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What does prey harvest composition signal to a social audience?: Experimental studies with Aché hunter-gatherers of Paraguay

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ABSTRACT

In small-scale societies hunting is a high-risk, high-reward activity which impacts status and reproductive success. The question of whether men hunt to provision families or as a costly signal of their phenotypic qualities has been hotly debated in the anthropological literature. To shed new light on this question, we explored audience assessments of a hunter's phenotypic quality and desirability as a function of the composition of prey acquired by the hunter. A combination of ranking and forced-choice tasks were administered to 52 informants (46% female, aged 15–76 years) from the Aché hunter-gatherer tribe of Paraguay between May and July of 2015. Ratings of a hunter's provisioning ability, strength, fighting ability, disease resistance, and desirability as a mate or ally were all positively associated with killing large and hard-to-kill prey, and negatively associated with killing hard-to-find prey. However, killing a single large animal resulted in a worse assessment of hunter phenotype and desirability than killing an equivalent biomass of small animals. These findings highlight the potential of small prey hunting as a mechanism for advertising both quality and consistent provisioning ability. Critically, no conflict was observed between the goal of advertising quality/desirability and the goal of effective provisioning, since hunters who acquired more meat, even if the source of the meat was small game, were generally perceived as having better phenotypes and as more desirable.

1. Introduction

In hunter-gatherer societies hunted game is an important currency which has value not only as a source of nutrients and energy but also potentially as a vector for communicating information about a hunter. It is well established that good hunters are usually preferred as mates and social partners (Alvard & Gillespie, 2004; Gurven, Kaplan, & Gutierrez, 2006; Kaplan & Hill, 1985; Marlowe, 2004; Patton, 2005; Smith, 2004), and usually show higher reproductive success (but see Kraft, Venkataraman, Tacey, Dominy, & Endicott, 2019). It is an open question, however, whether hunting and associated high levels of meat-sharing are better characterized as a strategy of provisioning and parenting effort or as a signal designed to impress potential mates and social allies (Gurven & Hill, 2009; Hawkes, 1991; Hawkes & Bird, 2002; Patton, 2005; Stibbard-Hawkes, 2019; Stibbard-Hawkes, Smith, & Apicella, 2022; Trumble, Smith, O'Connor, Kaplan, & Gurven, 2014; Wood & Marlowe, 2014).

Hunting success requires both skill and luck, and results in high daily harvest variability, making it difficult to evaluate the relative abilities of individual hunters (Gurven et al., 2006; Hill & Kintigh, 2009; Stibbard-Hawkes, Attenborough, & Marlowe, 2018). For that reason, communities may develop rules-of-thumb about hunting success, by which they can evaluate the qualities of individual hunters. Here we explore the possibility that preferences for hunters are influenced by the composition of prey they harvest.

There are many hypotheses and a well-developed literature surrounding the question of how and why hunters share their kills; however, there are fewer hypotheses about what motivates hunters'

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preferences with regard to prey targeting strategies. Models from Optimal Foraging Theory (OFT) have been applied to human foragers to make explicit predictions about which prey species should be pursued upon encounter and which should be ignored if the goal of a forager is to maximize their harvest rate (Hawkes, Hill, & O'connell, 1982; Hill, Kaplan, Hawkes, & Hurtado, 1987; Smith et al., 1983). Alternatively, various signaling hypotheses have proposed that specific prey are targeted, at least in part, on the basis of their value as advertisements of the qualities of the hunter (Bliege Bird, Smith, & Bird, 2001; Hawkes, 1991; Hawkes & Bird, 2002; Smith, Bird, & Bird, 2003; Smith & Bird, 2000). Although the signaling versus provisioning debate is often framed as either-or, it seems likely that the correct answer may be a combination of both possibilities, with relative hunter motivations varying based on current circumstances and life history stage (Wood, 2006; Wood & Hill, 2000; Wood & Marlowe, 2013). Furthermore, hunters might use the same foraging strategy for both purposes. Two main hypotheses have dominated the discussion surrounding the above question.

First, the Family Provisioning Hypothesis proposes that men hunt as a form of cooperative specialization in which their goal is to efficiently provision protein/lipid-rich foods to complement the carbohydrate-based calories gathered by their mates (Gurven et al., 2006; Gurven & Hill, 2009, Hill, Kaplan, & Hawkes, 1993; Kaplan, Hill, Lancaster, & Hurtado, 2000; Marlowe, 1999; Trumble et al., 2014; Wood & Marlowe, 2013, 2014). Theoretical modeling shows that a hominin shift to energetically dense, but difficult-to-acquire, foods might lead to just such male-female cooperation and the emergence of paternal investment (Alger, Hooper, Cox, Stieglitz, & Kaplan, 2020).

