ARTICLE IN PRESS

Evolution and Human Behavior xxx (xxxx) xxx

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens

A cost for signaling: do Hadza hunter-gatherers forgo calories to show-off in an experimental context?

Duncan N.E. Stibbard-Hawkes [a,*], Dorsa Amir [b], Coren L. Apicella [c]

[a] Department of Anthropology, Durham University, Dawson Building, South Rd, Durham DH1 3LE, UK
[b] Boston College, Department of Psychology, Chestnut Hill 02467, MA, USA
[c] Department of Psychology, University of Pennsylvania, 3720 Walnut Street, Philadelphia, PA 19104, USA

ARTICLE INFO

Keywords:
Hunter-gatherers
Food-sharing
Costly signaling
Show-off
Hadza

ABSTRACT

Hadza food-sharing is extremely generous and often extends to individuals outside the household. Some anthropologists have proposed that individuals, especially men, share food beyond the household in order to signal foraging skill. While correlational data have been used to both evidence and critique this hypothesis, it has less often been experimentally tested. Here, we conducted an incentivised experiment to test whether Hadza adults are indeed willing to forgo caloric resources in order to signal their foraging skills. In this study, 196 Hadza adults were given the opportunity to participate in two games - an *aim game* and a *search game* - designed to advertise their skill as foragers. We varied the incentive structure of both games, adjusting i) whether there was a caloric cost (i.e., honey) to play, and ii) whether success in each game was rewarded with a prize (i.e., a colored bracelet), which functioned as a visible signal of skill. Although the aim game was universally popular when there was no cost to play, we found that individuals generally valued calories more than signaling opportunities and were unwilling to forgo caloric resources to continue participation in either game. In line with signaling theory, we did observe age and gender difference in willingness to wager calories for signaling opportunities. Men were more likely than women to forgo calories in order to participate. Younger people (<37), especially younger men, were also more likely to forgo calories to play than older people.

1. Introduction

Food sharing is ubiquitous among many foraging populations (Damas, 1972; Dowling, 1968; Kent, 1993; Lee, 1979; Sahlins, Graeber, Sahlins, & Graeber, 1972; Smith, 1985). Within these groups, men and women typically pursue different sets of resources, sometimes with little overlap (Bird, 1999; Bliege Bird & Power, 2015; Brown, 1970; Jochim, 1988; Marlowe, 2007). Often, men target high-risk, high-variance resources (e.g., large game) while women prioritize lower-risk, lower-variance resources (e.g., berries; tubers) (Blurton Jones, 2016; Codding, Bird, & Bird, 2011; Hawkes, O'Connell, & Blurton Jones, 1991; Hurtado, Hill, Hurtado, & Kaplan, 1992; Marlowe, 2007). Importantly, certain foods, especially those procured by men, are habitually redistributed widely beyond the immediate family of the procurer (Codding et al., 2011; Gurven, 2004; Gurven & Hill, 2009). These observations prompted anthropologists to consider why (Brown, 1970; Kaplan, Hill, & Cadeliña, 1985) foragers may be targeting high-risk foods and giving away caloric resources at a 'significant opportunity cost to their own families' (Hawkes, O'Connell, & Blurton Jones, 2014, p.596).

Many explanations for caloric redistribution among foragers hinge on considerations of long-term self-interest (Gurven, 2004; Hill, Kaplan, & Hawkes, 1993; Kaplan et al., 1985; Winterhalder, 1996b). For instance, some have proposed that food-sharing might be motivated by future reciprocal exchange (Cashdan, 1985; Gurven, 2004; Gurven, Allen-Arave, Hill, & Hurtado, 2000,Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000; Sahlins et al., 1972) which could smooth variance in the availability of otherwise unreliably attained resources (Winterhalder, 2001). Others argue that food-sharing is motivated by persistent requests and demands from camp-mates (Blurton Jones, 1991; Peterson, 1993 but see Kaplan & Gurven, 2005; Stibbard-Hawkes, Smith, & Apicella, 2022), especially where individuals procure surplus perishable food (Winterhalder, 1986, 1996a). Further, some propose that food redistribution might be motivated by inclusive fitness, such that resources flow to consanguineal kin (Wood & Marlowe, 2013, but see Allen-Arave, Gurven, & Hill, 2008; Hill et al., 2011) a pattern observed in certain studies of Hadza food redistribution (Wood & Marlowe, 2013

* Corresponding author.
E-mail address: duncan.stibbard-hawkes@durham.ac.uk (D.N.E. Stibbard-Hawkes).

https://doi.org/10.1016/j.evolhumbehav.2022.10.004
Received 12 January 2022; Received in revised form 5 October 2022; Accepted 27 October 2022

Please cite this article as: Duncan N.E. Stibbard-Hawkes, *Evolution and Human Behavior*, https://doi.org/10.1016/j.evolhumbehav.2022.10.004

but see Hawkes et al., 2014), and in gift-giving games (Apicella, Marlowe, Fowler, & Christakis, 2012). Finally, many researchers see hunting as foremost a nuclear family provisioning strategy (Lovejoy, 1981; Washburn & Lancaster, 1968; Wood & Marlowe, 2013; Wood, Pontzer, Raichlen, & Marlowe, 2014).

Among the most enduring explanations for forager food acquisition (Hawkes, O'Connell, & Blurton Jones, 2018, 2014), redistribution, and the sexual division of labor (Bird, 1999; Jochim, 1988; Marlowe, 2007) is the notion that men might gain reproductive benefits from their food sharing (Gurven & von Rueden, 2006; Kaplan et al., 1985). Two key formulations of this idea are the *show-off* and *costly signaling* hypotheses (Hawkes et al., 2018; Hawkes & Bird, 2002). These predict that large food packages, such as large animal carcasses, 'are more like public than like private goods' (Hawkes et al., 2018, p.78) but men continue to procure them to 'establish and maintain their relative social standing by showing off their hunting prowess' (p.59). By targeting such resources, men forsake caloric optimality to reveal 'information about an otherwise hidden quality' (Hawkes & Bird, 2002, p.59) to third parties, and gain fitness benefits by doing so. Public goods, such as food items, attract wide and general interest in a way that other forms of signaling with no direct benefit to the recipient do not (Hawkes et al., 2018). In this way, people forsake calories to publicly show-off.

Sex differences in resource acquisition were traditionally framed as cooperative labour specialization, where women prioritize resources which are and aren't compatible with nursing and/or childcare (Brown, 1970; Hurtado, Hawkes, Hill, & Kaplan, 1985; Lancaster & Lancaster, 1987). Costly signaling models, by contrast, often highlight inter-sexual conflict, proposing that women gain fitness benefits by prioritising reliable food, while men gain fitness benefits through pursuing sometimes calorically suboptimal resources that are more widely shared and, often, less reliably attained (see Hawkes et al., 2018). Indeed, male hunting success is associated with measures of reproductive success in many forager populations (e.g., Gurven & von Rueden, 2006; but see Kraft, Venkataraman, Tacey, Dominy, & Endicott, 2019). While data on the relationship between Hadza men's long term hunting income and reproductive success [RS] are lacking, there is indirect evidence that Hadza men with better hunting reputations have higher RS (Apicella, 2014; Blurton Jones, 2016), more sequential marriages (Blurton Jones, 2016) younger and harder-working wives (Blurton Jones, 2016; Hawkes, O'Connell, & Blurton Jones, 2001) and are preferred as husbands (Marlowe, 2010). Moreover, there is evidence from multiple populations that women tend to target foods which are more reliably attained and shared less widely (Codding et al., 2011 though see Starkweather, Shenk, & McElreath, 2020), a pattern observed among Hadza children (Crittenden, Conklin-Brittain, Zes, Schoeninger, & Marlowe, 2013). For instance, variance in Hadza boys' caloric returns steadily increases throughout childhood and adolescence, but for girls, it remains stable (Apicella, Crittenden, & Tobolsky, 2017), and among both adults and children there are clear sex differences in competitiveness (Apicella & Crittenden, 2015; Apicella & Dreber, 2015).

Barker, Power, Heap, Puurtinen, and Sosis (2019), provide a counterpoint for the view that signaling is exclusively the purview of men, and highlight links between female foraging effort and likelihood of being named as friends or best friends (Marlowe, 2010) as well as links between female generosity and network centrality (Apicella et al., 2012). For this reason, they propose that Hadza women's foraging, 'may additionally hold signal content of the skill and dedication of the forager, as well as her potential value as a foraging partner' (Barker et al., 2019, p.89). In support of this, in a picture ranking task, Hadza women themselves rated skill-signaling highly as a motivation for foraging (Stibbard-Hawkes et al., 2022).

The show-off and costly signaling hypotheses have been divisive (Gurven, 2004; Gurven & Hill, 2010; Hawkes et al., 2014; Hawkes, O'Connell, & Coxworth, 2010; Stibbard-Hawkes, 2019; Stibbard-Hawkes, Attenborough, & Marlowe, 2018; Wood, 2006; Wood & Marlowe, 2013) and there is no universal consensus on the extent to which foraging, and sharing are motivated by showing-off. Gurven (2004) and Gurven and Hill (2009) have argued that food redistribution is multicausal and varies based on circumstance. Moreover, as meat provides important nutrients not easily obtained from other sources (see, Milton, 2003; Tennie, Gilby, & Mundry, 2009; Watts, 2020), small quantities of meat may provide benefits to the procurer even when widely shared. The notion that large game are public goods, and that producers have minimal control over food distribution has been divisive (Hawkes et al., 2014; Wood & Marlowe, 2013; Woodburn, 1998) and varies across cultures (reviewed by Kaplan & Gurven, 2005; Testart, 1987). Wood and Hill (2000), Wood (2006) have found that men among the Aché and Hadza often state a preference for living with better hunters so that they get more food, suggesting intra-sexual cooperation trumps competition. Moreover, while assessments of hunting ability well predict success at tasks designed to test foraging skills (Apicella, 2014; Stibbard-Hawkes, 2019), and hunting reputations track individual return rates among Aché hunters (p.333 Hill & Hurtado, 1996), the error introduced by high stochasticity in acquisition (Hill & Hurtado, 2009) renders hunting a potentially noisy signal (Stibbard-Hawkes, 2019).

To date, most empirical support for the show-off and costly signaling hypotheses comes from cross-sectional or correlational research. This includes evidence that better hunters have higher status (von Rueden, Gurven, & Kaplan, 2008) and greater reproductive success (Gurven & von Rueden, 2006), or evidence that sharing is calorically costly or suboptimal (e.g., Hawkes et al., 2018, but see discussion in Stibbard-Hawkes, 2019). Apicella (2014) and Stibbard-Hawkes et al. (2018) both found statistically real but noisy associations between hunting reputation and tests of hunting skill, suggesting that hunters' skills are not entirely opaque. Moreover, Bishop (in press) measured the signaling value of prey harvest composition across two foraging societies and found that different prey types altered perceptions of the hunter.

Several further studies have used experimental methodologies to assess the motives underlying food sharing behaviour. In two computer-simulated resource optimisation experiments (Kaplan, Schniter, Smith, & Wilson, 2012, 2018), high variance resources leads to emergent reciprocal sharing relationships between participants, rather than relationships of tolerated theft. Moreover, economic games (dictator, ultimatum & public goods games) have been extensively used to assess giving behaviour in small-scale societies (e.g., Gurven, 2004; Henrich et al., 2005; Marlowe, 2005; Smith et al., 2019; Stagnaro, Stibbard-Hawkes, & Apicella, 2022). Notably, Gurven, Zanolini, and Schniter (2008) showed that public games giving was slightly increased relative to private games, indicating the importance of generosity. Wood and Hill (2000); Wood (2006) showed, in the context of interviews, that both Hadza and Ache men prefer residential camps/villages which maximize food availability rather than signaling opportunities. However, we know of no other studies that have given participants the opportunity to choose directly between caloric optimality and signaling opportunities in the context of a controlled, incentivised behavioural experiment.

