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Hunter-gatherer males are more risk-seeking than females, even in late childhood

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ABSTRACT

Observed economic and labor disparities between the sexes may, in part, result from evolved sex differences in risk preferences. Using incentivized economic games, we report on sex differences in risk preferences in the Hadza, a population of hunter-gatherers. One game played in 2010 ($n = 233$) found that more Hadza males than females prefer to gamble for a chance to earn more maize rather than settle for a sure, but smaller, amount. Similarly, a second game played in 2013 ($n = 102$) found that male Hadza gamble a greater proportion of honey for a chance to earn more compared to female Hadza. Effect sizes are small to medium. We find weak evidence that risk-taking increases in men as their mating opportunities increase. In both games, the sex difference widens throughout childhood and is greatest among adolescents; though note that child samples are small. We explore developmental trends further using observational data on food returns in children ($n = 357$). Our data suggest that while the mean number of calories boys bring to camp remains stable with age, the variance in their caloric returns increases. Among girls, the variance remains stable with increased age. Both the economic games and food return data are consistent with the sexual division of labor wherein boys, beginning in late childhood, begin to target riskier foods. To the extent that the Hadza allow us to make inferences about long-standing patterns of human behavior, we suggest that sex differences in risk preferences may have been present long before agriculture and the modern work environment.

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1. Introduction

Financial and labor disparities are observed between the sexes in all types of societies. Men typically attain more powerful, higher earning positions (Blau & Kahn, 2000; DiPrete & Buchmann, 2013; Bertrand & Hallock, 2001), despite the fact that in some societies and sectors women are, on average, more educated (Altbach, Reisberg, & Rumbley, 2009; Vincent-Lancrin, 2008). In 2014 for example, women working full-time earned about 79% of what men did (Blau & Kahn, 2016). While decompositions of the gender wage gap illustrate the importance of a variety of factors, a sizable disparity between men and women's pay remains unexplained by traditional economic variables (Blau & Kahn, 2016). As such, some researchers have suggested that labor inequalities may, in part, result from innate sex differences in psychological preferences such as willingness to compete, initiate negotiations, or take on risk (e.g., Apicella & Dreber, 2015; Babcock, Gelfand,

Small, & Stayn, 2006; Croson & Gneezy, 2009; Eckel & Grossman, 2008; Powell & Ansic, 1997; Saad, 2011).

While sex differences for some preferences, such as competitiveness, are generally large and robust, the results for risk-taking have been more heterogeneous, though most studies report a sex difference (for detailed review, Niederle, *in press*). Byrnes, Miller, and Schafer (1999) conducted a meta-analysis of 150 studies spanning three decades that compared men and women in various types of risk-taking behavior (e.g., driving and gambling). While the majority of risk categories showed a sex difference, many of the effects were small. Using a hypothetical questionnaire, where evolutionarily typical risks were presented using modern frames, Wang, Kruger, and Wilke (2009) found that men reported more risk-taking in all domains studied. Eckel and Grossman (2008) and Croson and Gneezy (2009) provide two broad reviews of studies that ask individuals to either make decisions between alternatives that vary in monetary risk or to make valuations of risky payoffs. Both reviews conclude that men generally exhibit higher levels of risk-taking but acknowledge that less consistent evidence is found when gambles are framed as losses. However, two more recent surveys of sex differences in risk-taking that analyzed studies with different methods of eliciting risk preferences reached markedly different

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conclusions about the existence of sex differences, suggesting that the method of elicitation may account for heterogeneity of the findings (Charness & Gneezy, 2012; Filippin & Crosetto, 2016).¹ The latest and most comprehensive survey of the literature (e.g., Niederle, *in press*) concludes that while sex differences in risk do likely exist, the difference may not be substantial in all settings.

A few cross-cultural examinations have been conducted. Charness and Gneezy (2012) assembled data from a number of studies, including students living in Sweden, USA and Turkey and villagers from China, India and Tanzania, and conclude that in 90% of the experiments men make relatively larger investments in risky assets. Cárdenas, Dreber, Von Essen, and Ranehill (2012) find that boys, ages 9–12, in both Sweden and Colombia were more risk-taking than their female counterparts. Similarly, Buser, Niederle, and Oosterbeek (2014) report that Dutch male high school students chose a significantly more risky lottery than did girls. Finally, a survey conducted with nearly 7000 university students, largely studying economics, from 53 different countries find significant and robust differences between men and women in their propensity to take risks in the gain domain (Rieger, Wang, & Hens, 2014). The opposite finding emerged when looking at losses. In this domain, women were less risk-averse. Again, this finding is not particularly surprising given the inconsistent results previously reported when gambles are framed as losses (e.g., Croson & Gneezy, 2009).

Although there is growing and admirable interest in how individuals living in small-scale societies make decisions involving risk, the majority of studies have relied on Western populations and students, leaving the generalizability and origins of these sex differences unknown. Here, we report on sex differences in risk preferences among the Hadza, one of the only remaining populations of hunter-gatherers who rely primarily on wild foods for subsistence. Given that the Hadza live in a social and physical environment that more closely approximates that of human origins than industrialized environments, their risk preferences may provide insight into the origins of sex differences (Apicella & Dreber, 2015; Apicella, Feinberg, & Marlowe, 2007; Cashdan, Marlowe, Crittenden, Porter, & Wood, 2012). If nothing else, the Hadza offer a valuable example of how men and women living in a subsistence economy – without farming or livestock – make decisions under conditions of risk.

Anthropologists, economists, and psychologists have used the term risk to mean different things. In the current study, we formalize risk preferences in the tradition of economics to represent the tradeoff between the variance and the expected value for a given resource. Our measures, therefore, involve asking participants to make choices between options that are less rewarding but more certain, and options that are less certain, but potentially more rewarding. This study focuses on risk in the domain of gains.

Nearly all species have evolved in environments with a substantial element of unpredictability. Consequently, decisions involving uncertain outcomes in diverse behaviors such as mating, foraging, or parenting are ubiquitously observed across taxa, and the outcomes of such behaviors can have measurable fitness consequences. In hunter-gatherers, for instance, decisions are made daily about which foods to target for consumption. Foods such as meat are risky since variance in hunting returns is high, while other foods, such as foraged plant items, are more

reliably procured but may be less energy dense (Cordain, Watkins, & Mann, 2001; Smith, 1988). Outside of the traditional realms of ethological study one can find analogies in the decision making of humans in industrialized societies, from career decisions to medical treatment options. In all of these instances, the degree to which choices have consequences to fitness, evolution can be expected to have an underlying role.

To the extent that men and women confronted different challenges in the past and that the same choices made under conditions of uncertainty would have yielded different returns based on sex, it is possible that natural selection shaped sex differences in risk preferences. The standard narrative for many observed sex differences from ornamentation (e.g., Darwin, 1871) to mate choice (e.g., Buss, 1989) is that they are evolutionary downstream consequences of sex differences in the patterning of reproduction, in which the costs of reproducing are higher for females (Trivers, 1972). This difference leads to higher potential rates of reproduction and reproductive skew for men (Bateman, 1948; Trivers, 1972); the corollary of this is that men are designed to compete for mates since this is the limiting factor for their reproductive success. Apicella et al. (2008), suggest that financial risk-taking may be a modern form of male-male competition for resources, which can then be used to attract mates. More generally, Wang et al. (2009) argue that increased acceptance of risk-taking in males facilitates male-male competition. Formalized evolutionary models for sex differences in risk preferences have been provided. Dekel and Scotchmer (1999) argue that sex differences in risk-taking will be selected in winner-take-all environments, where top males mate with the majority of females. Rubin and Paul (1979) show that in environments where only those males who are above a certain income threshold are attractive to females, sex difference in risk preferences will evolve. Robson (1996) expands on this model by including repeated thresholds that correspond to increasingly larger number of mates and shows that if males choose lotteries over wealth, they will choose very risky lotteries, if any. In hunter-gatherers, hunting for big game may be akin to choosing risky lotteries.

For nearly all forager populations for which detailed ethnographic data exist, we see a marked sexual division of labor wherein men primarily target high-risk resources such as game animals and women primarily target plant resources, the staple of the diet (Kelly, 2013).² The fact that better hunters experience greater reproductive success in a number of these societies, including the Hadza (Apicella, 2014; Hawkes, 2001; Marlowe, 1999), the Ache (Hill & Hurtado, 1996; Kaplan & Hill, 1985) and !Kung (Wiessner, 2002) supports the notion that hunting ability, which requires a protracted period of learning (Gurven, Kaplan, & Gutierrez, 2006; Blurton Jones & Marlowe, 2002), was evolutionarily selected. While women do value hunting ability in their mates (Marlowe, 2003a, 2003b, 2004a; Apicella & Crittenden, 2016), there is lively debate over how hunting increases men's reproductive success. It has long been viewed that hunting evolved to provision a man's pair-bonded family unit (e.g., Washburn & Lancaster, 1968). Indeed, evidence suggests that a hunter's family benefits directly by receiving choice cuts of meat – even in settings of communal sharing (Wood & Marlowe, 2013) – and by obtaining nutrients and protein not found in foraged foods (Domínguez-Rodrigo et al., 2013), but alternative explanations have been proposed. Specifically, it had been argued that hunting may instead serve as a costly signal for advertising mate quality (Hawkes & Bliege Bird, 2002; Smith, 2004) and/or building a reputation for generosity useful for fostering cooperative friendships (Gurven, Allen-Arave, Hill, & Hurtado, 2000). Since game meat is less reliable and shared widely in hunter-gatherer groups, these are plausible explanations. How this debate is settled may have implications for how we understand the evolution of sex differences in risk preferences in

¹ Filippin and Crosetto (2016) largely analyze papers employing the Holt-Laury task where participants are presented with a menu of paired lotteries and are asked to decide between a safer option and riskier option and where one decision in the list is randomly chosen for payment. These choices together, are then used to estimate risk attitudes. They find that this produces a gender gap in risk-aversion, but one so small that studies will need samples in excess of, and likely double, several hundred participants. The authors compare this to simpler methods such as the Investment Game constructed by Gneezy and Potters (1997) and an ordered lottery selection task used by Eckel and Grossman (2002). From this, they isolate two key characteristics that jointly correlate with the likelihood of observing a sex difference. The first is whether there is a safe option available within the choice set and the second is whether the lotteries use 50/50 fixed probabilities.

