawing general conclusions from findings limited to a given population (Henrich et al., 2001; Henrich, Heine, & Norenzayan, 2010). To date, studies on digit ratio and HGS, and their link to male-male competition, have come from industrialized western societies. Our aim was to broaden the perspective by providing data from

traditional societies and to verify the universality of the abovementioned findings. We expected hunting performance and warriorship status to be positively related to HGS and negatively to 2D:4D. Confirming these hypotheses in two different and distant societies would bring us ecologically valid evidence that digit ratio and HGS might be associated with the performance in male-male competition throughout human evolution.

2 | METHODS

The study was conducted according to the principles of the Declaration of Helsinki. The populations studied were illiterate and therefore a written consent could not be obtained. The participants gave verbal consent and were told that their participation was voluntary and that they could withdraw from the study at any time. The study protocol and consent procedure received ethical approval from the Institutional Review Board (IRB) of the Institute of Psychology (University of Wrocław) and the Ethics Committee of Moscow State University, ethical approval from the head of the local Yali community in West Papua, and ethical approval from the Tanzania Commission for Science and Technology (COSTECH).

2.1 | Participants

The Yali population inhabits the Baliem Valley of New Guinea. We collected our data in small villages surrounding the Piliam village (Papua—Indonesian province). The Yali population has little contact with Western cultures because of limited access to their lands. They are considered traditional horticulturalists (Koch, 1974). The Yali society is strongly male-dominated and polygynous. In their society, people tend to distinguish some highly influential men as big men (Koch, 1974; Sorokowski, Sorokowska, & Danel, 2013). Big men tend to be fit and charismatic, and they are able to provide pigs, which signify a man's wealth. As Koch (1974) describes, big men gain their high social position through competence in creating debt relationships not only with relatives, but also with men who are not relatives. Most Yali villages acknowledge one or two men as big men.

Koch (1974) thoroughly described Yali means of waging wars. By the Yali definition, warfare occurs when both parties use bows and arrows in combat. Initial attacks are almost always a form of retaliation. Raids can be followed by theft. According to three Yali men whom we interviewed independently, Yali wage wars against other Yali and Western Dani (Dani is a population located on the east of Yalimo) roughly every 2 to 3 years. They claim that participating in war is not obligatory, and people often refrain from participating because of fear. Those who fear participation in war are called "akol," which literally means "a coward." "Oloktek" is a word for "a warrior." The most frequently claimed reason for war is "to capture women." Females are taken by victorious men to their home villages and become their wives. Males also attack other groups as a form of retaliation—to take their food and land, and for political reasons, such as establishing authority. They confirmed that in combat they use bows and arrows with sharpened wooden foreshafts, knives, and axes.

Hunting is not a substantial source of food for Yali. Their diet consists mainly of tubers and other vegetables (Milliken, 1994). According to our interviews with Yali regarding their hunting practice, hunting is considered to be exclusive to men. They hunt at night, especially during the full moon when the light allows them to spot animals. They hunt for rodents and marsupials like cuscus and tree kangaroos using bows and arrows. Yali also use traps and dogs to support hunting. During the day Yali hunt for birds.

The Hadza population inhabits northern Tanzania, a territory around Lake Eyasi. We collected data in eight Hadza camps located in the savannah-woodland habitat of the Mangola region. The Hadza are traditional hunter-gatherers with a strong sexual division of labor. Men are responsible for hunting and women for foraging (Marlowe, 2010). Hadza are considered to be an egalitarian society with no clear hierarchy (Woodburn, 1982). They sometimes use physical aggression toward other Hadza (Butovskaya, Burkova, Karelin, & Fink, 2015). Although Hadza have historically been attacked by neighboring pastoralists, unlike Yali, they do not wage regular wars (Marlowe, 2002).

Hadza hunting practices were extensively described by Marlowe (2010). Among Hadza, hunting is a male-exclusive activity and better hunters have greater reproductive success (Hawkes, 2001; Marlowe, 1999). It is argued that Hadza men hunt mainly to signal their mating value (Hawkes & Bliege Bird, 2002), as the meat they bring to camp constitutes 30% of food consumed by the population (Marlowe, 2010). However, this is still debated (Wood, 2006).