Here, we explore how adults behave in a paradigm that pits caloric maximization against showing-off aspects of foraging skill (but not generosity). We introduced $n = 196$ Hadza adults (93 men; 93 women) to two games: the *aim game*, a test of target accuracy, and the *search game*, a test of search efficacy. Both games were designed to be challenging, but winnable. Although both tasks had elements of luck, both require skills relevant to hunting or gathering (hand-eye coordination in the first instance; search efficiency in the second). Success in each game was rewarded with a colored bracelet specific to that game. Campmates were aware that the bracelet denoted success at the corresponding task. Participants were given an initial allotment of honey sticks - a valued food resource. After playing the games once without cost, participants were able to pay for subsequent attempts at the game by trading in their honey sticks. Paying one honey stick meant one extra attempt at the game of their choice - a direct caloric cost in exchange for a signaling opportunity.

We predicted that if individuals were motivated specifically by skill signaling, they would be willing to forsake calories in return for an opportunity to visibly advertise foraging-relevant skill to campmates.

The second aim of our study is to assess sex differences in both willingness to participate and willingness to pay a cost to do so. Some propose men reap greater fitness benefits from allocating effort into status-seeking than into self- and nuclear-family-provisioning strategies (e.g., Hawkes et al., 2018; Hawkes, Rogers, & Charnov, 1995). Recent work has challenged or otherwise revised the notion that men and women have entirely conflicting motivations (Barker et al., 2019; Mulder & Ross, 2019; Starkweather et al., 2020; Stibbard-Hawkes et al., 2022). It would be useful to assess cost and risk tolerance in an experimental setting and to test whether, ceteris paribus, men are more willing to exchange calories to participate in a visible display of aim and dexterity than women.

Finally, the present study also affords the opportunity to explore age-related differences in willingness to pay caloric costs for signaling opportunities. If hunting is a means of advertising to prospective partners, we should expect younger people will be more likely to exchange calories to show off.

2. Methodology

2.1. Study population

The Hadza are an ethnolinguistic group with 1000 speakers living in the Lake Eyasi region of northern Tanzania. While estimates vary (Blurton Jones, 2016; Marlowe, 2010), some 150–250 Hadza still subsist by hunting and gathering for most of their diet. Although we did not collect returns data sufficient to quantify camp-level reliance on foraging vs cash-bought cultigens, our research was conducted in bush camps and all participants were involved in mixed-subsistence activities with habitual foraging. The majority of the foraged Hadza diet comes from five sources: meat, honey, underground storage organs (tubers), berries and baobab fruit (Crittenden, 2016; Marlowe, 2010). Hadza foraging labour is divided along gender lines. Men do almost all hunting, most always with poisoned arrows, and collect most honey. Women collect all tubers, dug from the ground with sticks, and collect most berries and baobab fruit. Foods not eaten in situ while foraging (Berbesque, Wood, Crittenden, Mabulla, & Marlowe, 2016) are brought back to a central place. Certain foods, especially meat and honey, may be widely shared with everyone in camp (Marlowe, 2010).

Honey is especially prized both among the Hadza and more broadly in numerous small-scale societies (Berbesque & Marlowe, 2009; Crittenden, 2011; Demps, 2019; Marlowe et al., 2014; Wood et al., 2014). It is eaten in such quantities (Berbesque et al., 2016) that Hadza men have high rates of dental carries (Crittenden, 2011). As elsewhere (Hooper, Demps, Gurven, Gerkey, & Kaplan, 2015; Kraft, Venkataraman, & Dominy, 2014), while the risks and skill associated with honey collection differ by bee species, Hadza honey collection can be a skill-intensive and dangerous activity. The Hadza recognise seven species of honeybee, six stingless (Wood et al., 2014). The most important honey producer is the seventh, the honey bee *Apis melifera* which builds its nest in the top of baobab trees (Marlowe et al., 2014). Honey from this species is almost exclusively collected by men, who climb to nests using hammered wooden pegs, and employ smoke from torches to pacify the bees (Woodburn, 1970). Stings are common and the activity is associated with substantial risk of injury from falling (Bennett, Barnicot, Woodburn, Pereira, & Henderson, 1973; Blurton-Jones & Marlowe, 2002; Wood et al., 2014).

It has been suggested that, after accounting for food-redistribution, Hadza men's hunting patterns do not maximize hunting returns for themselves or their families (Hawkes et al., 2018). Indeed, several studies identify no nutritional benefits to being or marrying a more highly regarded hunter (Blurton Jones, 2016; Stibbard-Hawkes, Attenborough, Mabulla, & Marlowe, 2020). However, null findings are not definitive (Stibbard-Hawkes & Attenborough, 2021) and the extent to which foods are preferentially channeled to the affinal and consanguineal relatives of the procurer remains a topic of debate (Hawkes et al., 2014; Wood et al., 2014). Although there is some noise and error, most adult Hadza, men and women, show high agreement concerning the very best hunters among their peers (Blurton Jones, 2016; Smith & Apicella, 2020; Stibbard-Hawkes et al., 2018) and state a preference for living in the same camps as better hunters (Smith & Apicella, 2020; Wood, 2006).

Data collection for this study took place during the dry seasons of 2014 and 2019. Instructions were administered in Swahili by a research assistant who was blind to the study's hypotheses. Games were played outside and, due to the nature of the field site and the attention generated by the methods, it was impossible to ensure that tests were conducted free of onlookers. We made a total of 17 camp visits, 14 in 2014 and 3 in 2019. All adult men and women in each camp were invited to take part in the study. All present claimed honey sticks. A total of 196 Hadza participated.

2.2. Procedure

We conducted two carnival-like games: the *search game* and the *aim game*. As we explained to participants, the games were designed to simulate gathering and hunting activities, respectively. We referred to these games with participants as the 'hunting' and 'gathering' games.

The *search game* was a search task. Drawing on methods from a previous study (Apicella & Dreber, 2015), it was designed to simulate search efficiency in the context of berry gathering. Participants were presented with five bowls of single-colored beads. In each bowl, there was also a single buried black bead. Participants were given the option of choosing one bowl and then were given five seconds to find the single black bead in that bowl (Fig. 1; left). We used plastic beads as they were both eye-catching and familiar to participants. Although the placement of the bead in the bowl introduced an element of luck to this task, systematic searching yielded better results and it is possible to greatly increase the probability of finding the bead in the allotted time limit through more systematic and efficient searches.

The *aim game* was an aiming task. Here, participants were presented with a corkboard with six three-inch, red target stickers spaced out evenly (Fig. 1; right). While standing ten feet away, participants attempted to hit a target using darts, starting from the target in the top right. Although aim is most often important in the context of bow hunting, the darts task requires similar hand-eye coordination, was accessible to both genders and did not require participants to supply their own bows.

The procedure was identical across all camps. First, a researcher or research assistant demonstrated how to play each game by first playing it themselves. Participants were given a maximum of five attempts, or 'rounds' for each game. Game order (foraging first or gathering first) was determined by a coin flip. We had access to no indoor spaces and so all games were conducted outside. As such, it proved impossible to exclude onlookers. We discuss these implications in section 4.6.

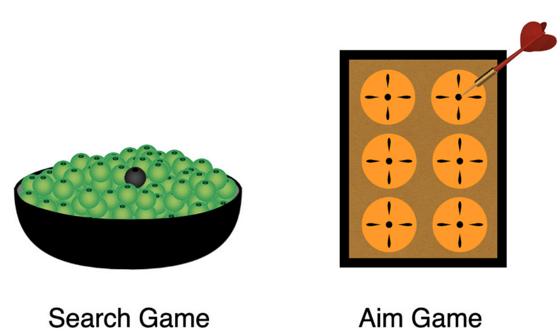

Fig. 1. Simplified illustrations of the *search game* and the *aim game*.

Although the aim and search games themselves were identical across camps, we experimentally varied game cost and reward structure. Costs were always paid in the form of honey sticks. These contained one teaspoon (approx. 20 kcal) of *Apis melifara* honey - a skill intensive resource in the wild (Wood et al., 2014). While this resource has plausible signaling value in some contexts, the medium of delivery made clear that these were the products of apiculture, and did not imply the same skill and risk tolerance as wild honey. We chose to use honey as a currency in the present experiment not due to signaling concerns but instead because it among the most energy dense foods in nature (80–95% sugar, 3049–3680 kcal per kg, see Crittenden, 2011; Marlowe et al., 2014), and the favourite food of both genders (Berbesque & Marlowe, 2009). Although the caloric cost of forsaking honey sticks is not as high as habitual meat-sharing it yet represent a palpable cost for signaling.

The signaling aspect of the game prohibited us from varying incentive structure between individuals, and we instead varied incentive structure between camps. We employed a total of three different incentive structures: A (costs, and rewards), B (costs, no rewards) and C (free, no rewards).

Incentive Structure A (ISA): After demonstrating game play, participants were given eight honey sticks. At this point, they were free to leave. We afforded each participant the opportunity to play up to one free round for each game type, followed by up to four paid rounds for each game type. After each attempt, participants were given the opportunity to play again (a maximum of five attempts, including the initial free round). However, for each attempt after the first, participants needed to pay one honey stick to play. ISA was employed in eleven of the camps we visited.

In ISA, a successful attempt - hitting the target with the dart or finding the black bead - earned the participants a prize that signaled their success to campmates: a colored rubber bracelet. The color of the bracelet, either green or red, corresponded to the game type: aim or search. We varied the color associated with each game type between camps, such that, in five camps, a red bracelet corresponded to the *aim game* and green to the *search game*. In six further camps, the color association was reversed. Each participant was also told that other adults in their camp would be given a chance to play the games, and that the colored bracelets signified a successful attempt. All camp members were made aware which bracelet color corresponded to which game.

Incentive Structure B (ISB): The cost structure for ISB was identical to that of ISA. After witnessing a demonstration, participants were given eight honey sticks. The first round involved no cost to play, and successive attempts cost one honey stick each. However, in ISB we did not reward successful attempts with prizes (bracelets) to signal successes. We employed incentive structure B (ISB) in three camps.

Incentive Structure C (ISC): Here there were no costs and no rewards. Instead, people were allowed to play up to five rounds for free. We employed incentive structure C in three camps.

Due to sample size constraints, we did not run a five-round method with prizes but no costs. Instead, we modelled no prize, no cost play probabilities using the 'free round' from incentive structure A (see Section 2.4).

Finally, we collected information on participant age and gender. In total, 196 Hadza (93 male) across 17 camp visits participated in the task. Ages ranged from 17 to 75, with a mean of 38.67 (SD = 14.21) and a median age of 37 (Fig. 2).

All data were recorded with a pen and paper in situ by research assistants blind to study aims and then later digitized. All data were included in the analysis.

2.3. Consent, permitting, and data availability

Verbal consent was attained both at the camp level and from each participant individually. Participants were instructed that they were free to drop out at any time. Research permission was granted the Institutional Review Board at the University of Pennsylvania (#833889) and the Tanzanian Commission for Science and Technology. Anonymised study data alongside code for statistical analyses are openly available online at the following url: https://github.com/DStibbardHawkes/CostSignallingAnalysis

2.4. Analyses and modelling strategy

We estimated the probability of playing each game with a series of binomial logistic regression models using the Bayesian Regression Models package in R (Burkner, 2017). In our analysis, each row of data corresponded to a single round.