² Notable exceptions do exist; in some ecological settings, such as with the Agta of the Philippines, women routinely hunt (Goodman, Griffin, Estioko-Griffin, & Grove, 1985).

humans if we think that the sexual division of labor reinforced or further promoted sex differences in risk-taking. That is, foraging may itself provide an additional selection pressure, but sex differences in risk-taking were likely present before the sexual division, as evinced by observations in numerous other species.

While different interpretations of Hadza men's foraging goals persist, we believe that insight can be generated from examining: 1) whether sex differences are present in the Hadza and, if so, 2) when during development they emerge. A developmental approach, notably, does not promise to isolate the role of culture versus biology on the development of sex differences. However, if sex differences emerge early in development, this provides some indication that the difference may be innate. Conversely, when sex differences emerge later in development, culture may contribute (e.g., social learning) but biological forces (e.g., puberty) cannot be ruled out. Still, combining developmental and cross-cultural data can be valuable when trying to identify species-typical features of our psychology (Apicella & Barrett, 2016).

Here we use two economic games to measure risk preferences and supplement these games by also analyzing variance in foraging yield as a more natural, albeit indirect, measure of risk-taking in children and adolescents. As boys get older, usually around the age of ten, they spend less time foraging with women and girls and begin to pursue game meat, which is more risky. For these reasons, we expect to see increased variance in food returns with age in boys but not girls. While these data would accord with a shift from stable to risky foraging behavior, the weakness of these data is that we neither know the particular foods targeted and subsequently missed, nor how much children worked/ate when away from camp.

There are some reasons to suspect that the characteristic sex difference in risk preferences may not be observed in the Hadza. Compared to many societies in the world, Hadza women enjoy a high level of autonomy, are vocal, and participate in making important decisions at the camp level (Marlowe, 2010). And a number of studies suggest the social and economic organization of groups is critical for the emergence of sex differences for some economic preferences. For instance, Booth and Nolen (2012) find that girls who attend same-sex schools are more likely to choose real stakes lotteries over sure bets compared to girls attending mixed-sex schools. Another study that highlights the role of culture finds that a gender difference in competitiveness observed among adults in a patriarchal society in Northeast India arises at puberty, but such a sex difference is not found in a nearby village that practices matrilineal inheritance (Andersen, Ertac, Gneezy, List, & Maximiano, 2013). In contrast however, Gong and Yang (2012) find that men are more risk-seeking in both matrilineal and patriarchal groups in China.

Studies have also examined biological determinants of risk preferences. For instance, it has been suggested that prenatal androgen exposure may influence risk preferences in adulthood, and consequently may explain some of the observed sex difference (for critique see Apicella, Carré and Dreber, 2015). These studies largely correlate digit ratio measurements (i.e., second to fourth digit or 2D:4D), a purported proxy of androgen exposure in utero, with risk preferences. While in a majority of populations 2D:4D is sexually dimorphic with males having a lower ratio than females, the Hadza do not exhibit this pattern (Apicella, Tobolsky, Marlowe, & Miller, 2016). In fact, the evidence suggests that, if anything, women have more masculine digit ratios (but see Butovskaya, Burkova, & Mabulla, 2010). It is unknown whether hormones underlie this unusual pattern of 2D:4D in the Hadza, but to the extent they do and to the extent that the association between 2D:4D and risk-taking is real, we may find that Hadza men and women behave similarly when faced with uncertainty. Likewise, current testosterone levels may also influence economic risk preferences – but this link too, is uncertain (Apicella et al., 2015) – and available evidence suggests that Hadza men may have lower testosterone than men in neighboring groups, such as the Datoga (Muller, Marlowe, Bugumba, & Ellison, 2009). This finding accords with observations that high investment in a pair-bond (Burnham et al., 2003; Gray et al., 2004; McIntyre et al.,

2006) and higher degrees of parental investment (Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002) tend to correlate with lower testosterone levels in men. While hormonal measurements have not been taken in Hadza women, Cashdan (2008) has argued that increased androgens might be favored in Hadza women, as evidenced by more masculine phenotypes, since their work is physically demanding, requiring strength and stamina. Accordingly, we would not be surprised to find Hadza men and women exhibiting comparable decision-making strategies when confronted with risk.

2. Methods

2.1. Subjects

The Hadza are a population of nomadic hunter-gatherers living in a savannah-woodland environment in Northern Tanzania. The Hadza live in temporary camps of about 30 individuals, but both camp residence and camp locations shift in response to resource availability. For this reason, many individuals know each other even when not currently living in the same camp (Apicella, Marlowe, Fowler, & Christakis, 2012). The Hadza target five main categories of wild foods: meat, honeycomb, baobab, berries, and tubers. These foods are either consumed while foraging or brought back to camp or shared widely with others. While there are about 1000 Hadza alive today, it is estimated that fewer than one third of them still practice a strict hunter-gatherer lifestyle in which less than 5% of their caloric intake is derived from agricultural or domesticated products (Marlowe, 2010).

There is a sexual division of labor wherein men primarily pursue animal-based resources, such as game and honey, and women pursue plant-based resources. Men generally hunt alone while women forage in small groups with their children. After weaning, small children spend a considerable portion of their time budget foraging for foods (Crittenden, Conklin-Brittain, Zes, Schoeninger, & Marlowe, 2013). Around the age of 10–11 boys begin to opt out of these foraging parties and begin solo hunting excursions. While strength and skill are important criterion for successful big game hunting (Apicella, 2014), juvenile males are able to target small mammals and birds. Children collect a sizable percentage of their daily energetic requirements (Crittenden et al., 2013) and older children share considerable amounts of food with younger children (Crittenden & Zes, 2015). Small bows and arrows and digging sticks are fashioned for boys and girls respectively, as soon as they begin walking.

Apart from the sexual division of labor, there are no other labor specializations (Marlowe, 2010). All Hadza women are capable of performing all female-typical tasks including foraging, food processing, and collecting firewood and water. Likewise, every man is capable of hunting, dismantling prey, creating fire, manufacturing his own bows and arrows and so on. Wealth inequality is discouraged (Marlowe, 2010). This is one possible reason why the Hadza show less attachment toward owned items (Apicella, Azevedo, Christakis, & Fowler, 2014). Finally, the Hadza are also non-hierarchical (Marlowe, 2010). While men are dominant to women, the difference is minor relative to other populations (Marlowe, 2010). Decisions are made in a group setting and both sexes are vocal participants.

The Hadza are familiar with games involving chance. For decades, the Hadza have played a luck-based game called *lukuchuko* (Woodburn, 1982). In this game, individuals compete against each other for small material possessions by throwing pieces of bark against a tree where the winner of the game is determined by how the bark lands. While there may be some throwing skill involved, there is a large element of chance to the game. Juvenile and teenage boys also play a version of this game, using recovered bottle caps in lieu of bark (Crittenden, 2016a). Finally, the Hadza are minimally religious and largely credulous of deities with supernatural powers such as the ability to control the outcomes of earthly events (Apicella, in press).

2.2. Procedures

Two economic games were used to elicit risk preferences in the Hadza over two separate field seasons (for full instructions, see appendix) by one of the authors (C.L.A.). Both risk games were simple, one-shot games that involved whole number multipliers. These methods were designed to facilitate increased understanding of the tasks. The vast majority of the Hadza are illiterate, and while many are able to count in Swahili, their number system in their native Hadzane does not include numbers greater than four. However, eliciting risk preferences does not require formal calculations; instead, it is based on subjective probabilities or degree of beliefs (Suppes, 1956).

All games were played in private and the researcher assured participants that their answers would remain confidential. The researcher also asked participants to refrain from telling others of their decisions.³ However, it should be noted that five cups of maize (awarded in the first game) is difficult to conceal, both for their bulk and for the processing they require to produce corn flour. For this reason, a second game involving small individually wrapped straws of honey was also played three years later. These honey sticks are easy for the Hadza to conceal in their garments. Honey has been listed as one of the most energy dense resources found in nature (Skinner, 1991) and the Hadza list it as their favorite food (Marlowe et al., 2014). Also, honey sticks (Apicella et al., 2012) and maize (Apicella & Dreber, 2015, Apicella, in press) have been successfully employed in economic games with the Hadza. The Hadza often report feeling hungry and so the outcomes of these games are not inconsequential. Finally, all adults were asked to name each of their living children and report whether they were currently married.