Second, the Costly Signaling Hypothesis proposes that men intentionally hunt difficult-to-acquire prey because their ability to capture such prey serves as an honest signal of phenotypic traits that would otherwise be difficult to observe such as strength, skill, fighting ability, health, leadership, generosity, or knowledge (Bliege Bird et al., 2001; Bliege Bird & Smith, 2005; Smith, 2004; Smith et al., 2003; Smith & Bird, 2000; Stibbard-Hawkes, 2019). For hunting to achieve this goal it should, "meet key criteria for costly signaling in being (1) differentially costly or beneficial in ways that are (2) honestly linked to signaler quality, and (3) designed to effectively broadcast the signal to the intended audience." (Bliege Bird et al., 2001). It should be noted, however, that difficult-to-acquire prey are not necessarily less efficient for provisioning, and therefore the Costly Signaling Hypothesis and the Family Provisioning Hypothesis do not necessarily lead to different predictions regarding prey choice. Furthermore, it is hard to empirically measure how difficult it is to acquire a given prey species, especially if only the most skilled hunters attempt to acquire such prey.

A third hypothesis, the "Showing-off" Hypothesis proposes that men hunt primarily with the goal of providing meat to a large audience, usually by hunting large-game which are presumed to be shared more widely, in order to gain attention and access to potential mates and allies (Hawkes, 1991; Hawkes & Bird, 2002). The "Showing-off" Hypothesis refers to provisioners, "One earns a steady mean income, with little variance. Daily totals are never very high and never low.", and show-offs, "The other strategy earns amounts which vary widely from day to day. The periodic bonanzas of the second strategy are visible to all." (Hawkes, 1991). Unlike the Costly Signaling Hypothesis, which proposes that potential mates and allies prefer skilled hunters because of the qualities they advertise, the "Showing-off" Hypothesis proposes that provisioners may be preferred as mates but that people may prefer to associate with show-offs out of a desire to receive shares of meat. "Even though a woman might prefer to be a provisioner and to have a provisioning husband, she would prefer the others in the community to bring in jackpots, that is, to behave as showoffs."(Hawkes, 1991).

Both the Costly Signaling Hypothesis and the "Showing-off" Hypothesis emphasize the importance of prey which can be shared widely, either to "attract the favorable attention of potential future mates and potential allies" (Hawkes, 1991) or to "broadcast the signal widely" (Bliege Bird et al., 2001). For this reason, large prey may be more favorable than small prey for showing-off or for signaling. However, when all harvested prey species regardless of size are shared evenly within a social group, as is the case with our study population while on forest treks (Gurven, Allen-Arave, Hill, & Hurtado, 2001), then both the Family Provisioning Hypothesis and "Showing-off" Hypothesis make the same predictions about which prey, or suites of prey, should be preferred by audiences and hunters alike. For this reason, our paper focuses on comparing the Family Provisioning Hypothesis and Costly Signaling Hypothesis.

Costly Signaling Theory, from which the Costly Signaling Hypothesis is derived, has been extensively modeled and examined in evolutionary biology (e.g. Grafen, 1990; Hamilton & Zuk, 1982; Zahavi, 1975). Models of costly signaling describe situations in which an organism produces a signal which honestly advertises an important phenotypic quality in order to gain a fitness benefit from the signal recipient, with stronger signals resulting in greater benefits. Early discussions of Costly Signaling Theory emphasized realized costs, meaning marginal costs are paid to produce the signal, as a way to assure the honesty of a signal. Higher quality signalers could afford to signal at a higher level because they either paid a lower differential or marginal cost to signal or because they were able to gain a greater benefit from signaling due to their quality. However, it has been repeatedly demonstrated that realized costs are not a necessary feature of honest costly signaling systems, nor are realized costs a reliable indicator that costly signaling is taking place (Grose, 2011; Smith, 1994; Számadó, 2011). Rather, the *potential* costs of over-signaling, meaning costs are paid only if the signal is dishonest, can assure the honesty of the signal (for discussion see: Barker, Power, Heap, Puurtinen, & Sosis, 2019; Higham, 2014; Penn & Számadó, 2020). An example of realized costs would be the energetic and nutritional costs of producing a male peacock's tail (Zahavi, 1975), while an example of potential costs would be the cost of coming home empty handed when an unskilled hunter attempts a turtle hunt (Bliege Bird et al., 2001).

Although costly signaling is one type of honest signal, it is important to remember that alternative mechanisms for honest signaling exist. Indices, for example, are behaviors or traits which are intrinsically linked to the quality of the signaler in a way which is impossible to fake (Maynard-Smith et al., 2003).