We created a 'condition' variable which took one of four values corresponding to whether that round had either a cost to play or a prize - either 'pay 1; prize 1' when there was a prize and a cost, 'pay 1; prize 0' when there was a cost to pay and no prize, 'pay 0; prize 1' for free rounds

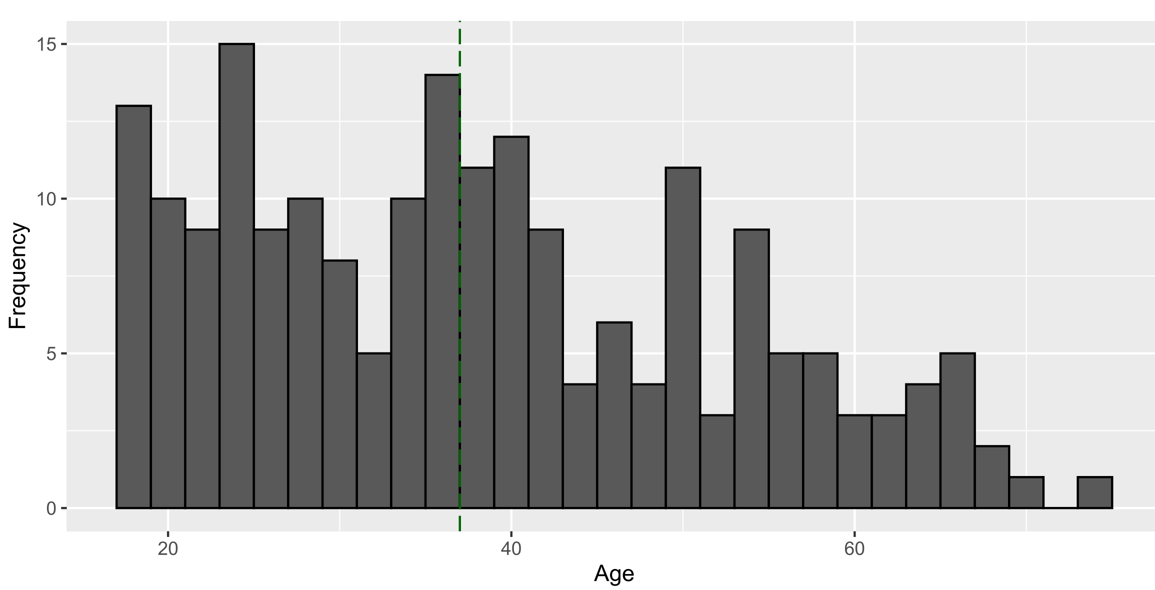

Fig. 2. Histogram showing age distribution in the study sample. Dashed green line represents median age. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

with a prize and 'pay 0; prize 0' for free rounds with no prize. For example, the free round in method A was coded as 'pay 0; prize 1', while the four paid rounds were coded as 'pay 1; prize 1'. We also used the median age split (i.e., 37 years) to create a binary variable to compare younger and older individuals.

We added our predictors stepwise in order of their theoretic importance (game type [hunting/gathering]; pay/prize condition; gender; age), at each step assessing the additional explanatory impact of each additional predictor in a leave-one-out cross-validation model selection. We built varying (i.e., random) effects models, with condition as a factor-variable predictor and game type, gender, and age as cross-classifying grouping variables. Each subsequent variable we added improved upon the previous model in our model selection, with the full model including all predictors being allotted the greatest Akaike weight (Table 1). We report results from the full model below.

Where appropriate, we also assessed the influence of potential methodological artefacts, including bracelet color, game order and round number. Though game order substantially improved model selection performance, none of these predictors substantively changed the findings.

3. Results

Our full model assessed the impact on per round play probabilities of game type (aim versus search game), game cost (free or costly), game reward structure (bracelets are prizes, or no prizes), participant gender (male or female) and participant age (above or below the median age split). We report these effects in detail. We also explore the impacts of several potential confounders - round number, bracelet color, previous round success rate and game order.

3.1. Aim versus search game

The experimental paradigm included two game types, giving participants the opportunity to signal hunting- and foraging-relevant skills. Game type substantially affected play probabilities, and the model including game-type substantially outperformed the baseline model in Leave-One-Out (LOO) model selection (Table 1). We expected that the *aim game* would be more popular among men, and the *search game* more popular among women. Instead, although participants were much more likely to win the search game than the aim game (15% of rounds vs 53% of rounds), we found that the *aim game* was more popular across both genders, pay/prize conditions, and ages. In the full model, participants were more likely to play the *aim game* in 12 of 16 contrasts, the only exception being the four no pay, prize contrasts where mean probabilities for both game types were close to one. Excluding these four contrasts, the mean absolute probability increase between the *search* and the *aim game* was $p = 0.09$ (90% CI = 0 to 0.2).

Table 1
Leave-one-out model selection results including expected log-predictive density differences, standard errors and Akaike weights. Left side model definitions provided in BRMs syntax.

Definition	ELPD Difference	SE Difference	Weights
0 + Condition + (0 + Condition | GameType) + (0 + Condition | Sex) + (0 + Condition | Age)	0.00	0.00	0.82
0 + Condition + (0 + Condition | GameType) + (0 + Condition | Sex)	−1.54	2.35	0.18
0 + Condition + (0 + Condition | GameType) + (0 + Condition | Age)	−57.88	10.35	0.00
0 + Condition + (0 + Condition | GameType)	−61.63	10.97	0.00
0 + GameType	−555.00	26.12	0.00
1	−560.82	25.94	0.00

3.2. Do foragers forgo calories for signaling opportunities?

Each round had either a cost or no cost to play (Pay 1/Pay 0) and either a prize or no prize for winning (Prize 1/Prize 0). We coded all four permutations as a single variable: condition. Conditions substantially influenced the probability of playing, and the model including experimental condition substantially outperformed the null and game type-only model in a LOO model selection (Table 1).

The free rounds, in every instance, had a higher play probability than paid rounds (Table 2; Fig. 3), in no cases with contrast distributions crossing zero. In the full model, the absolute increase in probabilities between paid (i.e., costly) and analogous free rounds was substantial (Fig. 5). In the prize condition, across genders, people were substantially more likely to participate in free rounds, with absolute mean estimated increases in probability ranging between $p = 0.86$ and $p = 0.96$ suggesting a very substantial influence of costs. For men, the contrasts in the no prize conditions were also large, with mean absolute increases between $p = 0.35$ and $p = 0.49$. Contrasts were smaller for women in the no prize conditions, ranging between 0.10 and 0.14, but still substantially above zero. In both paid conditions, across genders and age categories, most participants (74%) were unwilling to exchange caloric resources (honey sticks) for opportunities to signal (see Fig. 4). In the full model (Table 2), across age and gender categories, the mean predicted probability of paid attempts ranged from 0.27 (90% CI = 0.09 to 0.17) at its highest among men below the median age-split, playing the *aim game* in no prize rounds, to 0.03 (90% CIs = 0.01 to 0.04) at its lowest, among women above the median age-split (i.e. 'older') playing the *search game* in the no prize rounds ($p = 0$; 90% CIs = 0 to 0). Older men also had a near-zero probability of paying to play the *search game* in no prize rounds ($p = 0.01$; CIs: 0 to 0.02).

In most instances (14/16 contrasts), we also saw the expected increases in probability of playing when there was a prize (bracelet)

Table 2
Mean posterior probabilities with 90% confidence intervals of playing any round by game type, pay/prize condition, age and gender.

Condition	Age	Game	p Male	90%CI Male	p Female	90%CI Female
Pay1; Prize1	Younger	Search	0.06	0.04–0.09	0.04	0.02–0.06
Pay1; Prize1	Older	Search	0.04	0.02–0.06	0.03	0.01–0.04
Pay1; Prize1	Younger	Aim	0.13	0.09–0.17	0.09	0.06–0.13
Pay1; Prize1	Older	Aim	0.09	0.05–0.12	0.06	0.03–0.08
Pay1; Prize0	Younger	Search	0.02	0–0.04	0.00	0–0.01
Pay1; Prize0	Older	Search	0.01	0–0.02	0.00	0–0
Pay1; Prize0	Younger	Aim	0.27	0.15–0.39	0.04	0–0.09
Pay1; Prize0	Older	Aim	0.15	0.05–0.25	0.02	0–0.04
Pay0; Prize1	Younger	Search	0.99	0.99–1	0.99	0.98–1
Pay0; Prize1	Older	Search	0.99	0.98–1	0.99	0.97–1
Pay0; Prize1	Younger	Aim	1.00	0.99–1	0.99	0.99–1
Pay0; Prize1	Older	Aim	0.99	0.98–1	0.99	0.98–1
Pay0; Prize0	Younger	Search	0.49	0.41–0.57	0.11	0.07–0.15
Pay0; Prize0	Older	Search	0.46	0.38–0.54	0.10	0.07–0.13
Pay0; Prize0	Younger	Aim	0.62	0.54–0.7	0.18	0.13–0.23
Pay0; Prize0	Older	Aim	0.59	0.51–0.67	0.16	0.11–0.21

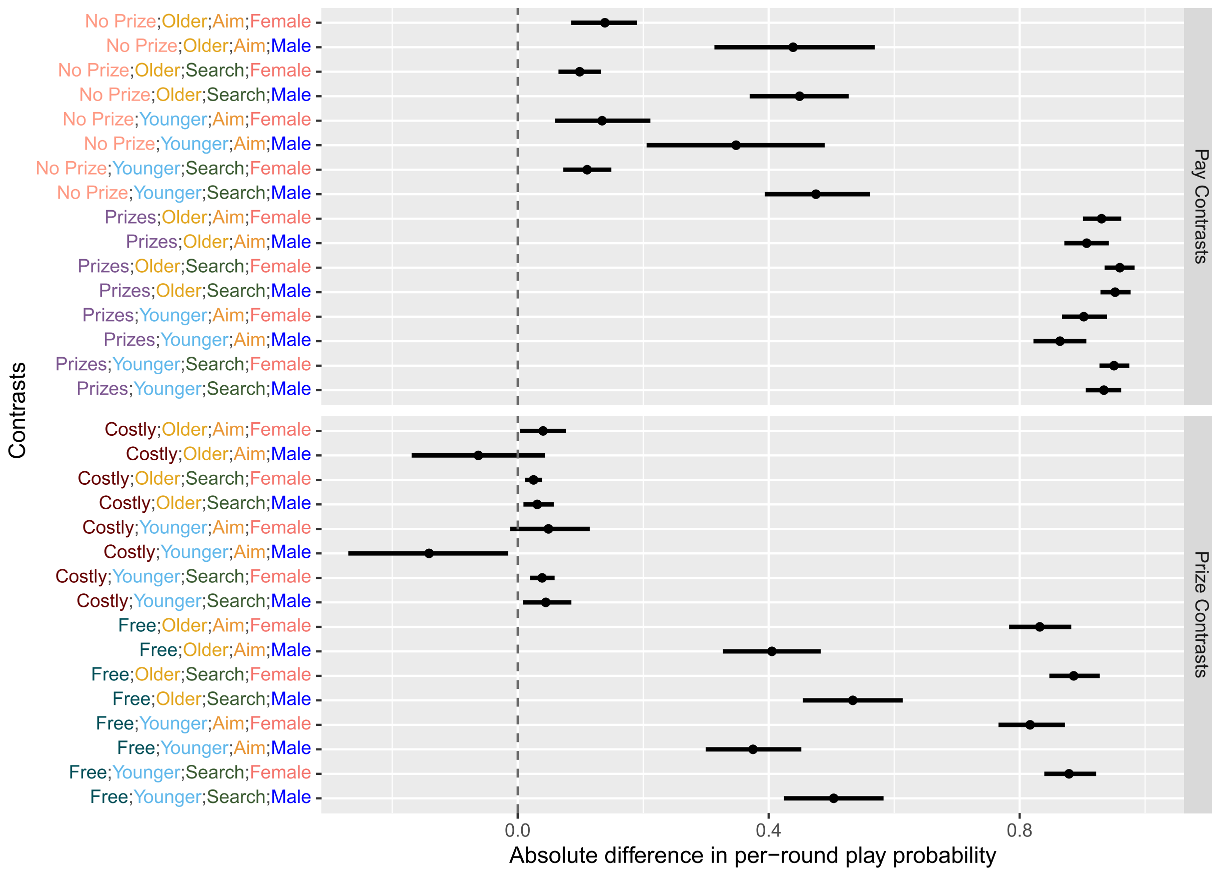

Fig. 3. Bar plots showing absolute difference in probability of playing any given round, moving from costly/paid to free (above) and no prize to prize (below). Points represent mean highest density absolute probability difference; bars represent 90% credibility intervals.