2.2.1. Game 1

During the summer of 2010, 233 Hadza participants from seventeen different camps around both the Eastern and Western side of Lake Eyasi were recruited to play a game involving cups of maize and a coin flip (see Fig. 1). Table 1 includes demographic information about the sample. Participants were asked to choose between two options: receiving five small cup of maize with certainty or five large cups of maize with a 50% probability of success. Participants were shown both sides of a 50 shilingi coin where one side displays a head (*kichwa*) and the other side, a rhinoceros (*kifaru*). Participants were also shown a small (4 oz) and large (8 oz) measuring cup and each participant observed the researcher fill the large cup with two small cups of maize to demonstrate that the larger cup was equal to two of the smaller cups. The maize was emptied from both cups and participants were asked if they wanted to try to win five large cups of maize where success is determined by the outcome of the coin flip or have five small cups of maize with certainty. Participants who chose the coin flip and lost did not receive any maize. The maximum amount of maize that could be won is 40 oz.

The Hadza grind the maize into cornmeal and add water to make porridge. According to the USDA's *National Nutrient Database for Standard Reference* (2008), 1 oz of cornmeal provides 103 kcal and 2 g of protein.

2.2.2. Game 2

During the summer of 2013, a second risk game involving straws filled with honey was played with 102 participants from ten different

Hadza camps (see Fig. 1). Table 1 includes demographic information about the sample. In this study, participants were asked how many sticks of honey (out of 4) they wanted to keep or allocate to a risky game of “double or nothing”. Success in the game was determined by the flip of a fair 50 shilingi coin.

Each honey stick provides about 15 cal. While honey collection is exclusively a men's foraging task, honeycomb is listed by all Hadza foragers (men, women, and children) as the most highly valued food (Berbesque & Marlowe, 2009). Honey represents approximately 11% of the Hadza diet (Crittenden, 2016b). Liquid honey is a concentrated source of fructose and glucose and contains approximately 80–95% sugar (Bogandov et al., 2008; Murray, Schoeninger, Bunn, Pickering, & Marlett, 2001) and trace amounts of several essential vitamins and minerals (Iskander, 1995; Terrab, Hernanz, & Heredia, 2004).

2.2.3. Foraging returns

Foraging data were collected in two Hadza camps, located approximately 40 km away from one another, over four non-sequential months during 2005 by one of the researchers (A.N.C.). Data were collected during both the wet season (from April through May) and the dry season (from October through November). Resource availability and general patterns of rainfall during these particular months map onto the greater resource availability throughout the wet and dry seasons of 2005 (Crittenden, 2009) and general seasonal trends in this region of Lake Eyasi over the past two decades (Marlowe, 2010). Mean foraging productivity was calculated for each participant in camp. Foraging returns were averaged for each participant over all days during the study period – this included the days in which the forager was successful and unsuccessful. Of the 70 total days of residence in the combined camps, at least one juvenile forager returned to camp with food on 65 days. All food brought back to camp was measured using a hanging spring scale. The kilocalorie values for all food (including small game meat, baobab, berries, legumes, nuts, and tubers) were determined by subtracting the inedible fraction and percent water content from the raw weight in grams and then converting to energy using published values for kilocalories/gram for each food type. The detailed methods for these conversions have been outlined in previous work on juvenile foraging returns (Crittenden, 2009, 2016b). The energy values for animal products, including birds and small game meat, were determined based on values in Clum, Fitzpatrick, & Dierenfeld, 1996 and Prange, Anderson, & Rahn, 1979; values for honey were determined based on values in Murray et al., 2001; and values for plant foods were determined based on values in Crittenden, 2009.

3. Results

Table 1 provides demographic statistics for the two risk games. Roughly 66% of male Hadza chose to take the gamble in the first game involving maize. This contrasts with the women and girls, wherein only 43.7% chose to take the gamble (see Fig. 2, Panel A). A chi-square test of independence was performed to examine the relation between sex and risk-taking in the maize game for the full sample of participants. The results indicate that a significantly greater proportion of male Hadza chose to take the risky option (χ^2 (2, $n = 233$) = 11.78, $p < 0.001$). The effect size described by phi and interpreted according to conventions set by Cohen (1988) is small to medium, $\Phi = 0.22$, 95% CI [0.095, 0.344]. Table 2 reports results from ordinary least square (OLS) regression analyses.⁴ After controlling for a number of other demographic variables, including age, age-squared, reproductive success

³ By concealing participants' choices, we attempted to isolate men and women's decisions from potential peer influences and the effects of knowing the outcomes of others' decisions. For instance, one could imagine that a woman going into the study might feel more pressure to behave in a certain way if she thinks her husband will learn of her decision or that men will feel peer pressured by other men to take the gamble. Also, knowledge of how others performed – whether they were lucky or unlucky – in the game may affect how later players make decisions. Of course, we cannot control what individuals say or do with the resources won once they leave.

⁴ While the dependent variable is binary, interaction effects are not well evaluated with logit regressions (Ai & Norton, 2003). That said, a logit regression with the same controls, provides qualitatively similar effects of sex on the decision to take a risk ($p < 0.003$).

(e.g., number of living children) and whether participants are married or single, sex remains a significant and strong predictor of whether individuals choose to gamble for more maize. We divide our sample into four age groups: young children (under 11 years), juveniles (11–17 years), adults (Berbesque & Marlowe, 2009; Bertrand & Hallock, 2001; Blau & Kahn, 2000; Blau & Kahn, 2016; Blurton Jones & Marlowe, 2002; Blurton Jones, 2016; Bogandov, Jurendic, Sieber, & Gallman, 2008; Booth & Nolen, 2012; Brown, 1970; Burnham et al., 2003; Buser et al., 2014; Buss, 1989; Butovskaya et al., 2010; Byrnes et al., 1999; Campbell, 1999; Cárdenas et al., 2012; Cashdan, 2008; Cashdan et al., 2012; Cesarini, Dawes, Johannesson, Lichtenstein, & Wallace, 2009; Charness & Gneezy, 2012; Charness, Gneezy, & Imas, 2013; Cheng, Tracy, & Henrich, 2010) and older adults (40 and older). Young children are categorized as those younger than 10, as boys begin going on solo hunts around this age. By the age of 18 most individuals are bringing in at least as many calories as they consume (Marlowe, 2004b). Also, this is roughly the age at which women typically first get married; for men the median age of first marriage is at least a few years later (Blurton Jones, 2016; Marlowe, 2010).

The point estimates in Fig. 2, panel B suggest that a greater proportion of male Hadza choose to take the risky option in every age category except the youngest Hadza. Thus, it would appear that the typical sex difference in risk preference appears in later childhood/adolescence, though our sample is too small to isolate the precise age at which boys become more risky. A test of proportions reveals that fewer boys (10 years and younger) (17%), choose the risky option compared to juvenile boys (11–17 year olds), wherein 71% chose the risky option ($\chi^2(1, n = 30) = 5.87, p = 0.015$). When comparing these same two age groups in girls, we see the reverse pattern. A greater number of girls (29%) chose the risky option compared to their older adolescent counterparts wherein none chose the risky option ($\chi^2(1, n = 13) = 6.98, p = 0.008$).

Male participants also risked significantly more sticks of honey ($M = 1.75, SD = 1.27$) than female Hadza ($M = 1.19, SD = 1.23$) ($t = 2.24, p = 0.03$), a result that is also robust to the inclusion of a number of controls, including age, age-squared, reproductive success and marital status (Table 2). The size of this effect ($d = 0.45$) represents a medium effect size according to conventions set by Cohen (1988). While the sample size here is smaller than in the maize game, the point estimates suggests that male Hadza are more risk-taking in every age category, but note the large error bars (see Fig. 2, panel C). While younger boys (10 and under) risked slightly fewer honey sticks than older boys (Apicella et al., 2007; Apicella et al., 2012; Apicella et al., 2016; Ariely & Loewenstein, 2006; Babcock et al., 2006; Baker & Maner, 2009; Bateman, 1948), this difference is not significant. Again, the sample size for male Hadza under 18 years is small ($n = 12$) so these results should be interpreted with caution. The point estimates suggest that the number of sticks of honey risked by female Hadza remains largely unchanged throughout life (Fig. 2, Panel C).

To explore risk preferences in children further, we also examined energy (kilocalories) obtained from 357 different foraging days made by 34 different individuals ($n = 20$ girls). We first calculated summary statistics of caloric returns for each individual by dividing the total number of calories they brought back for all days foraged by the number of days they foraged. Table 3 provides summary statistics for calories brought back to camp by older (11–17 years) and younger (10 and under) boys and girls. Table 3 also provides summary statistics on caloric returns yielded from every individual's foraging day broken down by sex and age. Fig. 2, panel D shows that variance in returns increases with age in boys and is relatively stable in girls. Independent Welch's t -tests were conducted to compare the mean standard deviations of calories obtained between male and female Hadza in both age groups. The results indicate that while the mean standard deviation of calories obtained by boys and girls (aged 10 and under) were similar (Welch's $t = -1.24$, rounded $df = 18, p = 0.23$), the mean standard deviation of calories obtained by juvenile boys was significantly higher than in

juvenile girls (Welch's $t = 2.17$, rounded $df = 6, p = 0.07$).⁵ Finally, we regressed age on mean standard deviation of caloric returns separately for men and women. While age did not predict the standard deviation in caloric returns in girls ($B = -19.31, p = 0.73$), it did in boys ($B = 64.80, p = 0.042$).