Study 1 was conducted among 22 Yali warriors (age $M = 39.8$; SD = 14.63) and a control group consisting of 27 Yali of a similar age who had not participated in wars (age $M = 42.7$; SD = 16.89). Study 2 was conducted among 47 Yali hunters (age $M = 40$; SD = 14.69) and 49 Hadza hunters (age $M = 36.39$; SD = 12.79). We invited every man in each village or camp to participate in our study, and we included all men willing to participate. Data from Yali were collected during the same expedition as reported by Marczak, Misiak, Sorokowska, and Sorokowski (2018). The measurement data for the Yali were gathered during May 2016, and the data for the Hadza was gathered during August 2017.

2.2 | Measures

2.2.1 | Digit ratio measurement

We measured digit ratio using a digital Vernier caliper with accuracy down to 0.01 mm. We took measures of the second and fourth finger from a mid-point on the ventral crease proximal to the palm to the tip of the finger. We measured both the left and right hand. We were unable to measure both hands of two Yali men and the left hands of three Hadza men because of hand injury or deformation. The Hadza had each hand measured twice, but the second measurement for Yali was performed using the digital photos of hands (3072 × 2304 pixel) to measure length of the index and the ring finger using a GNU Image Manipulation Program (GIMP) and its "measure" tool. Initially, we wanted to compare both methods of measurement in both populations (see Fink, Thanzami, Seydel, & Manning, 2006) but we did not manage to have appropriate equipment during the field study among the Hadza. We found high intraclass correlation coefficients for caliper digit ratio measures among the Hadza (right hand: $r = .93$, $P < .001$; left hand: $r = .95$, $P < .001$). For Yali, we tested the reliability of the digit ratios from the two methods of measurement using intraclass correlation coefficients. These were high for both the right ($r = .86$, $P < .001$) and left hand ($r = .97$, $P < .001$). To avoid comparing digit ratios measured with two different methods, we averaged measures for the Hadza, and for the Yali we only analyzed the measures obtained using digital calipers.

2.2.2 | Hand grip strength measurement

We measured maximum voluntary contraction of the grip flexors, commonly known as hand grip strength. We used a Harpenden spring dynamometer (Balogun, Adenlola, & Akinloye, 1991). Each participant was instructed to take a comfortable position and squeeze the dynamometer with his dominant hand as hard as he could, with the dominant hand raised and not supported by other parts of the body. We repeated the measurement three times. One Yali man refused to take part in the hand grip strength measurement. Measurements had a high intraclass correlation coefficient both for the right hand ($r = .82$, $P < .001$) and the left hand ($r = .87$, $P < .001$). We planned to analyze the strongest hand grip strength and the mean hand grip strength independently, but we found a strong correlation ($r = .98$) between these variables. Finally, to analyze hand grip strength, we used the mean of the three grips.

2.2.3 | Warriorship status

We found 22 men that declared their warrior status, that is, taking part in tribal wars. We asked one of the big men to confirm that the men who claimed to be warriors indeed took part in wars. Each declaration was confirmed. Furthermore, we found 27 men who declared that they were not warriors, and they served as a control group. Their non-warrior status was also confirmed by the big man.

2.2.4 | Hunting performance

To assess hunting performance we asked each man two questions: (a) what animals, not including birds, did you hunt during your last hunt (for Yali), or during the last 7 days (for Hadza)? (b) What birds did you hunt during your last bird hunt (for Yali), or during the last 7 days (for Hadza)? We added the number of animals and the number of birds independently. Yali hunt approximately once a month, and thus we could not ask them about the previous week's hunting performance. To the contrary, Hadza hunt relatively often (Marlowe, 1999), therefore asking about hunts over the last month could potentially confuse them. We asked about mammals and birds separately, as birds are available in the nearby environment for both populations. Mammals are harder to hunt, and hunting them may be more unpredictable, as the effort put into hunting does not necessarily predict the hunting outcome (Hawkes, O'Connell, & Jones, 2001). According to the participants, all healthy men of both populations participate regularly in hunting. We ensured that men understood our questions, as they described animals they hunt. The animals that Yali most frequently mentioned were cuscus and tree kangaroos, and Hadza mostly mentioned baboons and dik-dik antelopes.