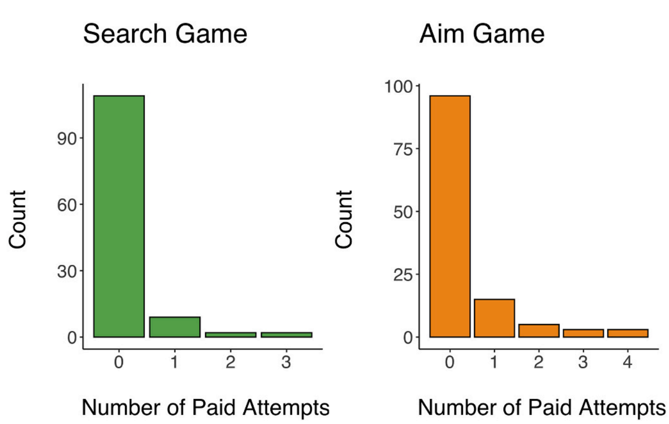

Fig. 4. (A) Raw frequencies of total paid attempts in the *search game*, (B) frequencies of total paid attempts in the *aim game* in the paid condition with prizes.

available (Fig. 3). Absolute probability increases were large in the free conditions, ranging from $p=0.38$ to 0.89. Absolute probability increases were smaller in the pay conditions, though in all but two cases positive, ranging between 0.3 and 0.5, with lower-bound credibility intervals for most contrasts above zero. However, there were two notable and unexpected exceptions: for men playing the *aim game*, the absolute probability of playing decreased in the prize rounds, by -0.14 for younger (<37 years) men (90%CIs: -0.26 to -0.01) and -0.06 for older men (90%CIs: -0.16 to 0.05).

3.3. Are there gender differences in play probabilities?

We next assessed whether men were more likely than women to play, and forgo calories to do so. Models including gender as a predictor were substantially preferred to those excluding gender.

In the full model (see Table 2), in no instances were women more likely to play than men, across game types (hunting/gathering), median age split (i.e., 37 years) categories (younger/older), and conditions (free/paid). In the paid (costly) rounds, men were, in most cases, slightly more likely to play than women (Fig. 6). This was especially true for the *aim game* with absolute gender differences in probabilities of between 0.3 and 0.23, a mean absolute increase of $p=0.11$ (90% CIs -0.01 & 0.26) and few of the contrast distributions crossing zero. Gender difference in absolute play probability for paid rounds in the *search game* were substantially smaller, ranging from $p=0.01$ to 0.2.

In free rounds, there were substantial gender differences in the no prize condition, but few gender differences in the condition with prizes. The probability of playing the free round with prizes was close to 1 across genders with almost no differences between them (Fig. 6). However, for the free, no prize rounds, men in all instances were substantially more likely to play than were women: Here, across ages and game types, in absolute terms, men were between $p=0.36$ and $p=0.44$ more likely to play, and $p=0.4$ (90% CIs 0.31 & 0.49) more likely overall.

3.4. Are younger people more likely to play?

Finally, we explored the impact of age on probability of playing. We modelled age as a binary variable, taking the value ‘older’ for participants with ages above or equal to the median age split of 37 years and ‘younger’ for those below it. The model including age improved upon

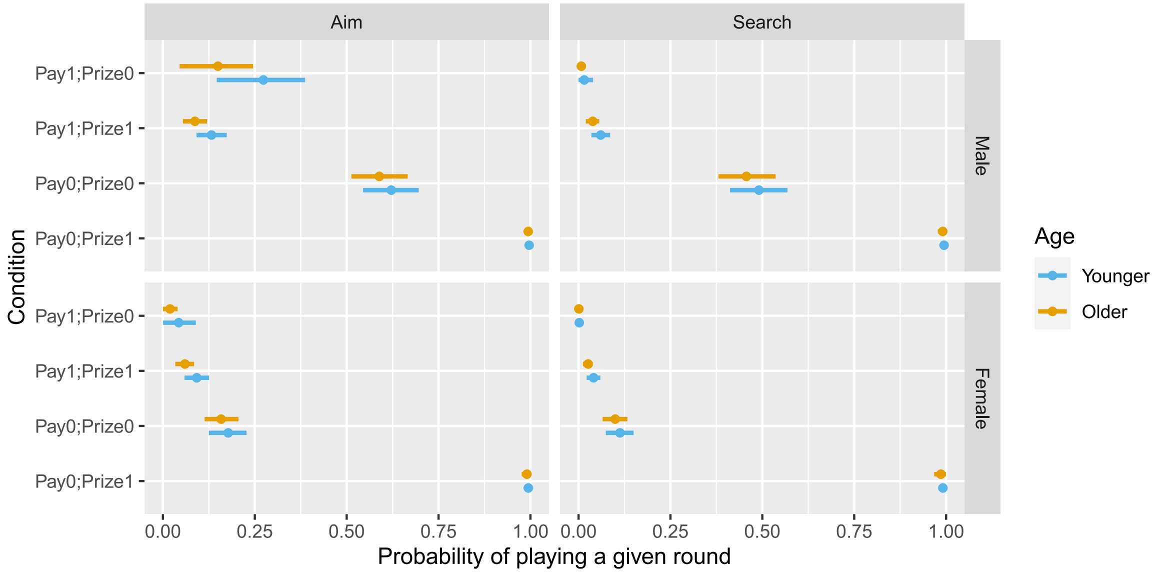

Fig. 5. Bar plots showing mean highest density probabilities for playing one round of either game, with 90% credibility intervals from the full model. Estimates for *aim game* right, *search game* left, men above and women below, with age categories indicated by line color.

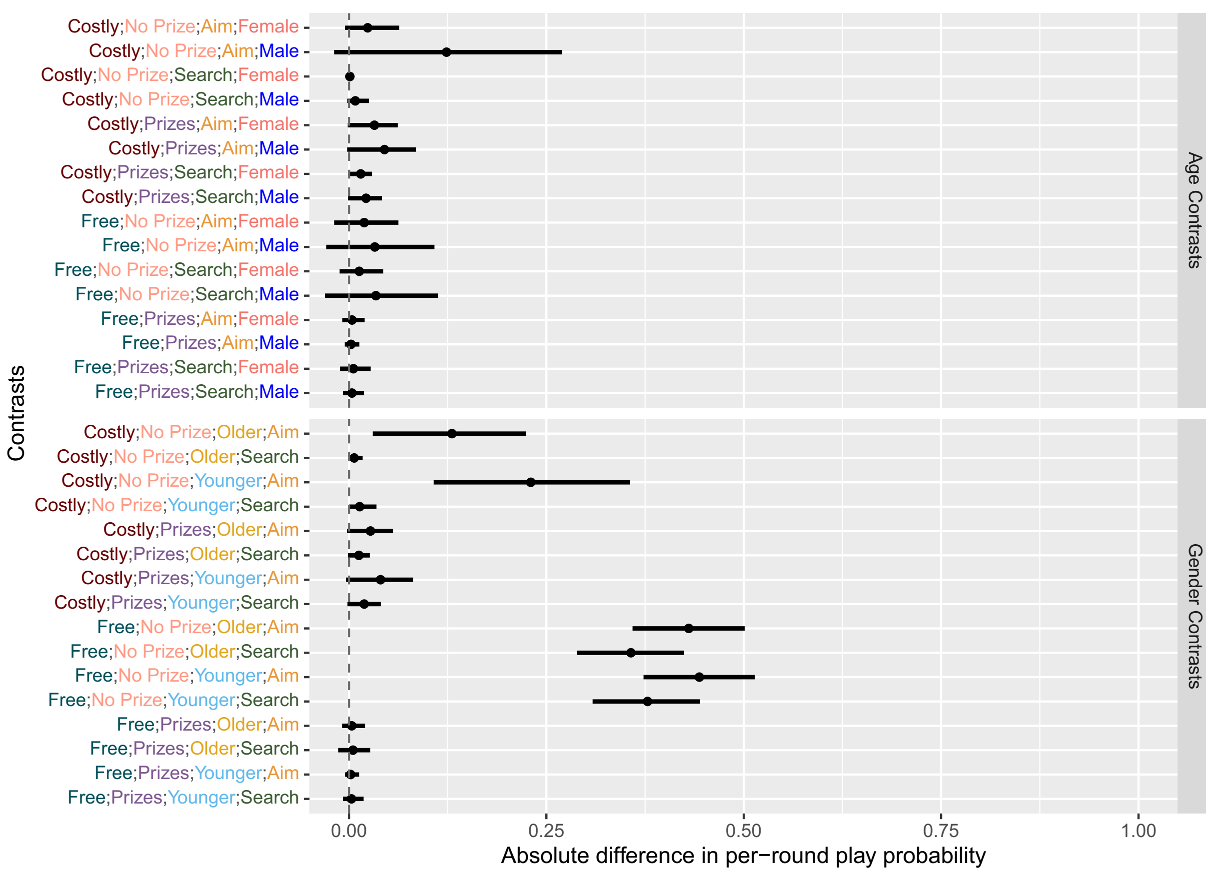

Fig. 6. Bar plots showing absolute difference in probability of playing any given round, moving from older (>37 years) to younger (<37 years; above) and female to male (below). Points represent mean highest density absolute probability difference; bars represent 90% credibility intervals.

the model without it (Table 1); though note that the model without age was allotted a minority of Akaike weight.

In no cases were older people more likely to play than younger people. In most cases, mean probability differences between age categories were close to zero (Fig. 6). However, in all four costly conditions with prizes, younger people showed small but statistically real increases in the absolute probability of playing, ranging between $p = 0.01$ and 0.04 in absolute terms. In several other instances, younger people were also more likely to play, but contrast estimates were wide, and 90% CIs crossed zero.

3.5. Were findings affected by methodological artefacts?

There were several methodological artefacts which had the potential to alter or confound results. These were prize color (whether participants received a green or a red bracelet), game order (whether participants played the aim or search game first) round-number (whether findings resulted from round order effects), and previous round results (whether participants won or lost the previous round). None of these substantively altered the key findings reported in the full model above, however some had an independent effect on play probabilities.