3.1. Exploratory analyses

We also examine whether the number of mating opportunities available to reproductive-age men in each camp in each year, affects their risk-taking. Similar to Marlowe (1999), we operationalize mating opportunities in two ways. First, we calculate the absolute number of reproductive-age women in each camp, defined as any women whose age is between 15 and 45 years old. Second we calculate the number of reproductive-age women per reproductive-age man in each camp. Reproductive-age men were defined as any man between the ages of 18 to 60. The average number of reproductive-age women in each camp in 2010 was 4.83 ($SD = 2.62$) and the average number of reproductive-age men was 5.44 ($SD = 2.85$). The OSR across camps ranged from 1.75 to 0.29 ($M = 0.95; SD = 0.45$). Similar ages have been used in other forager studies to encompass the entire period of mating competition (Hurtado & Hill, 1992; Marlowe, 1999). Binomial logistic regressions were run to determine whether either measure of mating opportunity predicted whether reproductive-age men ($n = 92$) chose to take the gamble in the maize study (e.g., game one). In the simple model, with only the number of reproductive-age women included as a predictor, we found that an increasing number of fertile women was not associated with an increased likelihood of choosing the risky option (Wald = 0.22, $df = 1, p = 0.64$). For every unit increase in number of fertile women, the log odds of choosing to risk decreased by 0.04. Likewise, in a second regression the Wald criterion demonstrated that the number of reproductive-age women per reproductive-age man in each camp also did not increase the likelihood of choosing the risky option (Wald = 0.26, $df = 1, p = 0.61$). We repeat both regressions adding marital status and age as predictors but the results remain unchanged. Nagelkerke's R^2 in all models ranged from 0.004 to 0.03 indicating that no relationship exists between our predictors and risk-taking in the maize game.

The average number of reproductive-age women in each camp in 2013 was 2.8 ($SD = 1.87$) and the average number of reproductive-age men was 4.8 ($SD = 1.69$). The OSR across camps ranged from 0.16 to 2 ($M = 0.67; SD = 0.55$). Separate ordinary least square regression analyses were performed to determine whether either measure of mating opportunity predicted how many sticks of honey reproductive-age men ($n = 40$) gambled in the honey game (i.e., game 2). Neither the absolute number of reproductive-age women ($\beta = 0.08, p = 0.62$) or the number of reproductive-age women per reproductive-age man in each camp ($\beta = 0.25, p = 0.12$) predicted the number of honey sticks risked in the simple models without controls. We repeat both regressions adding marital status and age as predictors. The results remain largely unchanged when age and relationship status were added as predictors to the first model. However, the number of reproductive-age women per reproductive-age man in each camp reaches significance in the full model ($\beta = 0.38, p = 0.02$). That is, when controlling for age and marital status, as the number of women per man increases in a camp, men risked more sticks of honey. Marital status ($\beta = -0.35, p = 0.03$) was also a significant predictor of honey sticks risked where single men risked more sticks of honey than married men. Age neared

⁵ We also examined whether the variance in calories obtained differs between the sexes at the observation level. Since calories obtained are highly skewed (skewness coefficient = 4.90) and violate assumptions of normality, we use Levene's test to compare whether the variances in caloric returns between male and female Hadza in both age groups are equal. We reject the null that the variance in caloric returns is the same for boys and girls ($W_0 = 5.06, p = 0.02$) or for male and female adolescents ($W_0 = 4.54, p = 0.04$).



Table 1
Basic demographics for the two risk games.

Risk game	Entire sample (n)		Age mean (SD)		Number of children (RS)		% Married		Sample under 11 years (n)		Sample 11–17 (n)	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Maize (n = 233)	130	103	32.82 (15.81)	34.04 (13.95)	2.83 (2.25)	3.23 (2.18)	56.2%	76.7%	6	7	24	6
Honey (n = 102)	55	47	32.64 16.42	31.81 16.81	2.31 2.48	2.57 2.58	49.1%	63.8%	10	5	2	7

significance ($\beta = 0.27$, $p = 0.09$). However, we ran eight separate regressions (four in each year) and with no correction for multiple tests, the chance of finding a result that is significant is around 15%. After correcting for this using a conservative Bonferroni adjustment, our results are no longer significant. Thus, this result should be interpreted with caution.

4. Discussion

Evidence from the current study shows that male Hadza are more likely to opt for a risky strategy rather than settle for a reduced but certain outcome as compared to female Hadza. About 33% more male Hadza chose to risk their maize in the first study. Likewise, males risked about 17% more of their endowed honey for a chance to earn more. Assuming the Hadza embody similar behavioral patterns to those used by many human societies before the advent of agriculture (see Apicella & Crittenden, 2016 for discussion), these results lend support to the supposition that sex differences in risk preferences were present thousands of years ago and have persisted across a wide array of human cultures and subsistence regimes. Still, it is important to stress that the effect sizes were small to medium and there was considerable overlap in the distributions.

Data from analyses presented here suggest that the sex difference is present prior to adulthood, and increases during development. In fact, in both risk games the largest difference between the sexes is observed in the juvenile age group, 11–17 years. In the maize study, juvenile boys chose the risky option significantly more than young boys, whereas juvenile girls were significantly more risk-averse than younger girls. A similar pattern is borne out when we examine food return data of children and juveniles. The variance in caloric returns increases with age in boys but for girls it remains relatively stable over time. These findings are consistent with the sexual division of labor, wherein pre-adolescent boys begin hunting, to the almost abandonment of plant foraging, around the age of 10 or 11 years. Lastly, the point estimates for the honey game also suggest that juvenile boys ages 11–17 take on more risk than their younger male counterparts, though this is not significant; note, however, that we rely on about half the sample size of children here relative to the maize game.

The sexual division of labor and sex differences in risk preferences may have been reciprocally reinforcing during our evolution. It is possible that men were relatively more risk-taking before the sexual division of labor, but that subsequent selection for hunting strengthened this. Hunter-gatherer men routinely target high-risk food items that are often characterized by a low probability of success but are calorically dense and highly nutritious. Relative to the boom and bust strategy of men, women target more stable resources and typically bring in more calories over time. The median percent of the diet coming from gathering and hunting are 67% and 32% respectively in African foragers (Marlowe, 2010).

While early arguments for the sexual division of labor suggest that women were precluded from hunting big game animals due to the

reproductive constraints of pregnancy and breastfeeding (Brown, 1970), recent analyses suggest that differences in resources targeted may also stem from different mating and parenting goals between the sexes (Panter-Brick, 2002). To date, the evolution of sex differences in risk preferences have only been modeled in polygynous environments (e.g., Dekel and Scotchmer; Robson, 1996) despite ample debate about whether selection has favored increased monogamy in the human lineage. Evidence of selection for increased monogamy includes decreased body size dimorphism between the sexes, reduced testes size, and the observation that in only 30% of foraging populations do more than 20% of married men have more than one wife (for discussion see Apicella & Crittenden, 2016; Chapais, 2013; Low, 2003; Lovejoy, 1981; Marlowe, 2003a, 2003b; White et al., 1988). The presumption that the sexual division of labor was a potential driver of sex differences in risk preferences still does not reconcile whether selection for hunting in men evolved because it afforded advantages in attracting mates or allies via costly signaling or whether it provided nutritional benefits within the pair-bond.

There is some evidence to suggest that the Hadza hunt in order to provision their families. Hadza men report that they would prefer to join a group of good hunters over bad hunters, implying that familial provisioning is a greater driver than other motivators (Wood, 2006). As Hadza women decrease the food they gather, due to pregnancy and lactation, they are compensated by increased returns by their husbands (Marlowe, 2003a, 2003b). While this may imply that Hadza men are motivated to provision their families, it still does not explain why men hunt; indeed, evidence suggests that Hadza men hunt less and forage more when they have young children for whom to provide (Marlowe, 2003a, 2003b; Marlowe, 2010). Conversely, many researchers suggest that men take risks, more generally, as part of a mating strategy. Indeed, a number of studies have documented an uptick in risk-taking in males of many species during their breeding season (Wingfield, Hegner, Dufty, & Ball, 1990). In men, risk-taking has been shown to increase during sexual arousal (Ariely and Loewenstein, 2006), when in the presence of attractive women (Dreber, Gerdes, & Gränsmark, 2013; Ronay & von Hippel, 2010) and potential romantic partners (Baker & Maner, 2009). In the Hadza, male parental care has also been shown to decrease as the number of potential mating opportunities, measured by the operational sex ratio in a camp, increases (Marlowe, 1999). This suggests that men can and do trade off parenting effort for mating effort. Our exploratory analyses find mixed evidence for this. In the maize game, we find that neither the absolute number of reproductive-age women or reproductive-age women per reproductive-age men predicted whether men choose the risky gamble. For the honey game, we find that as the number of reproductive age women per reproductive-age men increases, the number of honey sticks risked also increases. However, this is only significant in the full model with the controls and does not survive a correction for performing multiple tests. Here, we use two crude measures of mating opportunity, which largely assume that mating opportunities only exist at the level of the camp, when in fact they extend outside of the camp. Also, both studies were conducted in

Fig. 1. Panel A depicts the proportion of men and women (18 and up) and children (under 18) choosing to risk maize for a chance to double the amount. Panel B shows the proportion of male and female Hadza in different age categories that chose the risky maize option. Panel C shows the average number of honey sticks invested by men and women in a gamble of “double or nothing” in different age categories. Panel D depicts a scatterplot of the coefficient of variation in number of calories boys and girls bring back to camp by age. Error bars: ± 2 standard errors of the mean.