Costly Signaling Theory has been widely applied in anthropology and archeology to explain hunting and other behaviors which are either less efficient at achieving their goal than alternative options or which seem to serve no obvious adaptive function besides prestige enhancement (e.g. Bird & O'Connell, 2006; Boone, 1998, 2000; Codding & Jones, 2007; Plourde, 2008). The application of Costly Signaling Theory to hunting was intended to explain an apparent mismatch between the observed foraging behavior of the Aché (Hawkes, 1991; Hawkes, O'Connell, & Coxworth, 2010), Hadza (Hawkes, O'Connell, & Blurton Jones, 2001b, 2014), and Meriam Islanders (Bliege Bird et al., 2001), and the foraging behaviors which would most efficiently provision families. Whether or not such a mismatch exists among the Aché (Gurven & Hill, 2009) and Hadza (Wood & Marlowe, 2013, 2014) has been the subject of debate, however, the idea that hunting could be a useful vector for signaling is worthy of investigation.

Despite scientific interest in the emergence of the sexual division of labor in humans, the question of what motivates men to hunt, and the potential role of costly signaling in men's foraging decisions, there is little research directly addressing the information conveyed by different hunting outcomes. The size, number, and species of prey harvested as well as the difficulty of finding and killing said prey species could all impact audience beliefs about the hunter's observable or hidden traits.

Although factors such as the marital status of hunters (Marlowe, 1999; Wood, 2006; Wood & Hill, 2000) or the nature of hunting different prey species (Bliege Bird et al., 2001; Smith et al., 2003; Smith & Bird, 2000) have been considered, research on this topic has traditionally emphasized the means and variances of hunting income and how meat is transferred in order to assess whether hunter choices enhance, or undermine, family provisioning (e.g. Gurven & Hill, 2009;

Gurven & Jaeggi, 2015; Hawkes, 1991; Hill et al., 1993; Marlowe, 1999; Smith & Bird, 2000; Wood & Marlowe, 2013, 2014). Some research has also examined hunter motivations (Stibbard-Hawkes et al., 2022; Wood, 2006; Wood & Hill, 2000), and correlations between measures of hunting reputation and other traits (Apicella, 2014). But, to date there have been few studies systematically querying audiences about the relationship between the harvest of unique combinations of species and perceptions of hunter quality and desirability (Jones, 2016; Stibbard-Hawkes et al., 2018; Wood, 2006; Wood & Hill, 2000).

The goal of this research is three-fold: 1) to assess how hunting outcomes, specifically size and number of prey killed as well as the difficulty of finding and killing each species, impact perceptions of a hunter's provisioning ability, strength, fighting ability, and disease susceptibility; 2) to assess the impact of perceived hunter quality on assessments of the mate value and social partner value of a hunter; 3) to examine the implications of these findings for the Family Provisioning Hypothesis and Costly Signaling Hypothesis.

The four aspects of hunter phenotype examined in this study were chosen because of their obvious relevance to hunting or because of their prominence within the broader costly signaling literature. There is likely to be a direct link between the strength and aerobic endurance of a hunter and their ability to successfully pursue prey (Stibbard-Hawkes et al., 2018). Likewise, a hunter's ability to successfully kill difficult prey (provisioning ability) is likely to be predictive of their ability to kill prey in the future. Although hunting ability and fighting ability might not be directly linked, it is possible that hunting requires strength, courage, and skill with weapons, all of which could result in successful hunters being viewed as better fighters. Disease susceptibility was chosen, not because of any obvious link to hunting ability, but because many prior studies of costly signaling have examined costly signals of health (Folstad & Karter, 1992; Hamilton & Zuk, 1982), and because signals of health may play a role in human mate choice (Tybur & Gangestad, 2011).

The current study examines audience evaluations of hunter quality in three simple contexts allowing us to independently assess the impacts of prey characteristics, prey body size, and number of animals killed on audience assessments of hunter quality. These contexts consist of: 1) prey-by-prey comparisons; 2) comparisons of the harvest of single large animals vs multiple small animals; and 3) the comparison of hunters who adopt a large-game vs small-game specialization. Sharing breadth and depth were not considered in this study because, while on forest treks, the Aché generally share animals with equal depth and breadth regardless of the size of the animal (Gurven, Hill, & Kaplan, 2002) and because sharing breadth and depth are more likely to be relevant when signaling generosity or cooperative intent, neither of which were examined in this study.

Informants judged between hypothetical hunters (depicted in drawings) based on changes in their prey acquisition in each of these contexts. Informants were asked to judge which of a pair of depicted hunters: 1) would bring home more meat in the future ("future provisioning"); 2) was physically stronger; 3) would win in a fight; 4) was less susceptible to infectious disease. Additionally, informants were asked to indicate which hunter they would prefer as a mate or a social partner for themselves or their children, (or in the case of young unmarried men, which hunter they would prefer to be). We treat the responses of young unmarried men as though they are indicative of which hunter has higher mate value, however, this assumption may not be correct if young men's preferences are driven by some other priority besides the desire to attract a mate. The degree to which killing certain species or combinations of prey species predicts judgements about hunter quality is hereafter referred to as the signal value of the species or prey set.