We found that bracelet color had very little impact on play probability, and the mean-only model outperformed the model including prize color in a leave-one-out (LOO) model selection (model weights = 0.69 vs 0.31, ELPD Difference = −0.78). Similarly, the model including game type and game order did not substantially outperform the model including game type only and both were allotted comparable Akaike weight in a leave-one-out model selection (model weights = 0.59 vs 0.41, ELDP Difference = −0.35), indicating little strong effect of game order.

Previous round success did not have a strong influence on play probability. The model excluding previous round win/lose data outperformed the model including the variable in a LOO model selection (weights = 0.6 vs 0.4, ELPD Difference = −0.4). Across, conditions, genders and ages, play-probabilities in rounds with a previous loss were approximately the same as those with a previous win. The only exception was rounds where prize bracelets were available; here, people were marginally more likely to play if they had lost the previous round. However, probability increases were small and estimates substantially overlapped. Fitted model visualisations are provided in the associated 'Experimental Confounds and Artefacts' analysis document.

The model including pay/prize condition and round-number substantially outperformed the model including condition only, and adding round-number substantially improved upon the full model. As expected, each subsequent round decreased probability of playing. Moreover, due to condition-level imbalances in sample size between rounds, condition specific credibility intervals for changed with increasing round number: the uncertainty over the free, prize condition decreases with each round, while the certainty for the pay conditions (which were never round increases). These findings were both the expected byproducts of study design and including round-number in the statistical model did not otherwise substantially alter findings or change study inferences. Fitted model visualisations are provided in the associated 'Experimental Confounds and Artefacts' analysis document.

4. Discussion

4.1. Summary of findings

The current study yields several important findings. In line with expectations, the *aim game* was more popular than the *search game* for men and, contrary to expectations, also for women. As expected, in most cases the conditions with prizes were more popular than the conditions without, often substantially, although this trend did not hold for men playing the *aim game* in the pay condition. Overall, most individuals (74%) of both genders were highly unlikely to forsake caloric resources to play either game. The free rounds were in all cases more popular than the paid rounds, often by a substantial margin. Further, we show clear gender differences in probability of playing, such that men were reliably more likely to play the *aim game* in paid rounds, and substantially more likely to play both games in the free, no prize rounds. Finally, we found small age differences in play probability, such that younger (<37 years) men were more likely to play the *aim game* in paid rounds. We discuss these findings below.

4.2. Costly skill signaling

Anthropologists (e.g., Hawkes et al., 2018; Hawkes & Bird, 2002; Kaplan et al., 1985; Kaplan & Hill, 1985) have asked why, if hunters expect certain food items will be widely redistributed, they pursue such resources in the first place. The costly signaling hypothesis is one proposed solution to this puzzle. Although recent formulations of the costly signaling hypothesis have broadened their scope to consider, for example, the signaling value held by acts without large associated realized costs (Barker et al., 2019; Bird, Ready, & Power, 2018), classic formulations predict that men sacrifice caloric optimality for opportunities to conspicuously show-off elements of hunting prowess (Hawkes et al., 2018, 2014; Hawkes & Bird, 2002).

Evidence for this has been based on cross-sectional data, especially assessments of the costliness of male food acquisition patterns (Hawkes et al., 2018, 2014, 2010). For example, Hawkes et al. (2018) have inferred that, because of the high opportunity costs involved in sharing food (e.g., Hawkes et al., 2014), and the fact that a father's hunting reputation has few positive effects on his child's growth (Blurton Jones, 2016) or spouse's nutrition (see Blurton Jones, 2016; Stibbard-Hawkes et al., 2020), hunting and food-sharing might instead be motivated by mating effort. Although such findings may reasonably be taken as evidence against a strict family provisioning model, they provide less direct support that men are motivated to forsake caloric optimality in order to showing-off (Stibbard-Hawkes, 2019; Stibbard-Hawkes et al., 2020). The present study, by giving individuals an opportunity to forsake calories to show-off skill in a behavioural experiment, attempts to directly assess this tradeoff. Current results do not support the prediction that individuals are *often* willing to sacrifice calories to show-off foraging skills.

Although participants, especially men, were highly likely to participate in the *aim game* when they did not have to pay caloric resources to do so, a substantial majority of individuals in the study (74%), men (66%) and women (81%), opted not to forsake any calories to play either game. This indicates that honey sticks were more valuable than opportunities to show-off skill for most participants of both genders. Given the high value placed on honey by both men and women (Berbesque & Marlowe, 2009), this may be unsurprising. Certainly, it is consistent with the finding that men eat much of the honey they acquire immediately out of camp, instead of showing-off their honey-gathering prowess by bringing it to a central place for later sharing (Berbesque et al., 2016). It further concords with evidence from other small-scale societies showing general unwillingness to risk food resources (e.g., Amir et al., 2020) and is consistent with the fact that, when asked directly about their motivations for hunting and gathering, men and women both ranked family provisioning above signaling as their primary motive (Stibbard-Hawkes et al., 2022).

The focus of both carnival-like games was skill in resource acquisition. The *aim game* was designed to mimic elements of physical coordination, distance-judging and aim, integral to hunting wild animals. The *search game* was similarly designed to test searching efficacy, a skill essential to, for example, ripe berry-gathering, a critical seasonal food source (Marlowe, 2010). Many formulations of the show-off and costly signaling hypothesis have specifically framed hunting and the forsaking of caloric optimality/maximization via sharing as means by which individuals might 'demonstrate their skill' (Hawkes, commenting on Bliege Bird & Bird, 2008) or 'hunting prowess' Hawkes & Bird, 2002). Present findings did not support this notion. Of course, as with any behavioural experiment, ecological validity is a concern, and it is possible that present methods did not capture the skills that people aim to signal. We discuss this further in Section 4.6.

4.3. Gender, risk, competition and signaling

Sex differences in human risk-tolerance and competitiveness have been observed broadly across the evolutionary, psychological and economic sciences (Eckel & Grossman, 2008; Powell & Ansic, 1997; Wilson & Daly, 1985), and findings are typically robust across age (Buser & Niederle, 2014), time (Byrnes, Miller, & Schafer, 1999) and cultural contexts (Charness & Gneezy, 2012; Gray, 2004). Many formulations of the costly signaling hypothesis seek to explain sex differences in resource acquisition (Hawkes et al., 2018; Hawkes & Bird, 2002) and predict sex differences in motivation to show-off (Hawkes, 1991; Hawkes et al., 2018). Some recent work suggests that sex-differences in foraging motivation or risk tolerance may be lower than originally thought (Barker et al., 2019; Mulder & Ross, 2019; Starkweather et al., 2020; Stibbard-Hawkes et al., 2022). The present study provides an opportunity to test this directly by exploring sex difference in willingness to participate and pay a cost to do so.

The aim task involved elements of both risk and competition. In no conditions were women more likely to play than men. Probabilities of playing in the free rounds with prizes were close to one across genders with no gender differences. However, in free rounds without prizes, men were much more likely to play than women (absolute increase in $p = 0.4$; 90% CIs = 0.31 to 0.49). Moreover, in paid rounds, although probability of playing was low for both genders, in the *aim game* men were 8–9 times more likely to exchange resources to participate in paid attempts with no prizes (and 1.5 times more likely with prizes) than were women.

Food items prioritized by men across numerous forager groups have a high risk of daily shortfall (e.g., Gurven & Hill, 2009). A study of resource prioritization in three forager populations (the Ache, Martu and Meriam; Codding et al., 2011) showed that men were willing to take on greatly more risk of failure in pursuit of high-energy resource types than were women, especially when high-energy resources were unreliably attained. Moreover, results are further consistent with research among the Hadza showing strong sex differences both in the proclivity for risk-taking in games of chance (Apicella et al., 2017) and in the motivation to compete (Apicella & Dreber, 2015). Although men and women both found signaling to be important and gave precedence to family provisioning as a self-reported motive for foraging, it is notable that men are more likely to rank signaling as a primary motive than women (Stibbard-Hawkes et al., 2022).

In the current study, guaranteed resources could be exchanged to participate in a game with no guaranteed reward and, for example, success rate on the *aim game* was 15%. While this is substantially higher than daily success rates for Hadza large game hunting (1–3%; Blurton Jones, 2016; Hawkes, 1991), the high failure rate was, perhaps, one reason that so few participants of either sex were willing to forsake resources to participate.

Regardless, present results support the finding that men are generally more willing to take risks (Apicella et al., 2017; Charness & Gneezy, 2012; Gray, 2004; Gurven & Hill, 2009) and adopt risky high variance strategies (Hawkes et al., 2018, p.794), both among small-scale societies and more broadly.

4.4. *Age effects in participation*

Age effects on likelihood of participation were smaller than gender effects, but still notable. In no instances were older participants (i.e., those above the median age split of 37 years) more likely to play than younger participants (i.e., those below). In 12 of 16 contrasts, younger individuals were more likely to play, though in nine cases there was overlap between distributions. The most notable differences between age groups were seen in the paid rounds, especially the *aim games*. Here, for example, men below the median age split (37 years) were close to 1.6 times more likely to forsake calories to participate in the *aim game* than those above (an absolute increase of $p = 0.04$; 90% CIs = 0.0 to 0.09) and over twice as likely in no prize rounds (absolute increase $p = 0.12$; 90% CIs: −0.02 to 0.27).

Hadza women have, in previous studies, listed hunting skill as an important characteristic in prospective marriage partners (Apicella & Crittenden, 2015; Marlowe, 2004). Marlowe (2001, 2010) argues that younger, unmarried Hadza men channel more energy into showing-off to prospective partners than do married men, who prioritize spousal and family provisioning. If skill displays are indeed a form of showing-off to prospective partners (Hawkes et al., 2018), current results are consistent with the notion that younger men prioritize opportunities to advertise their skills relative to older men.

4.5. *Considering generosity signaling*

The tasks in the present study were designed to assess hunting and gathering skill. We did not assess generosity. The notion that sharing and prosocial behaviour mighty yield signaling benefits has a long history, and is the basis of the theories of costly or competitive altruism (Barclay & Willer, 2007; Hardy, 2006; Roberts, 1998; Zahavi, 1995) and indirect reciprocity (Alexander, 1985; Nowak & Sigmund, 1998; Roberts et al., 2021). It is alternatively possible that foraging effort in certain contexts might signal not hunting skill, but some aspect of the sharer's magnanimity or pro-sociality (Gurven, Allen-Arave, et al., 2000; Smith, 2004; Smith & Bird, 2000) and this idea is considered explicitly in the earliest literature on the show-off hypothesis (Hawkes, 1991). Some work on hunting and costly signaling (Bliege Bird & Bird, 2008; Bliege Bird & Power, 2015) has brought these predictions to the fore, highlighting the value of hunting, food-sharing and 'disengagement from property' as a signal of generosity or magnanimity. Our experimental games provided opportunities to signal elements of foraging skill only. Present findings do not show whether individuals are willing to forsake calories to demonstrate their generosity (see Bliege Bird & Bird, 2008; Bliege Bird & Power, 2015; Stibbard-Hawkes, 2019). Indeed, although people were unwilling to forsake honey sticks to participate in foraging skill games, we noticed individuals of both genders sharing the honey sticks they had acquired once the game had concluded. Unfortunately, we were unable to measure or further report on secondary-sharing patterns (sensu Wiessner, 2009).