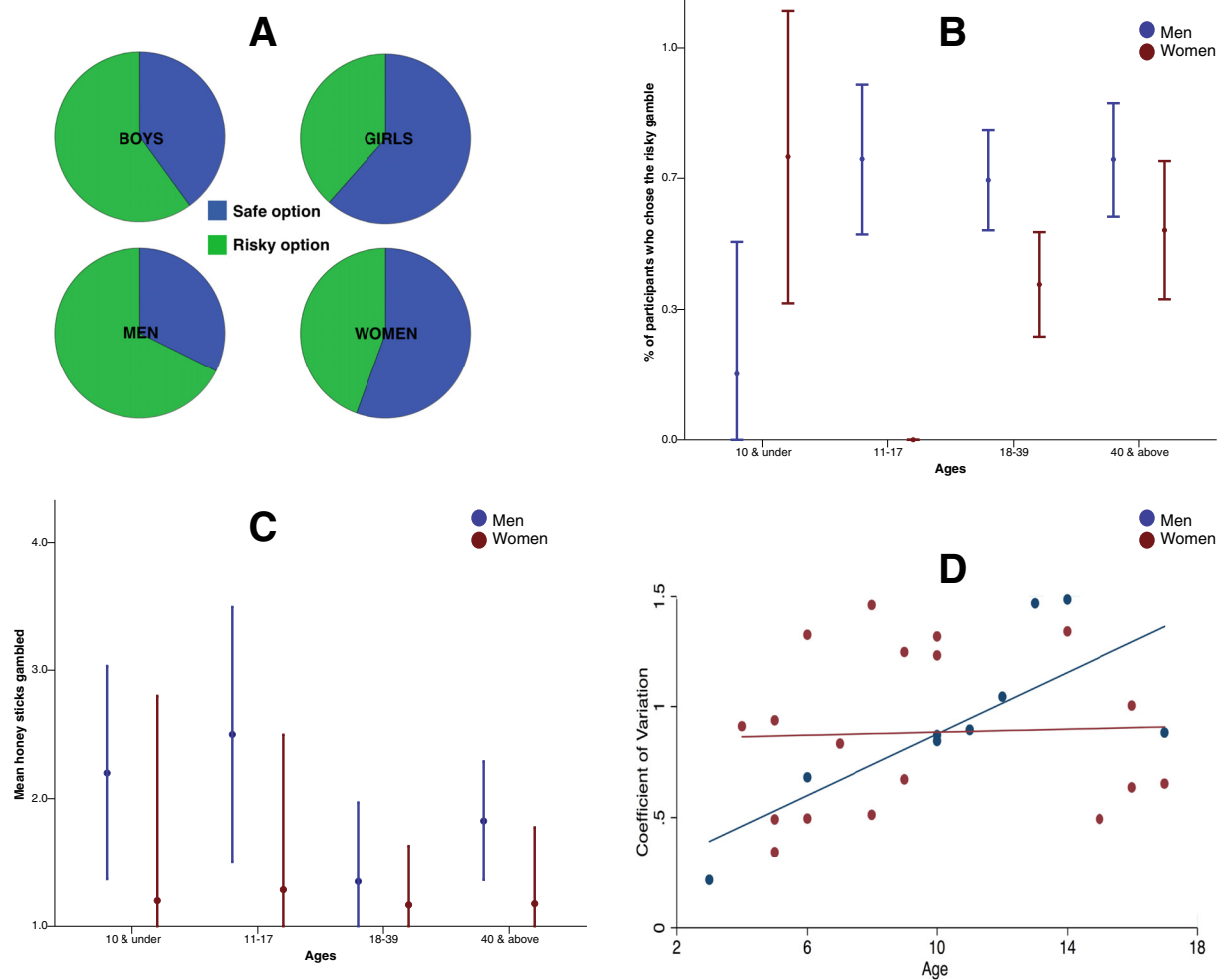


Fig. 2. The top panel is a map of Hadzaland depicting the location (based on GPS coordinates) of the seventeen Hadza camps visited in 2010 (in red) and the ten Hadza camps visited in 2013 (in blue). The middle panel shows a young boy listening to the experimenter's instructions for the maize task. The bottom left panel shows a young woman deciding whether to receive five 4 oz. cups with certainty or five 8 oz. cups of maize with 50% probability. The bottom right panel shows a Hadza man eating sticks of honey after the honey game. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

private. It would be interesting to see what would happen if men and women were required to make the decisions in the presence of their campmates. For instance, would men become more risk-seeking in the presence of women? Potentially, risk-taking has communicatory value. That is, it provides a signal to conspecifics about the underlying quality of the decision-maker. Future research may benefit from linking risk-taking in men with measures of quality – a link that is necessary for testing a signaling argument. Finally, future work would benefit from documenting the number of possible mating opportunities available to

each man in each camp by taking into account relatedness of individuals – many men live with their close female relatives whom are not viable mating partners – and the current reproductive state of women, since men may not consider women who are pregnant/breast-feeding as suitable mates.

Risk-taking, more generally, could have undergone positive selection in males as a result of increasing expected payoffs from other risky behaviors independent of food acquisition, such as physically fighting for resources and mates. Conversely, a “staying alive” explanation has been proposed for greater risk-aversion in women (Campbell, 1999). In this view, the costs of risk are weighted more heavily for

Table 2

Summary of simple regression analyses for variables predicting risk in the maize game and honey game.

Variable	Maize game			Honey game		
	B	SE B	β	B	SE B	β
Sex	−0.23	0.08	−0.23**	−0.52	0.26	−0.21*
Age	0.04	0.02	0.83	−0.02	0.04	−0.20
Age squared	0.00	0.00	−0.71	0.00	0.00	0.12
Reproductive success	0.02	0.02	0.11	0.05	0.07	0.11
Marital status	0.03	0.10	0.03	−0.30	0.34	−0.12
R ²	0.11			0.07		
F	3.65**			1.35		

* $p < 0.05$.

** $p < 0.01$.

Table 3

Summary statistics of caloric returns broken down by sex and age at both the individual level and foraging day level.

	11–17 years		3–10 years	
	Mean (SD)		Mean (SD)	
Caloric food returns (individual level)	♂	♀	♂	♀
	518.34 (743.43)	500.80 (389.16)		766.75 (948.12)
	n = 8	n = 5		n = 15
Caloric food returns (foraging day level)	♂	♀	♂	♀
	665.47 (871.95)	490.51 (441.27)	665.01 (692.83)	1016.22 (1799.51)
	n = 88	n = 39	n = 53	n = 177

women, since infant survival depends more on their care than paternal care. In a number of evolutionarily relevant domains (e.g., male–male competition, reproduction, mating) men report being more risk-seeking (Wang et al., 2009). In some settings (e.g., wartime), physical risk-taking or fighting may have had a reproductive advantage (e.g., Glowacki & Wrangham, 2015; but see Zefferman, Baldini, & Mathew, 2015), although there is some evidence to suggest that the fitness advantages of fighting were reduced in the human lineage. For example, there has been selection in humans for reduced overall body size and canine dimorphism between the sexes, which is presumed to be indicative of decreased selection for male–male combat (Plavcan, 2001; Plavcan & van Schaik, 1997). Interestingly, upper-body strength in humans remains highly sexually dimorphic, though this may be due to selection for good hunters rather than male–male fighting, since upper-body strength is an important predictor of hunting success (Apicella, 2014). While high status generally reaps reproductive dividends, this also may more strongly correlate with prestige (i.e., hunting) rather than dominance (i.e., competition), the latter of which is frequently viewed unfavorably in foragers (see Cheng et al., 2010 for discussion). Moreover, raiding, while not absent, is less common among foragers as compared to farmers (Wrangham, Wilson, & Muller, 2006) and the Hadza themselves have been described as peaceful by many anthropologists. In a thirty-year period, it was estimated that there were only two killings among the Hadza, a rate approximated at 6.6 per 100,000 (Marlowe, 2010). And while the Hadza report that they are continually on guard for possible war with neighboring groups (e.g., Obst, 1912), such fighting has not been observed.

We suggest that the increasing variance in food returns with age in boys may be due to boys targeting larger animals since these large animals provide more variable returns.⁶ Still, we cannot rule out other causes such as time spent foraging and number of hunting attempts which were not recorded in this study. Nevertheless, this developmental trajectory is consistent with known changes in behavior wherein boys begin hunting around the age of ten. Future work should aim to capture foraging attempts versus successes. It is unknown to what extent these contrasting patterns of variance between the sexes hold across the life span, although this also merits further exploration. Hunting success generally increases with age in males, peaking in mid-life, suggesting that learning is an important component of hunting (e.g., Blurton Jones & Marlowe, 2002; Gurven et al., 2006). Both skill and the types of animals pursued could affect the variance in caloric outcomes.

The data from the present studies suggest that the sex difference in risk preferences increases in juveniles at a time when they begin to take on the normative social roles of their group. However, biological factors may also play a role, the most notable being the hormone testosterone, which increases at puberty in boys. Indeed, other work suggests that sex differences emerge in middle childhood and may be hormonally mediated (e.g. Del Giudice, 2009). There is also large literature linking testosterone to economic risk preferences, though the nature of the relationship is far from certain (for review, Apicella et al., 2015). The onset of puberty, marked by accelerations in the rate of release of luteinizing hormone, occurs later in Hadza children relative to children in industrialized populations. In Hadza boys, the median age of accelerating LH release is 13.5, while for girls it is 11.5 (Worthman & Stallings, 1997).

Additional work comprising a larger sample of children with accompanying hormonal data could help tease apart these different influences.