We measured the height and weight of each participant to determine their body mass index (BMI). BMI is an indicator of nutritional status, which can influence hand grip strength (Chilima & Ismail, 2001), so we aimed to control it. We also asked about the participants' age to include it in our models since hand grip strength decreases with age (Massy-Westropp, Gill, Taylor, Bohannon, & Hill, 2011). The Yali men were also asked about their number of children.

2.3 | Statistical analysis

We conducted our analyses in the Bayesian framework. Although the majority of studies on digit ratio and hand grip strength were analyzed through the frequentist framework (eg, Null Hypothesis Significance Testing), we decided to conduct Bayesian analyses, as they allow for reaching meaningful conclusions from small sample sizes (Jarosz & Wiley, 2014). Furthermore, the Bayesian framework allows for the update of knowledge. Future models built from the studies on small-scale traditional populations may be informed by the Bayes Factors obtained in this study (Zyphur & Oswald, 2015).

Bayes factors allow for robustly quantifying the degree by which the observed data favor the alternative hypothesis regardless of sample size (Jarosz & Wiley, 2014). BF_{10} are reported to quantify the extent to which the data favor the alternative hypothesis relative to the null hypothesis ($BF_{10} > 1$ provides evidence in favor of the alternative hypothesis; $BF_{10} < 1$ provides evidence in favor of the null hypothesis; $BF_{10} = 1$ provides equal support for alternative and null hypotheses). We used a default Cauchy prior width of 0.707 and interpreted the results based on the canonical interpretations of the Bayes factor (Jeffereys, 1961). All of the analyses were conducted using JASP 0.9.1.0 software (JASP Team, 2018).

2.3.1 | Study 1

To test the alternative hypotheses concerning warriorship status, we examined two Bayesian regression models. The first and second Bayesian regression models tested whether right hand digit ratio and left hand digit ratio were associated with the warriorship status in Yali males. The third Bayesian regression model tested whether the mean hand grip strength (BMI and age included in the null model) was associated with the warriorship status in Yali males. The warriorship status in all models was dummy coded, where 0 meant a man is not a warrior and 1 meant a man is a warrior.

2.3.2 | Study 2

To test the alternative hypotheses concerning the hunting performance, we conducted Bayesian regression models (Table 3). The first models tested whether right hand digit ratio and left hand digit ratio were associated with the number of mammals (including marsupials in the case of Yali) and birds hunted. The subsequent models tested whether the mean hand grip strength (BMI and age included in the null model) were associated with the number of mammals and the number of birds hunted.

Additionally, we conducted Bayesian and frequentist regression (as it is most commonly used for assessing allometry in digit ratio) analyses to establish whether digit ratio may be associated with an allometric shift in finger length (Forstmeier, 2011). We used digit ratio as a dependent variable and the mean of second and fourth digit length as a predictor. We also dummy coded the population variable and controlled for it.

3 | RESULTS

3.1 | Study 1

The descriptive statistics are presented in Table 1. We found that models which included right hand digit ratio and left hand digit ratio do not support the alternative hypothesis (right hand: $BF_{10} = 0.29$; left hand: $BF_{10} = 0.29$). In this case, Bayes factor suggests that it is only 0.29 times more likely that there is a relationship between right hand digit ratio or left hand digit ratio and warriorship status in comparison to the null hypothesis, thus providing evidence for the null hypothesis according to the canonical interpretations of the Bayes factor (Jeffereys, 1961).

A Bayes Factor estimation showed that the model that included mean hand grip strength (age and BMI added to the null model) does not provide evidence for the alternative hypothesis ($BF_{10} = 0.43$). This means that it is only 0.43 more likely for the alternative hypothesis to be true, which is insufficient to claim that HGS may relate to warriorship status in any way. However, it appeared that BMI is a sole predictor of warriorship status. After including the other variables in the null model, we found substantial evidence ($BF_{10} = 5.02$) for the hypothesis that higher BMI predicts that a man is a warrior.

TABLE 1 Descriptive statistics and group comparisons for study 1

	Nonwarriors (n = 25) Mean (SD)	Warriors (n = 22) Mean (SD)	Bayesian independent samples *T*-test BF_{10}	Independent samples *T*-test *t*
Right hand digit ratio	0.95 (.061)	0.96 (.043)	0.29	−0.06
Left hand digit ratio	0.97 (.070)	0.97 (.067)	0.29	−0.08
Mean HGS	45.91 (25.115)	48.32 (22.320)	0.32	−0.57
BMI	24.99 (1.622)	26.13 (1.645)	4.90	−2.69*
Age	42.12 (16.496)	39.82 (14.634)	0.34	0.63

Note. *$P < .05$; BF10 > 1 provides evidence in favor of the alternative hypothesis; BF10 < 1 provides evidence in favor of the null hypothesis; BF10 = 1 provides equal support for alternative and null hypotheses.
Abbreviations: BMI, body mass index; HGS, hand grip strength.