Investigating generosity-signaling could be a fruitful avenue for further research. Public economic and allocation games, where people can donate resources without remuneration, have often been used among the Hadza to assess generosity (e.g., Marlowe, Apicella, & Reed, 2005; Smith, Larroucau, Mabulla, & Apicella, 2018; Stagnaro et al., 2022). Such studies often show that people willingly donate resources to others for little personal gain. In a 2005 Hadza study, modal offers in a dyadic 'dictator' game using cash, at 10%, were low relative to other populations (Marlowe et al., 2005) although only a minority (<20%) of individuals donated nothing. Moreover, when honey sticks were used in a public goods game, which is more similar to real-world patterns of food-sharing than dyadic cash transfers, mean voluntary donations to the public good were often close to or higher than 50% (e.g., a mean of 2.3/4, 1.7/4, 2.5/4 and 2.2/4 honey sticks donated in 2010, 2013, 2014 and 2016 public goods games respectively; Smith et al., 2018).

Conversely, there is little agreement between individuals when ranking other's reputations for generosity (Smith & Apicella, 2019), and only minor benefit to being percieved as generous in the context of resource sharing (Smith, Mabulla, & Apicella, 2022). Moreover, most Hadza do not state a preference for living with people who are more generous (Apicella et al., 2012; Smith & Apicella, 2019) instead preferring better foragers as camp mates (see Smith & Apicella, 2019; Wood, 2006). It may be that strong redistributive norms (see Hawkes et al., 2018) render generosity a relatively unimportant trait.

It would yet be enlightening to conduct a public goods game where people are given the choice between participating in a skill signaling opportunity or donating resources to others. Currently it is simply notable that, although in this study people were unwilling to forsake resources to show-off, participants in previous studies were willing to anonymously donate a greater proportion of comparable resources to the public good in exchange for no reward or recognition. Moreover, while present findings are at odds with skill signaling models of hunting motive, they are not inconsistent with generosity signaling.

4.6. Study limitations

The present investigation had several limitations. First is the relevance of signaling opportunities. Both tasks required hunting/gathering-relevant skills including aim, dexterity, and hand-eye coordination. Moreover, we presented these games to participants as '*the hunting game*' and '*the gathering game*' and made clear that games aimed to simulate these aptitudes. It is yet possible, even were food sharing motivated by a desire to show-off elements of foraging skill, that neither of the games captured those specific skills that individuals seek to advertise. It has, for example, been proposed that hunting might depend on resource location knowledge (Smith & Bliege Bird, 2005) or stealthy movement (Blurton Jones, 2016; Stibbard-Hawkes et al., 2018). Moreover, hunting and honey collection carry risk of injury (Marlowe, 2010; Wood et al., 2014) and participation in these tasks might plausibly signal physical risk tolerance. Neither game tested these attributes. Moreover, although both games required elements of luck mediated by skill, the search game required more luck (due to the random placement of the black bead) and may have been less popular for this reason.

To address this issue, it would be plausible to conduct a variant of this experiment using different tasks. Deciding upon an alternative task is, however, difficult. Some authors have provided general predictions concerning the signaling value of hunting in certain circumstances e.g., 'vigor, intelligence, economic productivity, and/or fighting ability' (Smith, 2004, p.353) or 'ethological knowledge, visual acuity [or] stamina' (Smith & Bliege Bird, 2005). However, predictions vary between sources and ethnographic contexts, and often authors discuss 'hunting prowess' in broad terms (see Stibbard-Hawkes, 2019). Without more specific predictions, empirical investigations into the signaling motivations of foragers will continue to encounter difficulties.

Relatedly, it is plausible that tasks lacked ecological validity. Although both games involved skills relevant to real-life foraging, under experimental conditions it was not possible to provide an exact test of the skills required for either hunting or gathering. It is possible, for example, that both sexes were more likely to play the 'aim' game not because of the underlying set of skills it represented, but simply because it was more engaging. Future research could address this by using more naturalistic tasks - for example an archery contest in lieu of a dart throwing contest, or a digging task contest in lieu of the search task — though such tasks would require substantially more time and energy investment from participants.

Second, as fieldwork is conducted outside in an environment with few buildings or other private locations, and due to the attention generated by both games, it was not possible to exclude onlookers. Rather than being a strict limitation, the presence of onlookers in fact ensured that camp members were aware which bracelet color corresponded with which game. Furthermore, the excitement generated by the free round of both games indicates that the reason people were unwilling to pay for extra opportunities to play was not because the games weren't enjoyable. However, we could not, for example, control audience size and composition. Moreover, by necessity, the study audience also included two researchers. There may be unaccounted for motives to impress the data collectors with skill (even when there are no prize) alongside potential social payoffs among co-resident camp members for spending time with potentially high-status extra-community individuals. Unmeasured observer effects may account for the unexpected finding that for aim games, men were slightly more likely to play in paid no prize rounds than in paid rounds with prizes.

Third, there were sample-size imbalances between conditions. We ran many more paid rounds with prizes (976), than either free rounds without prizes (526), paid rounds without prizes (264) and free rounds with prizes (244). This was deliberate. Our total sample size was limited. The paid round with prizes (i.e., costs and signals) were not only the most theoretically important condition but were also zero inflated and so more difficult to estimate. As estimates between pay-prize conditions were, in most cases, non-overlapping (Fig. 3) this does not represent a severe limitation, but it yet merits consideration.

Last, we altered study conditions (prize/pay structure) at the camp level. This was a necessity of the study design - for signaling to occur we required all camp member to know and understand the rules of and rewards for both games. However, it means that we could not control for camp-level differences in sharing norms, reported elsewhere (e.g. Gurven et al., 2008) nor easily control for other camp level effects (e.g. camp size, composition. Due to high levels of residential mixing (Marlowe, 2010; Smith et al., 2018), this is probably less of an issue than among more sedentary populations (Gurven et al., 2008), although in light of evidence cooperative assortment (Smith et al., 2018), it yet represents a concern.

Relatedly, we did not measure individual food access or camp-level foraging returns during the study period. It is possible that camp-level differences in food availability and/or subsistence activities created uncontrolled variation in willingness to forsake calories to play the games. Our choice of food item, honey sticks, somewhat addresses this concern. Honey is the favourite food of both genders (Berbesque & Marlowe, 2009), and is often eaten in extremely large quantities with a very high upper limit for satiation (e.g. a mean 3582 kcal and an upper range of 20,776 kcal per foray Berbesque et al., 2016). For this reason, we expect that satiation is not a severe concern in this study, yet this is still a notable limitation.

4.7. Conclusions

The current study found that, while men were more willing to exchange caloric resources for opportunities to 'show off' in a game of hunting skill than were women (see Hawkes et al., 2018), this was only a relative difference. Overall, few individuals of either gender willingly traded calories to exhibit their skill, and caloric maximization was more important than skill signaling. These result match Hadza self-report data showing that, while skill signaling was important for both genders, and slightly more important for men, it was universally less important than family provisioning (Stibbard-Hawkes et al., 2022). While some studies of signaling have employed both paired choices (Bishop, 2019; Wood & Hill, 2000), and ranking tasks (Bishop, In press; Stibbard-Hawkes et al., 2018), this study is, to our knowledge, the first time that these the choice between caloric optimality and skill-signaling has been tested in a controlled, incentivised, behavioural experiment.

Although success in both games required important hunting and gathering-related skills, it is possible that neither game required proficiencies that individuals were motivated to signal and didn't represent ecologically valid or valued signaling opportunities. For instance, it is yet possible that people are motivated to advertise generosity or magnanimity (Barker et al., 2019; Bliege Bird & Bird, 2008) and the current study did not address this directly. If hunting and the forsaking of calories via food-sharing are indeed motivated by skill signaling concerns, then clearer, operational predictions are needed regarding the exact skills or attributes being signaled. If costly skill signaling theories are to be tested further, predictions about precise the nature of signaled aptitudes (e.g., see Bishop, in press, this issue) are vital.

Among those who did choose to forsake calories to play the signaling games, results were more consistent with predictions of the show-off model (Hawkes et al., 2018), especially the finding that men are more likely to forsake calories for opportunities to signal hunting skill. The age differences observed in the probability of paying to play were also notable and consistent with the notion that young, unmarried men channel more energy into signaling effort than do older men (Marlowe, 2010).

However, despite the clear sex and age differences in likelihood of participation in games, this study finds that calories were in most cases not worth exchanging for opportunities to show-off, at least in the context of the current experiment. There was great demand for honey but, where there was a caloric cost to play, relatively little demand for skill signaling.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Alexander, R. D. (1985). A biological interpretation of moral systems. *Zygon, 20*, 3–20. https://doi.org/10.1111/j.1467-9744.1985.tb00574.x

Allen-Arave, W., Gurven, M., & Hill, K. (2008). Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an ache reservation. *Evolution and Human Behavior, 29*, 305–318. https://doi.org/10.1016/j.evolhumbehav.2008.03.002

Amir, D., Jordan, M. R., Mcauliffe, K., Valeggia, C. R., Sugiyama, L. S., Bribiescas, R. G., … Dunham, Y. (2020). The developmental origins of risk and time preferences across diverse societies. *Journal of Experimental Psychology: General, 149*, 650–661.

Apicella, C. L. (2014). Upper-body strength predicts hunting reputation and reproductive success in Hadza hunter-gatherers. *Evolution and Human Behavior, 35*, 508–518. https://doi.org/10.1016/j.evolhumbehav.2014.07.001

Apicella, C. L., & Crittenden, A. N. (2015). Hunter-gatherer families and parenting. In D. M. Buss (Ed.), *The handbook of evolutionary psychology chapter 23* (pp. 578–597). New York: Wiley Online Library.

Apicella, C. L., Crittenden, A. N., & Tobolsky, V. A. (2017). Evolution and human behavior hunter-gatherer males are more risk-seeking than females, even in late childhood. *Evolution and Human Behavior, 38*, 592–603.

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. https://doi.org/10.1007/s40750-014-0015-z

Apicella, C. L., Marlowe, F. W., Fowler, J. H., & Christakis, N. A. (2012). Social networks and cooperation in hunter-gatherers. *Nature, 481*, 497–501.

Barclay, P., & Willer, R. (2007). Partner choice creates competitive altruism in humans. *Proceedings of the Royal Society B: Biological Sciences, 274*, 749–753. https://doi.org/10.1098/rspb.2006.0209

Barker, J. L., Power, E. A., Heap, S., Puurtinen, M., & Sosis, R. (2019). Content, cost, and context: A framework for understanding human signaling systems. *Evolutionary Anthropology, 28*, 86–99. https://doi.org/10.1002/evan.21768

Bennett, F. J., Barnicot, N. A., Woodburn, J. C., Pereira, M. S., & Henderson, B. E. (1973). Studies on viral, bacterial, rickettsial and treponemal diseases in the Hadza of Tanzania and a note on injuries. *Human Biology, 45*, 243–272.

Berbesque, J., & Marlowe, F. W. (2009). Sex differences in food preferences of Hadza hunter-gatherers. *Evolutionary Psychology, 7*, 601–616.

Berbesque, J. C., Wood, B. M., Crittenden, A. N., Mabulla, A., & Marlowe, F. W. (2016). Eat first, share later: Hadza hunter-gatherer men consume more while foraging than in central places. *Evolution and Human Behavior, 37*, 1–6. https://doi.org/10.1016/j.evolhumbehav.2016.01.003

Bird, R. (1999). Cooperation and conflict: The behavioral ecology of the sexual division of labor. *Evolutionary Anthropology, 8*, 65–75. https://doi.org/10.1002/(SICI)1520-6505(1999)8:2<65::AID-EVAN5>3.0.CO;2-3

Bird, R. B., Ready, E., & Power, E. A. (2018). The social significance of subtle signals. *Nature Human Behaviour, 2*, 452–457. https://doi.org/10.1038/s41562-018-0298-3

Bishop, A. (2019). *Costly signaling and prey choice: The signaling value of hunted game*. Ph. D. thesis. Arizona State University.