Related work on sex differences in the Hadza has found that men are also more competitive than women in both male-centric and gender-neutral tasks (Apicella & Dreber, 2015). For instance, when faced with two payment options for rewarding performance, Hadza men were more likely to choose a competitive (i.e., tournament style) payment scheme whereas women were more likely to choose the piece-rate scheme based on individual performance. There have also been observations of Hadza men gambling, which fit with the current data. Woodburn (1982) describes a gambling game played by men called *lukuchuko*, which involves throwing bark against a tree where the winner is determined by which way the bark lands. Woodburn (1982) suggests that the game was played often. Conversely, Marlowe (2010) has only witnessed this game on a few occasions and Brian Wood (personal communication, 11/26/2016) has only seen Hadza play this once. Blurton Jones (2016) claims to have observed men gamble on two occasions but does not make explicit reference to *lukuchuko*. Similarly, two of us (Apicella & Crittenden) have worked with the Hadza for the last decade, and have not witnessed adult men play this game though one of us (Crittenden) has observed juvenile boys play it. We have, however, observed men play a game which involved tossing coins, scraps of metal or bottle caps into a small hole in the ground where the winners collect the coins/metal/bottle caps, though the exact rules of the game remain unknown (i.e., do winners keep the coins or are they redistributed?). Additionally, Wood (personal communication, 11/26/2016), has observed Hadza men engaging in target shooting contests that involve wagering arrows. None of us know of any games played by women that involve gambling.

Here we presented two studies that employ different methods to elicit risk preferences. Both techniques were easy to understand and share some similarities with other elicitation techniques previously employed such as the Investment Game constructed by Gneezy and Potters (1997) and a lottery selection task used by Eckel and Grossman (2002). Both of these methods have produced robust sex differences in risk preferences (Charness and Gneezy, 2012; Eckel & Grossman, 2008) but another technique (e.g., Holt-Laury), which does not provide a safe option, produces a significant, but minute sex difference (Filippin & Crosetto, 2016). The Holt-Laury task typically involves ten pairwise choices between two lotteries (A and B). Both lotteries yield a positive outcome and have an equal chance of obtaining the higher outcome, but one lottery has less variance in outcomes than the other. For each pairwise decision the subject makes, the possible payoffs for each gamble remain unchanged but the probability associated with each payoff changes, thus altering the expected value of payoffs of option A and B in each lottery. The crossover point where subjects choose the high-risk lottery is then used to estimate risk preferences. Economists like this method because it can provide an interval for the risk coefficient, under the assumption of constant relative risk-aversion (CRRA), which can then be used to classify individuals as risk-averse, loving or neutral (Charness et al., 2013). However, this technique has some drawbacks with the most significant being its complexity and the danger that participants will not understand the task. While the tasks we employed were easy to understand, their drawback is that they do not allow for fine-grained estimates. Still, simple methods are convenient for capturing group differences and treatment effects (Charness et al., 2013), which is what we did. Future work examining sex differences in risk preferences in the Hadza would benefit from designing additional tasks to test whether the sex differences we report is robust to other elicitation methods.

The suggestion that evolved sex differences in economic preferences may be responsible for some of the labor and economic disparities that exist in modern work environments is a real possibility. However, environment and culture almost certainly modify the expression of this difference. Twin studies reveal that shared genes account for only 25% of variation in risk preferences (Cesarini et al., 2009). Additionally,

⁶ There is some debate about whether Hadza specialize in big game hunting at the expense of small prey. Hawkes, O'Connell, and Blurton Jones (1991, 2001) suggest that men exclude small prey to specialize in big game and use experimental and theoretical data to show that hunting of smaller game would yield a higher success rate with more food being delivered to the producer's family. In contrast, Wood and Marlowe (2013) observed many small animals being brought back to camp by hunters – roughly every 12–13 days – and claim that men do not bypass small game. Hawkes, O'Connell and Jones (2014) claim that this result is still consistent with their view that men should be bringing in more small prey and that hunting of big game is sub-optimal with respect to family provisioning.

evolutionary explanations for why animals even perceive risk suggest that it affords animals the ability to take advantage of different payoff structures in their environments (McDermott, Fowler, & Smirnov, 2008; Stephens, 1981; Stephens and Krebs, 1986). Similarly, Robson (2001) theorized that preferences themselves evolved because they provide agents with increased flexibility to cope with new and changing environments. This supposition is supported by decades of research demonstrating that humans and other animals are exquisitely attuned to social and physical features of their environments that offer information about risk and reward (Watson & Platt, 2008). In foragers, flexibility in foraging choices has been observed. A recent detailed examination of how energetic value between resources can vary – as well as the risk around the return rates of particular resources – suggests that male and female foraging goals map onto one another when high quality resources can be readily acquired, but deviate when these resources are tethered to higher levels of risk (Coddington, Bird, & Bird, 2011).

Here we report the first study on sex differences in risk preferences in a population of hunter-gatherers occupying a subsistence environment that is more similar to that in which the human species originated and thrived for thousands of generations. In so doing, we add to the growing body of research on the evolution of risk preference and provide additional evidence that this difference is a uniform characteristic of our species that was present well before the advent of agriculture. This does not imply that this sex difference is necessarily large, non-overlapping, or permanent. However, it does suggest that modern day economic sex inequalities may find roots in evolutionarily selected, species-typical patterns of behavior, originating from reproductive asymmetries between the sexes. Thus, in order to remedy the pernicious persistence of economic sexual inequality cross-culturally, the most sagacious route forward in any policy undertaking will be to develop a more nuanced understanding of the origins of sex differences in a variety of circumstances. In this way, we may begin to more effectively address the root conditions that may stimulate specific patterns of behavior in our policy prescriptions, rather than adopting the idealistic, but fictitious, tabula rasa view of humankind.

Contributions

C.L.A., A.N.C. and V.A.T. wrote the paper. C.L.A. conceived of the study. C.L.A. and A.N.C. collected data. A.N.C. calculated caloric values. C.L.A. performed the statistical analyses.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.evolhumbehav.2017.01.003>.

References

- Ai, C., & Norton, E. C. (2003). Interaction terms in logit and probit models. *Economics Letters*, 80(1), 123–129.
- Altbach, P. G., Reisberg, L., & Rumbley, L. E. (2009). *Trends in global higher education: Tracking an academic revolution*. Paris: UNESCO.
- Andersen, S., Ertac, S., Gneezy, U., List, J. A., & Maximiano, S. (2013). Gender, competitiveness, and socialization at a young age: Evidence from a matrilineal and a patriarchal society. *The Review of Economics and Statistics*, 95(4), 1438–1443.
- Apicella, C. L. (2014). Upper-body strength predicts hunting reputation and reproductive success in Hadza hunter-gatherers. *Evolution and Human Behavior*, 35(6), 508–518.
- Apicella, C. L. (2017). High levels of rule bending in a minimally religious population of hunter-gatherers. *Religion, Brain and Behavior*. <http://dx.doi.org/10.1080/2153599X.2016.1267034> (in press).
- Apicella, C. L., & Barrett, H. C. (2016). Cross-cultural evolutionary psychology. *Current Opinion in Psychology*, 7, 92–97.
- Apicella, C. L., & Crittenden, A. N. (2016). Hunter-Gatherer families and parenting. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 578–597). Hoboken, New Jersey: John Wiley and Sons, Inc.
- Apicella, C. L., & Dreber, A. (2015). Sex differences in competitiveness: Hunter-gatherer women and girls compete less in gender-neutral and male-centric tasks. *Adaptive Human Behavior and Physiology*, 1, 247–269.
- Apicella, C. L., Feinberg, D. R., & Marlowe, F. W. (2007). Voice pitch predicts reproductive success in male hunter-gatherers. *Biology Letters*, 3(6), 682–684.
- Apicella, C. L., Dreber, A., Campbell, B., Gray, P. B., Hoffman, M., & Little, A. C. (2008). Testosterone and financial risk preferences. *Evolution and Human Behavior*, 29, 384–390.
- Apicella, C. L., Marlowe, F. W., Fowler, J. H., & Christakis, N. A. (2012). Social networks and cooperation in hunter-gatherers. *Nature*, 481, 497–501.
- Apicella, C. L., Azevedo, E. M., Christakis, N. A., & Fowler, J. H. (2014). Evolutionary origins of the endowment effect: Evidence from hunter-gatherers. *American Economic Review*, 104(6), 1793–1805.
- Apicella, C. L., Carré, J. M., & Dreber, A. (2015). Testosterone and economic risk-taking: A review. *Adaptive Human Behavior and Physiology*, 1, 358–385.
- Apicella, C. L., Tobolsky, V. A., Marlowe, F. W., & Miller, K. W. (2016). Hadza hunter-gatherer men do not have more masculine digit ratios (2D:4D). *American Journal of Physical Anthropology*, 159, 223–232.
- Ariely, D., & Loewenstein, G. (2006). The heat of the moment: The effect of sexual arousal on sexual decision making. *Journal of Behavioral Decision Making*, 19, 87–98.
- Babcock, L., Gelfand, M., Small, D., & Stayn, H. (2006). Gender differences in the propensity to initiate negotiations. In D. D. Crèmer, M. Zeelenberg, & J. K. Murnighan (Eds.), *Social psychology and economics* (pp. 239–259). Mahwah, NJ: Lawrence Erlbaum.
- Baker, M. D., & Maner, J. K. (2009). Male risk-taking as a context-sensitive signaling device. *Journal of Experimental Social Psychology*, 45, 1136–1139.
- Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, 2(Pt. 3), 349–368.
- Berbesque, J. C., & Marlowe, F. W. (2009). Sex differences in food preferences of Hadza hunter-gatherers. *Evolutionary Psychology*, 7, 601–616.
- Bertrand, M., & Hallock, K. F. (2001). The gender gap in top corporate jobs. *Industrial and Labor Relations Review*, 55(1), 3–21.
- Blau, F. D., & Kahn, L. M. (2000). Gender differences in pay. *The Journal of Economic Perspectives*, 14(4), 75–99.
- Blau, F. D., & Kahn, L. M. (2016). The gender wage gap: extent, trends and explanations. *NBER working paper no. 21913*.
- Blurton Jones, N. (2016). *Demography and evolutionary ecology of hadza hunter-gatherers, vol. 71*. Cambridge University Press.
- Blurton Jones, N. G., & Marlowe, F. W. (2002). Selection for delayed maturity: Does it take 20 years to learn to hunt and gather? *Human Nature*, 13, 199–238.
- Bogandov, S., Jurendic, T., Sieber, R., & Gallman, P. (2008). Honey for nutrition and health: A review. *American College of Nutrition*, 27, 677–689.
- Booth, A. L., & Nolen, P. (2012). Gender differences in risk behaviour: does nurture matter? *The Economic Journal*, 122, F56–F78.
- Brown, J. (1970). A note on the division of labor by sex. *American Anthropologist*, 72, 1073–1078.
- Burnham, T. C., Chapman, J. F., Gray, P. B., McIntyre, M. H., Lipson, S. F., & Ellison, P. T. (2003). Men in committed, romantic relationships have lower testosterone. *Hormones and Behavior*, 44, 119–122.
- Buser, T., Niederle, M., & Oosterbeek, H. (2014). Gender, competitiveness and career choices. *The Quarterly Journal of Economics*, 129(3), 1409–1447.
- Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12(01), 1–14.
- Butovskaya, M. L., Burkova, V., & Mabulla, A. (2010). Sex differences in 2D:4D ratio, aggression and conflict resolution in African children and adolescents: a cross-cultural study. *Journal of Aggression, Conflict and Peace Research*, 2, 17–31.
- Byrnes, J. P., Miller, D. C., & Schafer, W. D. (1999). Gender differences in risk-taking: A meta-analysis. *Psychological Bulletin*, 125(3), 367.
- Campbell, A. (1999). Staying alive: Evolution, culture, and women's intrasexual aggression. *Behavioral and Brain Sciences*, 22, 203–214.
- Cárdenas, J. C., Dreber, A., Von Essen, E., & Ranehill, E. (2012). Gender differences in competitiveness and risk-taking: Comparing children in Colombia and Sweden. *Journal of Economic Behavior and Organization*, 83(1), 11–23.
- Cashdan, E. (2008). Waist-to-hip ratio across cultures: Trade-offs between androgen- and estrogen-dependent traits. *Current Anthropology*, 49(6), 1099–1107.
- Cashdan, E., Marlowe, F. W., Crittenden, A., Porter, C., & Wood, B. M. (2012). Sex differences in spatial cognition among Hadza foragers. *Evolution and Human Behavior*, 33, 274–284.
- Cesarini, D., Dawes, C. T., Johannesson, M., Lichtenstein, P., & Wallace, B. (2009). Genetic variation in preferences for giving and risk taking. *The Quarterly Journal of Economics*, 809–842.
- Charness, G., & Gneezy, U. (2012). Strong evidence for gender differences in risk-taking. *Journal of Economic Behavior and Organization*, 83(1), 50–58.
- Charness, G., Gneezy, U., & Imas, A. (2013). Experimental methods: Eliciting risk preferences. *Journal of Economic Behavior & Organization*, 87, 43–51.
- Chapais, B. (2013). Monogamy, strongly bonded groups, and the evolution of human social structure. *Evolutionary Anthropology: Issues, News, and Reviews*, 22(2), 52–65.