3.2 | Study 2

The descriptive statistics are presented in Table 2. An estimation of the Bayes factor showed that it is unlikely for hunting success to be associated with digit ratio or hand grip strength—except for the Hadza hunting mammals and birds (Table 3). According to canonical interpretations of Bayes factors, we found substantial evidence for the relationship between mean HGS (BMI and age included in the null model) and the number of hunted mammals in the Hadza population ($BF_{10} = 3.60$). This meant that Hadza with a stronger mean HGS are 3.60 times more likely to hunt more mammals. We also found anecdotal evidence for the relationship between the left hand digit ratio and the number of hunted birds. This means that Hadza with higher digit ratio (less masculine) are 1.23 times more likely to hunt more birds.

Additionally, we verified whether digit ratio is linked to allometric shift (Table 4). We conducted Bayesian and frequentist regression analyses. Yali have longer fingers than Hadza, so we controlled for population in the frequentist model, and we included the population in the Bayesian null model. We found that estimation of the Bayes Factor provides substantial evidence for the association between right hand mean finger length and right hand digit ratio ($BF_{10} = 7.91$). It also provides anecdotal evidence for the association between left hand mean finger length and left hand digit ratio ($BF_{10} = 2.32$). Frequentist linear regression provides evidence that the right hand mean finger length is associated with the right hand digit ratio ($\beta = .29$; $P < .01$) and the left hand mean digit length is associated with the left hand digit ratio ($\beta = .23$; $P < .05$).

Marczak et al. (2018) reported a small negative correlation between right hand digit ratio and the number of

TABLE 2 Descriptive statistics and group comparisons for study 2

	Yali Mean (SD)	Hadza Mean (SD)	Bayesian independent samples *T*-test BF_{10}	Independent samples *T*-test *t*
2D:4D Models	n = 47	n = 46		
Right hand digit ratio	0.95 (0.053)	0.96 (0.041)	0.27	−0.69
Left hand digit ratio	0.97 (0.068)	0.97 (0.040)	0.23	0.33
Hunting—mammals	6.34 (5.168)	2.78 (3.425)	115.93	3.90**
Hunting—birds	9.60 (7.798)	3.30 (4.496)	2788.80	4.75**
HGS Models	n = 49	n = 49		
Mean HGS	46.189 (23.527)	41.707 (6.633)	0.44	1.28
Age	41.43 (15.826)	36.39 (12.798)	0.80	1.73
BMI	25.425 (1.759)	21.23 (1.831)	4.25	11.54**
Hunting—mammals	6.29 (5.066)	2.90 (3.484)	115.93	3.86**
Hunting—birds	9.53 (7.652)	3.39 (4.667)	2788.80	4.80**

Note. Mammals—mammals hunted during the last hunt (for Yali), or during the week preceding the study (for Hadza); Birds—birds hunted during your last hunt (for Yali), or during the week preceding the study (for Hadza); BF10 > 1 provides evidence in favor of the alternative hypothesis; BF10 < 1 provides evidence in favor of the null hypothesis; BF10 = 1 provides equal support for alternative and null hypotheses.
Abbreviations: BMI, body mass index; HGS, hand grip strength.
**$P < .001$.

TABLE 3 Bayes factors (BF_{10}) for alternative regression models concerning digit ratio, hand grip strength, and hunting success

	Yali		Hadza	
	Mammals	Birds	Mammals	Birds
Right hand digit ratio	0.31	0.35	0.29	0.54
Left hand digit ratio	0.31	0.35	0.31	1.26
Age + BMI included in the null model				
Mean HGS	0.46	0.47	3.60	0.68

Note. Mammals—mammals hunted during the last hunt (for Yali), or during the week preceding the study (for Hadza); Birds—birds hunted during your last hunt (for Yali), or during the week preceding the study (for Hadza); BF10 > 1 provides evidence in favor of the alternative hypothesis; BF10 < 1 provides evidence in favor of the null hypothesis; BF10 = 1 provides equal support for alternative and null hypotheses.
Abbreviations: BMI, body mass index; HGS, hand grip strength.