Bishop, A. (in press). What does prey harvest composition signal to a social audience?: Experimental studies with Aché hunter-gatherers of paraguay. Evolution and Human Behavior. doi:10.1016/j.evolhumbehav.2022.10.001. In press.

Bliege Bird, R., & Bird, D. W. (2008). Why women hunt: Risk and contemporary foraging in a Western Desert aboriginal community. *Current Anthropology, 49*, 655–693. https://doi.org/10.1086/587700

Bliege Bird, R., & Power, E. A. (2015). Prosocial signaling and cooperation among Martu hunters. *Evolution and Human Behavior, 36*, 389–397. https://doi.org/10.1016/j.evolhumbehav.2015.02.003

Blurton Jones, N. G. (1991). Tolerated theft suggestions about the ecology and evolution of sharing, hoarding, and scrounging. In G. Schubert, & R. D. Masters (Eds.), *Primate politics chapter 7* (1st ed., pp. 170–206). Carbondale: Southern Illinois University Press.

Blurton Jones, N. G. (2016). *Demography and evolutionary ecology of Hadza hunter-gatherers*. Cambridge: Cambridge University Press.

Blurton-Jones, N. G., & Marlowe, F. W. (2002). Selection for delayed maturity. *Human Nature, 13*, 199–238.

Brown, J. K. (1970). A note on the division of labour by sex. *American Anthropologist, 72*, 1073–1078.

Burkner, P.-C. (2017). BRMs: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software, 80*, 1–28.

Buser, T., & Niederle, M. (2014). Gender, competitiveness and career choices. *The Quarterly Journal of Economics, 29*, 1409–1447.

Byrnes, J. P., Miller, D. C., & Schafer, W. D. (1999). Gender differences in risk taking: A meta-analysis. *Psychological Bulletin, 125*, 367–383. https://doi.org/10.1037/0033-2909.125.3.367

Cashdan, E. A. (1985). Coping with risk: Reciprocity among the Basarwa of northern Botswana. *Man, 20*, 454–474. https://doi.org/10.2307/2802441

Charness, G., & Gneezy, U. (2012). Strong evidence for gender differences in risk taking. *Journal of Economic Behavior and Organization, 83*, 50–58. https://doi.org/10.1016/j.jebo.2011.06.007

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 B: Biological Sciences, 278*, 2502–2509. https://doi.org/10.1098/rspb.2010.2403

Crittenden, A. N. (2011). The importance of honey consumption in human evolution. *Food and Foodways, 19*, 257–273. https://doi.org/10.1080/07409710.2011.630618

Crittenden, A. N. (2016). Ethnobotany in evolutionary perspective: Wild plants in diet composition and daily use among Hadza hunter-gatherers. In K. Hardy, & L. Kubiak-Martens (Eds.), *Wild harvest: Plants in the hominin and pre-agrarian human worlds chapter 16* (pp. 319–339). Oxford: Oxbow Books.

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. https://doi.org/10.1016/j.evolhumbehav.2013.04.004

Damas, D. (1972). University of Pittsburgh-of the commonwealth system of higher education central Eskimo systems of food sharing. *Source: Ethnology, 11*, 220–240.

Demps, K. E. (2019). *Dynamics of social learning: Socialization into a honey-collecting tribe and the ecology of cultural knowledge transmission*. Ph.D. thesis. University of California Davis.

Dowling, J. H. (1968). Individual ownership and the sharing of game in hunting societies. *American Anthropologist, 70*, 502–507. URL: http://doi.wiley.com/10.1525/aa.1968.70.3.02a00040 https://doi.org/10.1525/aa.1968.70.3.02a00040.

Eckel, C. C., & Grossman, P. J. (2008). Men, women and risk aversion: Experimental evidence. *Handbook of Experimental Economics Results, 1*, 1061–1073. https://doi.org/10.1016/S1574-0722(07)00113-8

Gray, P. B. (2004). Evolutionary and cross-cultural perspectives on gambling. *Journal of Gambling Studies, 20*, 347–371. https://doi.org/10.1007/s10899-004-4579-6

Gurven, M. (2004). To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences, 27*, 543–583.

Gurven, 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*, 263–282. https://doi.org/10.5840/filmphil2012163

Gurven, M., & Hill, K. (2009). Why do men hunt? *Current Anthropology, 50*, 51–74. https://doi.org/10.1086/595620

Gurven, M., & Hill, K. (2010). Moving beyond stereotypes of men's foraging goals: Reply to hawkes, o'connell, and coxworth. *Current Anthropology, 51*, 265–267. https://doi.org/10.1086/651291

Gurven, M., Hill, K., Kaplan, H., Hurtado, A., & Lyles, R. (2000). Food transfers among Hiwi foragers of Venezuela: Tests of reciprocity. *Human Ecology, 28*, 171–218.

Gurven, M., & von Rueden, C. (2006). Hunting, social status and biological fitness. *Social Biology, 53*, 81–99. https://doi.org/10.1080/19485565.2006.9989118

Gurven, M., Zanolini, A., & Schniter, E. (2008). Culture sometimes matters: Intra-cultural variation in pro-social behavior among Tsimane Amerindians. *Journal of Economic Behavior and Organization, 67*, 587–607. https://doi.org/10.1016/j.jebo.2007.09.005

Hardy, C. L. (2006). Nice guys finish first: The competitive altruism hypothesis. *Personality and Social Psychology Bulletin, 32*, 1402–1413. URL: http://psp.sagepub.com/cgi/doi/10.1177/0146167206291006 https://doi.org/10.1177/0146167206291006.

Hawkes, K. (1991). Showing off. *Ethology and Sociobiology, 12*, 29–54. URL: http://linkinghub.elsevier.com/retrieve/pii/016230959190011E https://doi.org/10.1016/0162-3095(91)90011-E.

Hawkes, K., & Bird, R. B. (2002). Showing off, handicap signaling, and the evolution of Men's work. *Evolutionary Anthropology, 11*, 58–67.

Hawkes, K., O'Connell, J., & Blurton Jones, N. (2018). Hunter-gatherer studies and human evolution: A very selective review. *American Journal of Physical Anthropology, 165*, 777–800. https://doi.org/10.1002/ajpa.23403

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1991). Hunting income patterns among the Hadza: Big game, common goods, foraging goals and the evolution of the human diet. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 334*. https://doi.org/10.1098/rstb.1991.0113, 243–250; discussion 250–251.

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (2001). Hunting and nuclear families: Some lessons from the Hadza about men's work. *Current Anthropology, 42*, 681–709. https://doi.org/10.1086/322559

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (2014). More lessons from the Hadza about men's work. *Human Nature, 25*, 596–619. https://doi.org/10.1007/s12110-014-9212-5

Hawkes, K., O'Connell, J. F., & Coxworth, J. E. (2010). Family provisioning is not the only reason men hunt. *Current Anthropology, 51*, 259–264. https://doi.org/10.1086/651074

Hawkes, K., Rogers, A. R., & Charnov, E. L. (1995). The male's dilemma: Increased offspring production is more paternity to steal. *Evolutionary Ecology, 9*, 662–677. URL:.

Henrich, J., Boyd, R., Bowles, S., Camerer, C. F., Fehr, E., Gintis, H., … Tracer, D. (2005). "economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences, 28*, 795–815. discussion 815–55. https://doi.org/10.1017/S0140525X05000142

Hill, K., & Hurtado, A. M. (1996). *Ache life history: The ecology and demography of a foraging people*. Hawthorne: Aldine de Gruyter.

Hill, K., & Hurtado, A. M. (2009). Cooperative breeding in south American hunter-gatherers. *Proceedings of the Royal Society B: Biological Sciences, 276*, 3863–3870.

Hill, K., Kaplan, H., & Hawkes, K. (1993). On why male foragers hunt and share food. *Current Anthropology, 34*, 701. https://doi.org/10.1086/204213

Hill, K. R., Walker, R. S., Bozicević, M., Eder, J., Headland, T., Hewlett, B., … Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science (New York, N.Y.), 331*, 1286–1289. https://doi.org/10.1126/science.1199071

Hooper, P. L., Demps, K., Gurven, M., Gerkey, D., & Kaplan, H. S. (2015). Skills, division of labour and economies of scale among Amazonian hunters and south Indian honey collectors. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 370*. https://doi.org/10.1098/rstb.2015.0008

Hurtado, A. M., Hawkes, K., Hill, K., & Kaplan, H. (1985). Female subsistence strategies among ache hunter-gatherers of eastern Paraguay. *Human Ecology, 13*, 1–28. https://doi.org/10.1007/BF01531086

Hurtado, A. M., Hill, K., Hurtado, I., & Kaplan, H. (1992). Trade-offs between female food acquisition and child care among hiwi and ache foragers. *Human Nature, 3*, 185–216. https://doi.org/10.1007/BF02692239

Jochim, M. A. (1988). Optimal foraging and the division of labor. *American Anthropologist, 90*, 130–136. https://doi.org/10.1525/aa.1988.90.1.02a00100

Kaplan, H., & Gurven, M. (2005). The natural history of human food sharing and cooperation: A review and a new Milti-individual approach to the negotiation of norms. In H. Gintis, S. Bowles, R. Boyd, & E. Fehr (Eds.), *Moral sentiments and material interests chapter 3* (1st ed., p. 404). London: MIT Press. https://doi.org/10.1007/s10997-007-9032-7. URL: http://www.anth.ucsb.edu/faculty/gurven/papers/kaplangurvensharing.pdf.

Kaplan, H., & Hill, K. (1985). Hunting ability and reproductive success among male ache foragers: Preliminary results. *Current Anthropology, 26*, 131–133.

Kaplan, H., Hill, K., & Cadeliña, R. (1985). Food sharing among ache foragers - tests of explanatory hypothesis. *Current Anthropology, 26*, 223–233.

Kaplan, H. S., Schniter, E., Smith, V. L., & Wilson, B. J. (2012). Risk and the evolution of human exchange. *Proceedings of the Royal Society B: Biological Sciences, 279*, 2930–2935. https://doi.org/10.1098/rspb.2011.2614

Kaplan, H. S., Schniter, E., Smith, V. L., & Wilson, B. J. (2018). Experimental tests of the tolerated theft and risk-reduction theories of resource exchange. *Nature Human Behaviour, 2*, 383–388. URL: https://doi.org/10.1038/s41562-018-0356-x https://doi.org/10.1038/s41562-018-0356-x.

Kent, S. (1993). Sharing in an egalitarian kalahari community. *Man, 28*, 479–514.

Kraft, T. S., Venkataraman, V. V., & Dominy, N. J. (2014). A natural history of human tree climbing. *Journal of Human Evolution, 71*, 105–118. https://doi.org/10.1016/j.jhevol.2014.02.002

Kraft, T. S., Venkataraman, V. V., Tacey, I., Dominy, N. J., & Endicott, K. M. (2019). Foraging performance, Prosociality, and kin presence do not predict lifetime reproductive success in Batek hunter-gatherers. *Human Nature, 30*, 71–97. https://doi.org/10.1007/s12110-018-9334-2

Lancaster, J. B., & Lancaster, C. B. (1987). The watershed: Change in parental-investment and family-formation strategies in the course of human evolution. In J. B. Lancaster, J. Altmann, A. S. Rossi, & L. Sherrod (Eds.), *Parenting across the life span: Biosocial dimensions chapter 7* (1st ed., pp. 187–205). New York: Aldine de Gruyter.