- Cheng, J. T., Tracy, J. L., & Henrich, J. (2010). Pride, personality, and the evolutionary foundations of human social status. *Evolution and Human Behavior*, 31, 334–347.
- Clum, N. J., Fitzpatrick, M. P., & Dierenfeld, E. S. (1996). Effects of diet on nutritional content of whole vertebrate prey. *Zoo Biology*, 15, 525–537.
- Codding, B. F., Bird, R. B., & Bird, D. W. (2011). Provisioning offspring and others: risk–energy trade-offs and gender differences in hunter–gatherer foraging strategies. *Proceedings of the Royal Society of London B: Biological Sciences*, 278, 2502–2509.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2 ed.). Hillsdale, NJ: Erlbaum.
- Cordain, L., Watkins, B. A., & Mann, N. J. (2001). Fatty acid composition and energy density of foods available to African hominids. In K. V. Pavlou, & A. M. Simopoulos (Eds.), *Nutrition and fitness: Metabolic studies in health and disease* (pp. 144–161). Karger Publishers.
- Crittenden, A. N. (2009). *Allomaternal care and juvenile foraging among the Hadza: Implications for the evolution of cooperative breeding in humans*. (Dissertation) University of California San Diego.
- Crittenden, A. N. (2016a). Children's foraging and play among the Hadza. In C. L. Meehan, & A. N. Crittenden (Eds.), *Origins and implications of the evolution of childhood* (pp. 155–172). Albuquerque: School of Advanced Research (SAR) Series, University of New Mexico Press.
- Crittenden, A. N. (2016b). Ethnobotany in evolutionary perspective: Wild plants in diet composition and daily use among Hadza hunter–gatherers. In K. Hardy, & L. K. Martens (Eds.), *Wild harvest: Plants in the hominin and pre-agrarian human worlds* (pp. 319–340). Oxford: Oxford University Press.
- Crittenden, A. N., & Zes, D. A. (2015). Food sharing among Hadza hunter–gatherer children. *PLoS One*, 10(7).
- Crittenden, A. N., Conklin-Brittain, N. L., Zes, D. A., Schoeninger, M. J., & Marlowe, F. W. (2013). Juvenile foraging among the Hadza: Implications for human life history. *Evolution and Human Behavior*, 34, 299–304.
- Crosby, R., & Gneezy, U. (2009). Gender differences in preferences. *Journal of Economic Literature*, 47(2), 448–474.
- Darwin, C. (1871). *Sexual selection and the descent of man*. London: Murray.
- Dekel, E., & Scotchmer, S. (1999). On the evolution of attitudes towards risk in winner–take-all games. *Journal of Economic Theory*, 87, 125–143.
- Del Giudice, M. (2009). Sex, attachment, and the development of reproductive strategies. *Behavioral and Brain Sciences*, 32, 1–67.
- DiPrete, T. A., & Buchmann, C. (2013). *The rise of women: The growing gender gap in education and what it means for American schools: the growing gender gap in education and what it means for American schools*. Russell Sage Foundation.
- Dominguez-Rodrigo, M., Bunn, H. T., Mabulla, A. Z. P., Baquedano, E., Uribealrrea, D., Pérez-González, A., ... Anson, M. (2013). On meat eating and human evolution: A taphonomic analysis of BK4b (Upper Bed II, Olduvai Gorge, Tanzania), and its bearing on hominin megafaunal consumption. *Quaternary International*, 322, 1–24.
- Dreber, A., Gerdes, C., & Gränsmark, P. (2013). Beauty queens and battling knights: Risk-taking and attractiveness in chess. *Journal of Economic Behavior and Organization*, 90, 1–18.
- Eckel, C. C., & Grossman, P. J. (2002). Sex differences and statistical stereotyping in attitudes toward financial risk. *Evolution and Human Behavior*, 23(4), 281–295.
- Eckel, C. C., & Grossman, P. J. (2008). Men, women and risk aversion: Experimental evidence. *Handbook of Experimental Economics Results*, 1, 1061–1073.
- Filippin, A., & Crosetto, P. (2016). A reconsideration of gender differences in risk attitudes. *Management Science*, 62(11), 3138–3160.
- Glowacki, L., & Wrangham, R. (2015). Warfare and reproductive success in a tribal population. *Proceedings of the National Academy of Sciences*, 112, 348–353.
- Gneezy, U., & Potters, J. (1997). An experiment on risk taking and evaluation periods. *The Quarterly Journal of Economics*, 112, 631–645.
- Gong, B., & Yang, C. L. (2012). Gender differences in risk attitudes: Field experiments on the matrilineal Mosuo and the patriarchal Yi. *Journal of Economic Behavior and Organization*, 83, 59–65.
- Goodman, M. J., Griffin, P. B., Estioko-Griffin, A. A., & Grove, J. S. (1985). The compatibility of hunting and mothering among the Agta hunter–gatherers of the Philippines. *Sex Roles*, 12, 1199–1209.
- Gray, P. B., Kahlenberg, S. M., Barrett, E. S., Lipson, S. F., & Ellison, P. T. (2002). Marriage and fatherhood are associated with lower testosterone in males. *Evolution and Human Behavior*, 23, 193–201.
- Gray, P. B., Chapman, J. F., Burnham, T. C., McIntyre, M. H., Lipson, S. F., & Ellison, P. T. (2004). Human male pair bonding and testosterone. *Human Nature*, 15, 119–131.
- Guven, M., Allen-Arave, W., Hill, K., & Hurtado, M. (2000). "It's a wonderful life": signaling generosity among the Ache of Paraguay. *Evolution and Human Behavior*, 21(4), 263–282.
- Guven, M., Kaplan, H., & Gutierrez, M. (2006). How long does it take to become a proficient hunter? Implications for the evolution of delayed growth. *Journal of Human Evolution*, 51, 454–470.
- Hawkes, K. (2001). Is meat the hunter's property? Big game, ownership, and explanations of hunting and sharing. In C. Stanford, & H. Bunn (Eds.), *Meat-eating and human evolution* (pp. 219–236). Oxford: Oxford University Press.
- Hawkes, K., & Bliege Bird, R. (2002). Showing off, handicap signaling, and the evolution of men's work. *Evolutionary Anthropology: Issues, News, and Reviews*, 11, 58.
- Hawkes, K., O'Connell, J., & Blurton Jones, N. G. (1991). Hunting income patterns among the hadza: Big game, common goods, foraging goals and evolution of the human diet. *Philosophical Transactions of the Royal Society of London B*, 334(1270), 243–251.
- Hawkes, K., O'Connell, J., & Blurton Jones, N. G. (2001). Hunting and nuclear families: Some lessons from the Hadza about men's work. *Current Anthropology*, 42, 681–709.
- Hawkes, K., O'Connell, J. F., & Jones, N. G. B. (2014). More lessons from the hadza about men's work. *Human Nature*, 25(4), 596–619.
- Hill, K., & Hurtado, A. M. (1996). *Aché life history: The ecology and demography of a foraging people*. Hawthorne, NY: Aldine de Gruyter.
- Hurtado, A. M., & Hill, K. (1992). Paternal effect on offspring survivorship among Ache and Hiwi hunter–gatherers: Implications for modeling pair–bond stability. In B. Hewlett (Ed.), *Father–child relations: Cultural and biosocial contexts*. Chicago: Aldine.
- Iskander, F. Y. (1995). Trace and minor elements in four commercial honey brands. *Journal of Radioanalytical and Nuclear Chemistry*, 201, 401–408.
- Kaplan, H., & Hill, K. (1985). Hunting ability and reproductive success among male Ache foragers: Preliminary results. *Current Anthropology*, 26, 131–133.
- Kelly, R. L. (2013). *The lifeways of hunter–gatherers: The foraging spectrum*. Cambridge, UK: Cambridge University Press.
- Lovejoy, C. O. (1981). The origin of man. *Science*, 211(4480), 341–350.
- Low, B. S. (2003). Ecological and social complexities in human monogamy. In U. H. Reichard, & C. Boesch (Eds.), *Monogamy: Mating strategies and partnerships in birds, humans and other mammals* (pp. 161–176). Cambridge: Cambridge University Press.
- Marlowe, F. (1999). Male care and mating effort among Hadza foragers. *Behavioral Ecology and Sociobiology*, 46, 57–64.
- Marlowe, F. W. (2003a). The mating system of foragers in the standard cross-cultural sample. *Cross-Cultural Research*, 37, 282–306.
- Marlowe, F. W. (2003b). A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior*, 24(3), 217–229.
- Marlowe, F. W. (2004a). Mate preferences among Hadza hunter–gatherers. *Human nature*, 15(4), 365–376.
- Marlowe, F. W. (2004b). What explains Hadza food sharing? *Research in Economic Anthropology*, 23, 69–88.
- Marlowe, F. (2010). *The Hadza: Hunter-gatherers of Tanzania*. Berkeley: University of California Press.
- Marlowe, F. W., Berbesque, J. C., Wood, B., Crittenden, A., Porter, C., & Mabulla, A. (2014). Honey, Hadza, hunter–gatherers, and human evolution. *Journal of Human Evolution*, 71, 119–128.
- McDermott, R., Fowler, J. H., & Smirnov, O. (2008). On the evolutionary origin of prospect theory preferences. *The Journal of Politics*, 70, 335–350.
- McIntyre, M., Gangestad, S. W., Gray, P. B., Chapman, J. F., Burnham, T. C., O'Rourke, M. T., & Thornhill, R. (2006). Romantic involvement often reduces men's testosterone levels–But not always: The moderating role of extrapair sexual interest. *Journal of Personality and Social Psychology*, 91, 642.
- Muller, M. N., Marlowe, F. W., Bugumba, R., & Ellison, P. T. (2009). Testosterone and paternal care in East African foragers and pastoralists. *Proceedings of the Royal Society of London B: Biological Sciences*, 276, 347–354.
- Murray, S. S., Schoeninger, M. J., Bunn, H. T., Pickering, T. R., & Marlett, J. A. (2001). Nutritional composition of some wild plant foods and honey used by Hadza foragers of Tanzania. *Journal of Food Composition and Analysis*, 14, 3–13.
- Niederle, M. (2017). In J. Kagel, & A. E. Roth (Eds.), "Gender" handbook of experimental economics (2nd ed.) (in press).
- Obst, E. (1912). Von Mkalama ins Land der Wakindiga. *Mitteilungen der Geographischen Gesellschaft in Hamburg*, 26, 1–45.
- Panther-Brick, C. (2002). Sexual division of labor: Energetic and evolutionary scenarios. *American Journal of Human Biology*, 14(5), 627–640.
- Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. *American Journal of Physical Anthropology*, 116, 25–53.
- Plavcan, J. M., & van Schaik, C. P. (1997). Interpreting hominid behavior on the basis of sexual dimorphism. *Journal of Human Evolution*, 32, 345–374.
- Powell, M., & Ansic, D. (1997). Gender differences in risk behaviour in financial decision-making: An experimental analysis. *Journal of Economic Psychology*, 18(6), 605–628.
- Prange, H. D., Anderson, J. F., & Rahn, H. (1979). Scaling of skeletal mass to body mass in birds and mammals. *The American Naturalist*, 113, 103–122.
- Rieger, M. O., Wang, M., & Hens, T. (2014). Risk preferences around the world. *Management Science*, 61, 637–648.
- Robson, A. J. (1996). The evolution of attitudes to risk: Lottery tickets and relative wealth. *Games and Economic Behavior*, 14, 190–207.
- Robson, A. J. (2001). The biological basis of economic behavior. *Journal of Economic Literature*, 39, 11–33.
- Ronay, R., & von Hippel, W. (2010). The presence of an attractive woman elevates testosterone and physical risk-taking in young men. *Social Psychological and Personality Science*, 1(1), 57–64.
- Rubin, P. H., & Paul, C. W., II (1979). An evolutionary model of taste for risk. *Economic Inquiry*, 17, 585–596.
- Saad, G. (Ed.). (2011). *Evolutionary psychology in the business sciences*, vol. 197. Springer Science and Business Media.
- Skinner, M. (1991). Bee brood consumption: An alternative explanation for hypervitaminosis A in KNM-ER 1808 (Homo erectus) from Koobi Fora, Kenya. *Journal of Human Evolution*, 20(6), 493–503.
- Smith, A. E. (1988). Risk and uncertainty in the "original affluent society": Evolutionary ecology of resource sharing and land tenure. In T. Engold, D. Richey, & J. Woodburn (Eds.), *Hunters and gatherers volume 1: History, evolution, and social change* (pp. 222–252). Oxford: Berg Publishers.
- Smith, E. A. (2004). Why do good hunters have higher reproductive success? *Human Nature*, 15(4), 343–364.
- Stephens, D. W. (1981). The logic of risk-sensitive foraging preferences. *Animal Behaviour*, 29(2), 628–629. [http://dx.doi.org/10.1016/S0003-3472\(81\)80128-5](http://dx.doi.org/10.1016/S0003-3472(81)80128-5).
- Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.
- Suppes, P. (1956). The role of subjective probability and utility in decision-making. *Proceedings of the third Berkeley symposium on mathematical statistics and probability, 1954–1955*, Vol. 5. (pp. 61–73).