TABLE 4 Standardized beta coefficients and Bayes Factors for models concerning mean finger length, population, and digit ratio

	Right hand digit ratio		Left hand digit ratio	
	***B* (SE)**	***β***	***B* (SE)**	***β***
Right hand model: $R^2 = .06$ Left hand model: $R^2 = .03$				
Constant	0.82 (0.071)		0.78 (0.064)	
Mean finger length	0.002 (8.623e-4)	0.29**	0.002 (9.646e-4)	0.23*
Population (0 = Yali, 1 = Hadza)	0.017 (0.010)	0.18	0.002 (0.012)	0.19
Bayes factor (BF_{10})				
Population included in the null model				
Mean finger length	7.91		2.32	

Note. *$P < .05$; **$P < .01$; BF10 > 1 provides evidence in favor of the alternative hypothesis; BF10 < 1 provides evidence in favor of the null hypothesis; BF10 = 1 provides equal support for alternative and null hypotheses.

children among Yali males. Although it is not directly related to this study, we attempted to further clarify this link by conducting a mediation analysis among the Yali participants (n = 47). We hypothesized an indirect effect of right hand digit ratio on the number of children through hunting success (measured through mammals hunted and birds hunted separately). Two mediation models were tested to verify if the number of mammals or the number of birds hunted mediates the relationship previously reported. Analyses were performed by means of the PROCESS macro developed for SPSS (Hayes, 2017). A bias-corrected bootstrap confidence interval for the indirect effect based on 5000 bootstrap samples indicated that there is no indirect effect of right hand digit ratio on the number of children, neither through mammals hunted ($b = -0.133$, BCa CI [−4.2586, 1.9605]) nor birds hunted ($b = 0.002$, BCa CI [−2.8028, 30 327]). We did not gather data on reproductive success among Hadza and, therefore, we were unable to conduct a similar analysis on Hadza.

4 | DISCUSSION

A great number of studies indicate a link between digit ratio, HGS, and male-male competition outcomes (ie, Gallup et al., 2007; Manning & Taylor, 2001). However, these studies did not include any traditional societies, where the ecology is much more similar to the ecology of the origins of human species. Here, we found evidence for the association of upper body strength with hunting success among the Hadza, a hunter-gatherer population in Tanzania. We did not, however, observe a significant relationship between digit ratio, HGS, and male-male competition outcomes in the male sample of the Yali, a horticulturalist population of New Guinea.

We found that Hadza hunter gatherers, who have greater hand grip strength, are more likely to hunt more mammals (but not birds). HGS is a marker of overall physical health, nutritional status, and level of circulating testosterone (Chin et al., 2012; Norman et al., 2011), which means that these biological characteristics might mitigate hunting. As for the Hadza, hunting requires endurance, as they practice pursuit methods of hunting. They often have to follow wounded animals for long distances and carry their carcasses back to the camp (Marlowe, 2010). Greater upper body strength may also enable Hadza males to launch more powerful shots from the large bows they use (Bartram, 1997). Yet, we did not observe any relationship between hand grip strength and bird hunting in the Hadza. It could be that upper body strength does not influence bird hunting outcome. Birds are more common, and they inhabit the near proximity of the Hadza camps, making them much easier to hunt than larger mammals, which have more unpredictable locations (Hawkes et al., 2001).

Our study reinforces the results reported by Apicella (2014). She found that stronger men have a reputation of being better hunters. Our study demonstrates that upper body strength is linked not only to reputation but to actual hunting performance. This finding confirms the hypothesis that upper body strength may serve as an indicator of physical male-male competitiveness.