2. Methods and results

2.1. Participants

Interview data were collected between May and July of 2015 with indigenous Aché informants from the communities of Arroyo Bandera, Kue Tuvy, and Chupa Pou. Permission to access the site and collect data was granted by Aché community leaders. A stratified sample of informants ($n = 52$ adults ages 15–76; 46% female), balanced by marital status and sex, were selected based on their immediate availability and willingness to participate. Data were not collected regarding the presence or absence of dependent offspring for any of the informants. Informants were approached on an individual basis, and offered modest compensation for participation in 4 interview tasks. All informants provided informed consent and all protocols were approved by the Arizona State University Institutional Review Board (Study ID: STUDY00001593). Special permission was granted to interview informants under the age of 18 due to a scarcity of unmarried women over the age of 18. Interviews were conducted by A.B. with single informants either in a closed room or outdoors near informant's homes. Interviews were conducted in the Aché language with the help of a male translator who was bilingual in Spanish and Aché. Some Aché interviews were conducted directly by K.H. (who is fluent in Aché) with a translator observing in order to learn interview protocol.

The Aché were chosen because of the abundance of quantitative data on their hunting behavior and food sharing practices (Gurven et al., 2001; Gurven, Allen-Arave, Hill, & Hurtado, 2000; Hurtado & Hill, 1996; Kaplan & Hill, 1985) and because of their historic role in the development of the "Showing-Off" Hypothesis (Hawkes, 1991; Hawkes et al., 2001b; Hawkes, O'Connell, & Blurton Jones, 2001a).

There are >2000 Aché currently spread across five reservation settlements in eastern Paraguay. The Northern Aché were an isolated hunter-gatherer society until the 1970s, when they were moved to reservations (Hurtado & Hill, 1996). While they continue to make regular trips into large forest reserves where they are permitted to hunt and fish and collect wild honey, fruit, palm starch, and other plant resources, they also engage in subsistence agriculture, and occasional wage labor.

Our study populations primarily exploited the Mbaracayú forest preserve, containing >60,000 ha of protected forest in the traditional Aché homeland. Because firearm use and hunting by all non-Aché people is prohibited within the reserve, bow hunting is still a common and well-maintained skill for many Aché men. Palmwood bows and hardwood-tipped (or metal-tipped) arrows were employed to harvest several dozen game species that provided roughly 78% of calories consumed during observed hunts in the 1980s and 1990s (Kaplan et al., 2000), while honey, and plants foods made up most of the rest. The most important game species (in order by weight harvested) are nine-banded armadillos, paca, tapir, capuchin monkeys, white-lipped peccary, coatimundi, red brocket deer, collared peccary, and tegu lizard. All other species make up <1% of the harvest biomass (Hill and Padwe, 2000). Prior research shows that food sharing is more extensive and egalitarian in the forest than on reservation settlements, with all band members usually receiving equal shares of the day's harvest regardless of their own personal success (Gurven et al., 2001). Based on non-systematic observations of food sharing both in the reservation settlements and while on forest treks, it was the impression of A.B. that this pattern of sharing was still in effect.

2.2. Task 1: Prey character rankings

2.2.1. Task 1: methods

Our interviews examine two characteristics of prey species that might form the basis for costly signaling. Informants ranked how hard animal species are to kill after they have been encountered, since killing difficult prey may be an indicator of strength, stamina, skill, coordination, and future success at hunting. Informants also ranked how difficult each prey species is to find, since the ability to find rare animals could indicate special cognitive abilities, knowledge of the local ecology, stealth, tracking skills, or superior ability at detecting cryptic species.

Prey species images were taken from non-watermarked, publicly available online sources and were then cropped and digitally altered (using Adobe Photoshop CS3) to appear consistent with one another and scaled to be approximately appropriately sized relative to an Aché hunter.

Individual informants sorted drawings of 16 prey species, presented one at a time in random order, (Fig. 1) into two rank ordered lists based upon how hard each species was to: 1) Find (Hard-to-Find); or 2) Kill after being found (Hard-to-Kill). Informants ranked prey based on Hard-to-Find before Hard-to-Kill. The prompts for these sorting tasks were the questions: "Which of these is harder to find?" and "Which of these is harder to kill once found?". The species selected for comparison represent a range of body sizes and included animals which were both common and rare in the diet, as well as animals rumored to be difficult to find or difficult to kill. Mean body weight upon harvest was estimated for each species (Table 1 in Section 2.2.3, see supplement for sources of body weight estimates). Weight refers to the body size of prey, not their edible biomass.

Individual informant rankings of all species were then recorded with higher rank numbers indicating that a species is harder to kill or find. Prey ranked as "tied" by informants were given the mean ranking of the set of prey species that had tied each other.

Fifty-one out of 52 informants completed the prey ranking tasks, and final prey rankings were taken as the mean of the individual informant ranks for each prey species.

Table 1
Task 1: Prey ranking results.