- Terrab, A., Hernanz, D., & Heredia, F. J. (2004). Inductively coupled plasma optical emission spectrometric determination of minerals in thyme honey and their contribution to geographical discrimination. *Journal of Agricultural Food Chemistry*, 52, 3441–3445.
- Trivers, R. (1972). *Parental investment and sexual selection*, vol. 136. (pp. 179). Biological Laboratories, Harvard University, 179.
- U.S. Department of Agriculture, & Agricultural Research Service (r). USDA National Nutrient Database for standard reference (2008) release 21. Nutrient Data Laboratory Home Page <http://www.ars.usda.gov/ba/bhnrc/ndl>
- Vincent-Lancrin, S. (2008). *The reversal of gender inequalities in higher education: An on-going trend. Higher education to 2030*, 265–298.
- Wang, X. T., Kruger, D. J., & Wilke, A. (2009). Life history variables and risk-taking propensity. *Evolution and Human Behavior*, 30(2), 77–84.
- Washburn, S., & Lancaster, C. (1968). The evolution of hunting. In R. B. Lee, & I. Devore (Eds.), *Man the Hunter* (pp. 293–303). Chicago: Aldine.
- Watson, K. K., & Platt, M. L. (2008). Neuroethology of reward and decision making. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 363(1511), 3825–3835.
- White, D. R., Betzig, L., Mulder, M. B., Chick, G., Hartung, J., Irons, W., ... Spencer, P. (1988). Rethinking polygyny: Co-wives, codes, and cultural systems. *Current Anthropology*, 29(4), 529–572.
- Wiessner, P. (2002). Hunting, healing, and hxaro exchange: A long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evolution and Human Behavior*, 23, 407–436.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr., & Ball, G. F. (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, 136, 829–846.
- Wood, B. M. (2006). Prestige or provisioning? A test of foraging goals among the Hadza. *Current Anthropology*, 47, 383–387.
- Wood, B. M., & Marlowe, F. W. (2013). Household and kin provisioning by Hadza men. *Human Nature*, 24, 280–317.
- Woodburn, J. (1982). Egalitarian societies. *Man*, 431–451.
- Worthman, C. M., & Stallings, J. F. (1997). Hormone measures in finger-prick blood spot samples: New field methods for reproductive endocrinology. *American Journal of Physical Anthropology*, 104, 1–21.
- 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., Baldini, R., & Mathew, S. (2015). Solving the puzzle of human warfare requires an explanation of battle raids and cultural institutions. *Proceedings of the National Academy of Sciences*, 112, E2557.