Lee, R. B. (1979). *The !Kung san: Men, women, and work in a foraging society* (1st ed.). Cambridge: Cambridge University Press.

Lovejoy, C. O. (1981). The origin of man. *Science, 211*, 341–350.

Marlowe, F. W. (2001). Male contribution to diet and female reproductive success among foragers. *Current Anthropology, 42*, 755–760.

Marlowe, F. W. (2004). Mate preferences among Hadza hunter-gatherers. *Human Nature, 15*, 365–376.

Marlowe, F. W. (2005). Dictators and ultimatums in an egalitarian society of hunter-gatherers: The Hadza of Tanzania. In J. Henrich, R. Boyd, S. Bowles, C. Camerer, E. Fehr, & H. Gintis (Eds.), *Foundations of human sociality: Economic experiments and ethnographic evidence from fifteen small-scale societies* (1st ed., pp. 167–192). Oxford: Oxford University Press. https://doi.org/10.1093/0199262055.003.0006 (arXiv: arXiv:1011.1669v3).

Marlowe, F. W. (2007). Hunting and gathering: The human sexual division of foraging labor. *Cross-Cultural Research, 41*, 170–195. https://doi.org/10.1177/1069397106297529

Marlowe, F. W. (2010). *The Hadza: Hunter-gatherers of Tanzania*. Los Angeles: University of California Press.

Marlowe, F. W., Apicella, C., & Reed, D. (2005). Men's preferences for women's profile waist-to-hip ratio in two societies. *Evolution and Human Behavior, 26*, 458–468. https://doi.org/10.1016/j.evolhumbehav.2005.07.005

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.

Milton, K. (2003). The critical role played by animal source foods in human (Homo) evolution. *Journal of Nutrition, 133*, 3875–3878. https://doi.org/10.1093/jn/133.11.3886s. URL: https://academic.oup.com/jn/article/133/11/3886S/4818038.

Mulder, M. B., & Ross, C. T. (2019). Unpacking mating success and testing Bateman's principles in a human population. *Proceedings of the Royal Society B: Biological Sciences, 286*. https://doi.org/10.1098/rspb.2019.1516

Nowak, M. A., & Sigmund, K. (1998). Evolution of indirect reciprocity by image scoring/the dynamics of indirect reciprocity. *Nature, 393*, 573–577.

Peterson, N. (1993). Demand sharing: Reciprocity and the pressure for generosity among foragers. *American Anthropologist, 95*, 860–874.

Powell, M., & Ansic, D. (1997). *Gender differences in risk behaviour in financial decision-making*.

Roberts, G. (1998). Competitive altruism: From reciprocity to the handicap principle. *Proceedings of the Royal Society, 265*, 427–431. URL: http://rspb.royalsocietypublishing.org/content/265/1394/427.short.

Roberts, G., Raihani, N., Bshary, R., Manrique, H. M., Farina, A., Samu, F., & Barclay, P. (2021). The benefits of being seen to help others: Indirect reciprocity and reputation-based partner choice. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 376*, 1–10. https://doi.org/10.1098/rstb.2020.0290

von Rueden, C., Gurven, M., & Kaplan, H. (2008). The multiple dimensions of male social status in an Amazonian society. *Evolution and Human Behavior, 29*, 402–415. https://doi.org/10.1016/j.evolhumbehav.2008.05.001. arXiv:NIHMS150003.

Sahlins, M., Graeber, D., Sahlins, M., & Graeber, D. (1972). On the sociology of primitive exchange. In *Stone age economics* (pp. 168–258). London: Routledge. https://doi.org/10.4324/9781315184951-5.

Smith, D., Dyble, M., Major, K., Page, A. E., Chaudhary, N., Salali, G. D., … Mace, R. (2019). A friend in need is a friend indeed: Need-based sharing, rather than cooperative assortment, predicts experimental resource transfers among Agta hunter-gatherers. *Evolution and Human Behavior, 40*, 82–89.

Smith, E. A. (1985). Inuit foraging groups: Some simple models incorporating conflicts of interest, relatedness, and central-place sharing. *Ethology and Sociobiology, 6*, 27–47. https://doi.org/10.1016/0162-3095(85)90039-1

Smith, E. A. (2004). Why do good hunters have higher reproductive success? *Human Nature, 15*, 343–364. https://doi.org/10.1007/s12110-004-1013-9

Smith, E. A., & Bird, R. (2000). Turtle hunting and tombstone opening: Public generosity as costly signaling. *Evolution and Human Behavior, 21*, 245–261.

Smith, E. A., & Bliege Bird, R. (2005). Costly signaling and cooperative behavior. In H. Gintis, S. Bowles, R. Boyd, & E. Fehr (Eds.), *Moral sentiments and material interests: On the foundations of cooperation in economic life chapter 4* (pp. 115–148). Cambridge: MIT Press. https://doi.org/10.1525/aa.2007.109.2.380.

Smith, K. M., & Apicella, C. L. (2019). Hadza hunter-gatherers disagree on perceptions of Moral character. *Social Psychological and Personality Science*. https://doi.org/10.1177/1948550619865051

Smith, K. M., & Apicella, C. L. (2020). Partner choice in human evolution: The role of cooperation, foraging ability, and culture in Hadza campmate preferences. *Evolution and Human Behavior, 41*, 354–366. https://doi.org/10.1016/j.evolhumbehav.2020.07.009

Smith, K. M., Larroucau, T., Mabulla, I. A., & Apicella, C. L. (2018). Hunter-gatherers maintain Assortativity in cooperation despite high levels of residential change and mixing. *Current Biology, 28*, 3152–3157.e4. https://doi.org/10.1016/j.cub.2018.07.064

Smith, K. M., Mabulla, I. A., & Apicella, C. L. (2022). Hadza hunter-gatherers with greater exposure to other cultures share more with generous campmates. *Biology Letters, 18*(7), 20220157. https://doi.org/10.1098/rsbl.2022.0157

Stagnaro, M. N., Stibbard-Hawkes, D. N., & Apicella, C. L. (2022). Do religious and market-based institutions promote cooperation in Hadza hunter-gatherers? *Religion, Brain and Behavior, 12*, 171–189. https://doi.org/10.1080/2153599X.2021.2006293

Starkweather, K. E., Shenk, M. K., & McElreath, R. (2020). Biological constraints and socioecological influences on women's pursuit of risk and the sexual division of labour. *Evolutionary Human Sciences, 2*, 17. https://doi.org/10.1017/ehs.2020.60

Stibbard-Hawkes, D. N. (2019). Costly signaling and the handicap principle in hunter-gatherer research: A critical review. *Evolutionary Anthropology, 28*, 144–157. https://doi.org/10.1002/evan.21767

Stibbard-Hawkes, D. N., & Attenborough, R. D. (2021). Some omissions, few confusions. A reply to Pinheiro 2021. *American Journal of Physical Anthropology, 174*, 392–395. https://doi.org/10.1002/ajpa.24223

Stibbard-Hawkes, D. N., Attenborough, R. D., Mabulla, I. A., & Marlowe, F. W. (2020). To the hunter go the spoils? No evidence of nutritional benefit to being or marrying a well-reputed Hadza hunter. *American Journal of Physical Anthropology, 173*, 61–79. https://doi.org/10.1002/ajpa.24027

Stibbard-Hawkes, D. N., Attenborough, R. D., & Marlowe, F. W. (2018). A Noisy signal: To what extent are Hadza hunting reputations predictive of actual hunting skills? *Evolution and Human Behavior, 39*, 639–651. https://doi.org/10.1016/j.evolhumbehav.2018.06.005

Stibbard-Hawkes, D. N., Smith, K. M., & Apicella, C. L. (2022). Why hunt? Why gather? Why share? Hadza assessments of foraging and food-sharing motive. *Evolution and Human Behavior, 43*, 257–272.

Tennie, C., Gilby, I. C., & Mundry, R. (2009). The meat-scrap hypothesis: Small quantities of meat may promote cooperative hunting in wild chimpanzees Pan troglodytes. *Behavioral Ecology and Sociobiology, 63*, 421–431.

Testart, A. (1987). Game sharing systems and kinship systems among hunter-gatherers. *Man, 22*, 287. https://doi.org/10.2307/2802866

Washburn, S., & Lancaster, C. (1968). The evolution of hunting. In R. B. Lee, & I. DeVore (Eds.), *Man the hunter* (2nd ed., pp. 293–303). Chicago: Aldine Publishing Company.

Watts, D. P. (2020). Meat eating by nonhuman primates: A review and synthesis. *Journal of Human Evolution, 149*. https://doi.org/10.1016/j.jhevol.2020.102882

Wiessner, P. (2009). Experimental games and games of life among the Ju/'hoan bushmen. *Current Anthropology, 50*, 133–138. https://doi.org/10.1086/595622

Wilson, M., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology, 6*, 59–73. https://doi.org/10.1016/0162-3095(85)90041-X

Winterhalder, B. (1986). Diet choice, risk, and food sharing in a stochastic environment. *Journal of Anthropological Archaeology, 5*, 369–392. https://doi.org/10.1016/0278-4165(86)90017-6

Winterhalder, B. (1996a). A marginal model of tolerated theft. *Ethology and Sociobiology, 17*, 37–53. https://doi.org/10.1016/0162-3095(95)00126-3

Winterhalder, B. (1996b). Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology: Issues, News, and Reviews, 5*, 46–57. URL: https://doi.org/10.1002/(SICI)1520-6505(1996)5:2%3C46::AID-EVAN4%3E3.0.CO2-U.

Winterhalder, B. (2001). The behavioural ecology of hunter-gatherers. In C. Panter-Brick, R. H. Layton, & P. Rowley-Conwy (Eds.), *Hunter-gatherers: An interdisciplinary perspective* (pp. 12–38). Cambridge: Cambridge University Press.

Wood, B., & Hill, K. (2000). A test of the "showing off" hypothesis with ache hunters. *Current Anthropology, 41*, 124–125. https://doi.org/10.1086/300111

Wood, B. M. (2006). Prestige or provisioning? A test of foraging goals among the Hadza. *Current Anthropology, 47*, 383–387. https://doi.org/10.1086/503068

Wood, B. M., & Marlowe, F. W. (2013). Household and kin provisioning by hadza men. *Human Nature, 24*, 280–317. https://doi.org/10.1007/s12110-013-9173-0

Wood, B. M., Pontzer, H., Raichlen, D. A., & Marlowe, F. W. (2014). Mutualism and manipulation in Hadza-honeyguide interactions. *Evolution and Human Behavior, 35*, 540–546. https://doi.org/10.1016/j.evolhumbehav.2014.07.007

Woodburn, J. (1970). *Hunters and gatherers: The material culture of the nomadic Hadza* (1st ed.). London: British Museum.

Woodburn, J. (1998). Sharing is not a form of exchange: An analysis of property-sharing in immediate-return hunter-gatherer societies. In C. M. Hann (Ed.), *Property relations: Renewing the anthropological tradition chapter 2* (pp. 48–63). Cambridge: Cambridge University Press.

Zahavi, A. (1995). Altruism as a handicap - the limitations of kin selection and reciprocity. *Journal of Avian Biology, 26*, 1–3.