We also found that left hand digit ratio was associated with the number of birds hunted. Hadza males with a higher digit ratio (less masculine) hunted more birds. This result, according to the canonical interpretation of Bayes Factor, provides only anecdotal evidence (Jeffereys, 1961). Surprisingly, contrary to our expectations, Hadza males with less masculinized digit ratio were more successful in bird hunting. This result must be interpreted with caution. Further research is needed to confirm this counterintuitive finding. If

our finding reflects the true effect of prenatal exposure to sex hormones on hunting performance among Hadza, it means that a new hypothesis is needed to explain this phenomenon. We want to highlight that this kind of evidence allows us only to speculate on the causes of such a pattern. One probable explanation could be that men with a higher digit ratio tend to be more risk averse (Stenstrom et al., 2011), as has been shown in previous studies. This, in turn, could prevent them from leaving the camp for big-game hunting and motivate them to forage in the near area of the camp where they can safely hunt for smaller prey-like birds.

We found no evidence for the link between HGS and digit ratio to hunting success or warriorship status among the Yali. Warriorship and hunting performance in Yali may be determined by quite different characteristics, independent of prenatal exposure to sex hormones or upper body strength. Such characteristics may be related to cognitive (ie, intelligence, creativity) and motivational functioning, as well as socialization toward activities, and associated with foraging and gaining higher social status (Hawkes, O'Connell, & Jones, 1995). Notably, the Yali ways of hunting may promote these psychological characteristics when using traps and dogs for night sneaking (Koch, 1974). The use of traps and dogs allows less physically fit individuals to participate in hunting. It could be argued that the Yali ways of hunting do not fit in the frame of the endurance hypothesis and digit ratio that was proposed by Longman et al. (2015).

We found only one characteristic that allowed us to predict performance in male-male competition among the Yali. It appeared that Yali men who took part in tribal wars had a higher BMI. The relationship between BMI and warriorship status is not straightforward. It could be argued that, because the Yali take part in wars voluntarily, only the healthiest and most sizable men decide to risk their lives in combat. However, warriors were able to achieve a higher BMI through the benefits and rewards of participation in warfare. Glowacki and Wrangham (2013) argue that men benefit from wars by gaining social status. Studies report that increased social status allows men to obtain more social support and wealth, including food (Gurven & von Rueden, 2006; von Rueden, Gurven, & Kaplan, 2008). This way, men who are wealthier can maintain a higher BMI. Still, the causal relationship between BMI and warriorship status requires further clarification.

We also observed an association between finger length and digit ratio. This means that a portion of the variance in digit ratio may be explained by the allometric shift. Apparently, this association is stronger in the right hand. This finding contributes to the debate on allometric shift in digit ratio (Forstmeier, 2011; Kratochvíl & Flegr, 2009; Lolli et al., 2017; Manning & Fink, 2018), providing data from traditional populations.

It could be argued that the sample size of our study was too small to demonstrate the links between digit ratio and performance in male-male competition outcomes, as correlations between digit ratio and performance in male-male competition explain only a small fraction of the variance (ie, Hönekopp & Schuster, 2010). To address this problem, we conducted our analysis according to Bayesian methods that are suitable for small samples (Jarosz & Wiley, 2014). Still, it may be possible that some subtle relationships may be found in larger samples. Fortunately, Bayesian methods allow for the update of knowledge through the accumulation of data (van de Schoot & Depaoli, 2014). Our study provides Bayes Factors that can be included as informative priors in Bayesian models of future studies on traditional populations.

Hunting performance in our study was self-reported. It seems possible that males were trying to manifest their abilities and distort the information about the number of animals they hunted. However, in most cases, the information obtained from a particular respondent had been confirmed by another man, as we were randomly inquiring about this.

Digit ratio and HGS is associated with performance in male-male competition outcomes in western societies, among men involved in various intrasex competitive activities (Bennett et al., 2010; Hansen et al., 1999; Hönekopp & Schuster, 2010; Kilduff et al., 2011; Longman et al., 2011, 2015; Manning & Taylor, 2001; Watts et al., 2003). Here, we show evidence that the hypothesis concerning hand grip strength finds support in the Hadza population, but does not hold true among the Yali of New Guinea. We also found that, contrary to our expectations, a higher digit ratio was associated with the number of hunted birds among the Hadza. The evidence for this, however, was very weak. Future research in different traditional populations should take into account other individual factors that may further explain mechanisms underlying performance in male-male competition in traditional societies.

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTIONS

M.M. and M.B. conceived the study. M.M., M.B., A.O., and P.S. collected the data. M.M. and A.O. were responsible for all statistical analyses, and M.M. drafted the manuscript. M.M., M.B., A.O., and P.S. all participated in manuscript revisions, and all authors approved the final manuscript.

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