Species	Weight (Kg)	Hard-to-Find		Hard-to-Kill	
		Mean	SD	Mean	SD
Tapir	177.0	10.87	2.70	12.28	3.14
Jaguar	88.0	12.70	2.35	**14.43**	1.66
Anaconda	50.0	**15.18**	1.24	**15.02**	2.31
Red Brocket Deer	25.8	8.72	2.51	10.34	2.83
White Lipped Peccary	24.9	7.61	3.16	9.26	3.34
Collared Peccary	16.3	8.32	2.77	8.83	2.95
Paca	6.7	5.27	2.86	6.60	2.90
Bush Dog	5.5	**14.46**	1.12	11.38	3.14
Tayra	4.0	10.42	3.00	9.98	3.24
Nine-Banded Armadillo	3.8	2.43	2.09	3.30	1.94
Coati	3.5	7.45	2.97	8.35	2.62
Capuchin Monkey	2.3	4.88	2.09	8.10	3.45
Tegu Lizard	2.3	5.82	3.41	5.31	2.91
Tortoise	1.0	12.82	3.64	5.93	4.69
Rusty-Margined Guan	0.8	5.92	3.06	7.61	3.38
Bothrops Snake	0.7	10.21	3.88	4.67	3.69

Note. – weight in Kg, mean rank Hard-to-Find, and mean rank Hard-to-Kill for prey species (in rank order of weight) calculated from informant responses. The two highest ranked species are **bolded**, the two lowest ranked species are underlined.

2.2.2. *Task 1: analyses*

To analyze prey trait rankings, the mean and standard deviation of rankings of Hard-to-Find and Hard-to-Kill were calculated for each species. The rank values calculated were the mean rank values for the species across all informants. The correlations were then estimated between mean Hard-to-Find rank and body weight, mean Hard-to-Kill rank and body weight, and between mean Hard-to-Find rank and mean Hard-to-Kill rank, in order to determine the independence of prey traits. Subsequently, each of the prey trait rankings were analyzed using Cultural Consensus Analysis (hereafter referred to as "CCA") in order to examine informant agreement about prey characteristics. CCA is a statistical method which is used to determine whether or not there is consensus among a group of informants about the answers to a set of questions (Romney, Weller, & Batchelder, 1986). If consensus is achieved, CCA will identify the consensus opinions of the group (the answer key), the degree to which each individual's responses conform to the consensus opinions (competency), the mean proportion of correct answers across all informants (mean competency), and the number of informants whose opinions do not, on average, conform to the consensus opinions of the group (negative competency). All CCA analyses referred to in this study were carried out using UCINET v. 6.636 (Borgatti,

Fig. 1. Drawings of 16 animal species were illustrated on flash cards and used for Aché interviews. An Aché hunter is depicted on each card for scale.

Everett, & Freeman, 2002).

2.2.3. Task 1: results

Rank order for 16 prey species (Table 1), shows a positive relationship between prey mean body weight and those that are ranked Hard-to-Kill ($r^2 = 0.37$, $P < 0.05$). Rank Hard-to-Find and Hard-to-Kill were also moderately correlated with each other ($r^2 = 0.48$, $P < 0.01$). No correlation was found between weight and Hard-to-Find. Despite the correlations among weight, Hard-to-Find, and Hard-to-Kill, multiple regression analyses could still be used on Task 2 data to disentangle their respective implications for the signaling value of a species. Some species represent only a small amount of food yet are considered extremely difficult to find (bushdog, tayra, tortoise, snake) or kill (bushdog). Conversely, some species are reasonably large, but are considered relatively easy to find (deer, peccaries) or kill (collared peccary).

Consensus was high among the Aché for rankings of both Hard-to-Find (n = 50, ratio first/s eigen value = 8.0, mean competency = 0.77, SD = 0.19, negative competencies = zero of 50), and Hard-to-Kill ($n = 50$, ratio first/s eigen value = 5.7, mean competency = 0.71, SD = 0.21, negative competencies = one of 50) (Supplement, Table S1).

2.3. Task 2: prey-by-prey comparisons

2.3.1. Task 2: methods

In order to examine the impact of killing different prey species on informant perceptions of hunter quality and desirability, informants were shown images depicting pairs of otherwise identical hunters each standing next to a single animal that they had reportedly killed (Fig. 2) and were asked to compare them on four aspects of quality and two aspects of desirability. Images were shown to informants in random order and the associated questions for each image were asked in random order. Old photos of Aché hunters (taken by K.H.) were digitally altered by A.B. using Adobe Photoshop CS3 to look like generic hunter drawings standing behind recognizable prey species at approximately correct scale. Participants were told: "*imagine you meet these two hunters in the forest standing by the animals they killed that day*." Informants were then asked six interview questions in randomized order comparing the depicted hunters (e.g. "*Which hunter do you think is stronger?" "Which hunter would you prefer your daughter to marry?*"). English translations of the six questions are shown in Table 2.

The four aspects of hunter phenotype that informants were asked to compare were Future Provisioning, Strength, Fighting Ability, and Disease Susceptibility. The Aché word for strength ("*chija*") implies both short burst strength as well as aerobic stamina. Traditionally the Aché practiced ritualized club fights, so questions about fighting ability

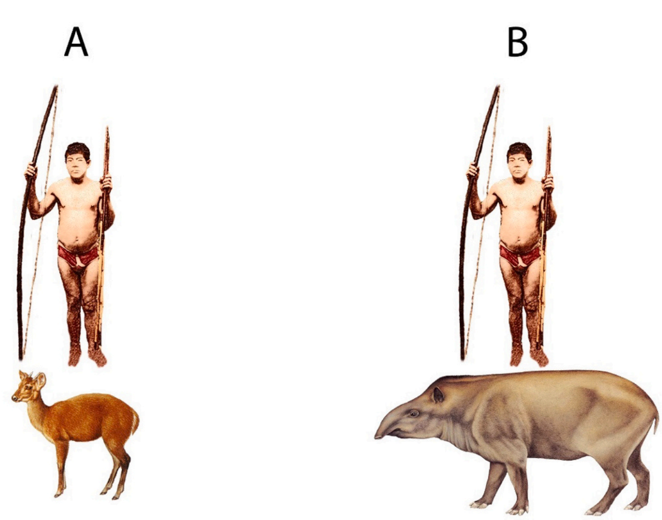

Fig. 2. Example images from Aché paired comparison task.

Table 2
Paired comparison interview questions in english.

Future Provisioning	Who will bring more meat in the future?
Physical strength	Who is stronger?
Fighting Ability	Who would win in a club fight?
Disease Susceptibility	If sickness comes to the community, which man will get sick first?
Mate	(Unmarried Women) Who would you prefer to marry? (Married Women and Men) Who would you prefer to have your daughter marry? (Unmarried Men) Which animal would you have preferred to kill?
Social Partner	Who would you rather go on a forest trek with?

Note. - Description of interview questions for Task 2, in English.

referenced that tradition, however, several informants (4 out of 52) declined to compare hunters on "fighting ability". The fourth question was intended to assess whether successfully hunting certain prey might signal immunocompetence, since this is one of the primary proposed functions of costly signaling in animals (Folstad & Karter, 1992). When asked to compare informants, however, some Aché informants (8 of 52) replied that they did not believe there was any connection between hunting success and disease susceptibility.

The paired comparisons also included two questions assessing the hunter's desirability as a mate or social partner. In order to couch social partnership in terms that are culturally relevant, informants were asked: *"which hunter would you prefer to go on a forest trek with?"* Questions about desirability as a mate were modified based on the sex and marital status of the informant being asked.

Participants were divided into four groups and each group was presented with 30 unique prey combinations. For each prey dyad, informants were asked four questions about hunter quality, and two questions about the desirability of the hunter as a mate or ally. For each question, informants responded by assigning greater quality or preference to hunter A or hunter B, or by indicating no difference between the hunters (tie), or by declining to answer based on a lack of knowledge (no answer = missing data). The responses of informants who stated that there is no connection between hunting returns and fighting ability or disease susceptibility were treated as ties. This was done to differentiate informants who failed to answer specific questions (no response) from those who answered by saying hunting isn't informative about the topic (tie). The result is that all six questions were answered for each possible prey dyad by 12–14 different informants. We were unable to ask each informant about all possible prey combinations in each interview because informants showed signs of fatigue due to the repetitive nature of this interview (six questions x 30 prey combinations = 180 comparisons per informant). However, the sample size for each possible prey combination ($n = 12$–14) is sufficient for statistical analyses.

2.3.2. Task 2 analyses

Paired-comparison data were analyzed with binomial logistic regression to determine the effects of prey characteristics (weight, Hard-to-Kill, Hard-to-Find) on informant beliefs about the phenotypes of the hunters who killed those prey (future provisioning, strength, fighting ability, disease susceptibility), and social preferences for such hunters (mate value, social partner value). In each model, the dependent variable was whether hunter A was chosen over B. The independent variables in the model were calculated differences, A – B, in prey weight, rank Hard-to-Find, or rank Hard-to-Kill for the pair of animals shown (e.g. Hard-to-Kill rank of prey killed by A – Hard-to-Kill rank of prey killed by B). In order to directly compare effect sizes of the three independent variables, the difference measures were all standardized [(measure prey A - measure prey B)/ std. deviation of interview sample)]. All binomial logistic regressions performed on Task 2 data were carried out using R statistical software (V. 4.1.1) (R Core Team, 2022).

In the prey ranking task, harder to find and harder to kill prey were always assigned the higher rank value (highest prey rank = 16, lowest prey rank = 1). This means that larger values for A indicated that animal A was higher than B on a given characteristic (weight, Hard-to-Find, Hard-to-Kill). The models allowed us to statistically determine whether informants were more likely to pick the hunter who killed prey type A as the strongest of the two hunters, or the most disease resistant, etc., if prey type A had a greater weight or higher rank Hard-to-Find or Hard-to-Kill.

A second set of analyses were performed on paired comparison data using binomial generalized linear models in order to determine whether hunters evaluated as having better phenotypes are also evaluated as having greater value as mates or social partners. For these analyses, the dependent variable was whether the informant chose hunter A as having higher mate value, or social partner value (yes = 1). The independent variable in each model is whether hunter A was rated by that informant as having greater future provisioning, strength, fighting ability, and disease susceptibility (yes = 1).

Finally, task 2 data were analyzed using CCA (using UCINET v. 6.636) (Borgatti et al., 2002) to determine whether informants were in agreement about their assessment of hunter qualities based on hunting outcomes. Because informants were divided into four groups, with each group answering questions about a unique set of prey dyads, CCA was performed independently for each group.

2.3.3. Task 2: results

Model results from analyses of Task 2 data suggest that standardized differences in weight, rank Hard-to-Find, and rank Hard-to-Kill were all significant predictors of informant ratings of hunter future provisioning, strength, fighting ability, and disease susceptibility. Hunters portrayed as having killed larger, or harder-to-kill animals were more likely to be rated as having greater future provisioning, strength, and fighting ability, and less likely to be rated as disease susceptible (Table 3; Supplement Figs. S1, S2, S3). Participants were also more likely to rank those hunters higher in terms of their mate value and value as social partners (Table 4; Supplement Figs. S4, S5, S6). On the other hand, hunters who harvested harder-to-find prey were generally perceived as having worse phenotypes, and as being less desirable as mates and social partners.

These results, based on dyadic comparisons of two individual prey items, suggest that the signal value of prey in Aché society is influenced by both the difficulty of hunting the species (Hard-to-Find, Hard-to-Kill), as well as its food value (weight). Aché hunters who wish to signal positive phenotypic traits should target large and/or hard-to-kill animals but should avoid hunting animals that are small and hard-to-find, such as pit vipers and tortoises. The relative sizes of standardized regression coefficients presented in Table 3 and Table 4 suggest that variation in Hard-to-Kill of hunted prey is slightly more important than variation in prey size for assessing the phenotypic quality and mate and social partner value of a hunter.

Importantly, despite the hesitance of a few informants to connect prey harvests with beliefs about hunter fighting ability or disease susceptibility, consensus analysis confirmed that informants achieved good agreement in their assessment of all hunter qualities examined based on the animals killed by each hunter (ratio first/s eigen value = 4.12–6.75, mean competency = 0.66–0.77, SD = 0.11–0.27, negative competencies = zero of 52; Supplement, Table S2).

Two additional generalized linear models examined relationships between informant assessment of hunter A's phenotype (e.g. stronger, greater future provisioning, etc.) and value as a mate or social partner (Table 5). Favorable assessments of a hunter's mate value were positively associated with the choice of that hunter as having greater future provisioning and strength, but not greater fighting ability or lesser disease susceptibility. Favorable assessments of a hunter's social partner value were associated with the same assessments of hunter phenotypic quality as mate value. The relative sizes of the standardized regression coefficients presented in Table 5 suggest that differences in perceived future provisioning ability have the greatest influence on mate value and social partner value.

Table 4
Task 2 regressions: mate and social partner value questions.

Standardized predictors (Animal A – Animal B)	Mate value		Social Partner Value	
	β	P <	β	P <
Diff. Body Weight	0.90	0.001	0.82	0.001
Diff. Hard-to-Find	−1.65	0.001	−1.71	0.001
Diff. Hard-to-Kill	1.26	0.001	1.34	0.001

Note. - Task 2 results of two binomial logistic regressions predicting the Mate and Social Partner value of the hunter based on differences between animals killed. For each model, the predictor variable is the standardized difference between the character value (weight, rank Hard-to-Find, rank Hard-to-Kill) for prey killed by hunter A and the character value for prey killed by hunter B. The outcome variable is whether informant preference was for hunter A.

2.4. Task 3: single large vs many small prey comparison

2.4.1. Task 3: methods

In order to examine the potential tradeoff between killing larger animals or a greater number of animals when total biomass harvested is equalized, participants were shown depictions of two hunters, one next to a single large animal and the other next to an approximately

Table 5
Mate Value and Social Partner Value by Hunter Traits.

Standardized Predictors	Mate Value		Social Partner Value	
	β	P <	β	P <
Future Provisioning	4.66	0.001	4.58	0.001
Strength	1.50	0.008	2.21	0.001
Fighting Ability	0.63	0.282	−0.09	0.869
Disease Susceptibility	−0.29	0.544	−0.12	0.793

Note. - Results of two Aché paired comparison GLM analyses examining the relationship between ascribed hunter phenotypes and assessments of mate value and social partner value. Mate Value and Social Partner Value represent unique models.

Table 3
Task 2 Regressions: Hunter Phenotype Questions.

Standardized Predictors (Animal A – Animal B) SD	Future Provisioning		Strength		Fighting Ability		Disease Susceptibility	
	β	P <	β	P <	β	P <	B	P <
Diff. Body Weight	0.94	0.001	0.88	0.001	0.91	0.001	−0.83	0.001
Diff. Hard-to-Find	−1.69	0.001	−1.24	0.001	−1.15	0.001	1.11	0.001
Diff. Hard-to-Kill	1.32	0.001	1.41	0.001	1.48	0.001	−1.30	0.001

Note. - Task 2 results of four binomial logistic regressions predicting perceptions of hunter phenotype (Future Provisioning, Strength, Fighting Ability, Disease Susceptibility) based on differences in the characteristics of animals killed. For each model, the predictor variable is the standardized difference between the character value (weight, rank Hard-to-Find, rank Hard-to-Kill) for prey killed by hunter A and the character value for prey killed by hunter B. The outcome variable is whether the informant chose hunter A as having greater future provisioning, strength, fighting ability or disease susceptibility.

equivalent weight of smaller animals of a single prey type (Fig. 3). For the remainder of this paper, we designate a hunter who kills one large prey as the "Large-Game Hunter", and a hunter that harvests many small animals as the "Small-Game Hunter". Informants were asked to imagine that they had encountered these two hunters and were told that the animals depicted were all of the animals killed by each hunter during a week. Informants were first asked, "which of these men has killed more meat?", as a way to verify that informants perceived total harvest by both hunters to be approximately equal. This was followed by the same six questions asked in the previous task.

Unlike the paired comparison task, not every possible combination of prey species could be examined (due to time constraints). Instead, we selected a variety of prey dyads that represent a mix of body sizes, ranks Hard-to-Find and Hard-to-Kill, and levels of importance in the Aché economy. Nine prey species were divided into three groups: large animals (tapir, anaconda, jaguar), medium sized animals, (deer, white lipped peccary, collared peccary), and small animals (armadillo, coatimundi, paca). Jaguars and anaconda, while considered edible and occasionally consumed, are not important in the Aché economy but potentially have high value as signals of strength and fighting ability. Indeed, jaguar tooth necklaces are often worn among the Aché and are highly prized by both men and women.

Prey combinations were compared across but not within size groups. Tapir could not, however, be compared directly to the animals in the smallest class, because the huge size difference made it impractical to fit an equivalent weight of smaller animals onto a single image card. The mean difference in total weight depicted between the prey sets killed by the Large-Game Hunter and Small-Game Hunter (weight of large prey – weight of small prey set) was low (mean = 2.19 kg, std. deviation = 4.54).

2.4.2. Task 3: analyses

Data from task 3 were first used to calculate the mean proportion of informants choosing the Large-Game Hunter or Small-Game Hunter as having killed more meat. These values should be approximately equal if informants were equally likely to perceive either hunter as having harvested a greater total biomass of game. Next, we calculated the mean proportion (and standard error) of informants choosing the Large-Game Hunter, as a more desirable mate or social partner or as having greater future provisioning, strength, fighting ability, and lower disease susceptibility. Informants who did not provide complete responses for all 24 prey combinations were excluded from the calculations.

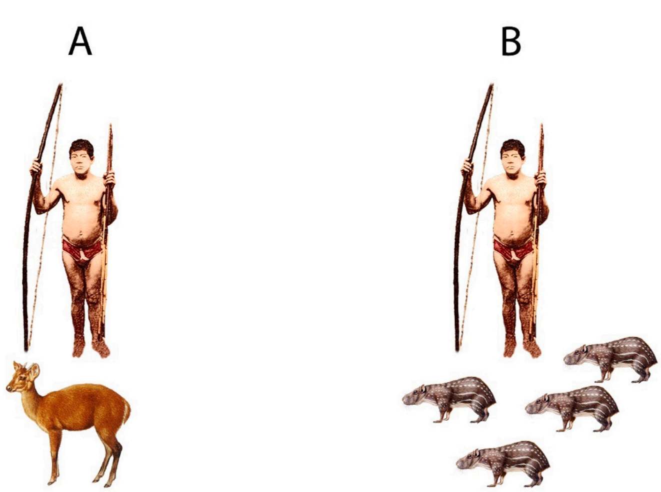

Fig. 3. Example of a comparison examined in task 3 - the multi-prey comparison.

2.4.3. Task 3: results

Informants chose the Large-Game Hunter prey set as containing a greater total biomass 51% of the time and the Small-Game Hunter prey set 33% of the time, with 16% of informants viewing the two prey sets as containing an approximately equal biomass (Supplement, Fig. S7). Importantly participants voiced a strong bias that the Small-Game Hunter had greater phenotypic quality and greater desirability as a mate or social partner than the Large-Game Hunter, despite the slightly greater odds of perceiving the Large-Game Hunter as having killed more meat. The Large-Game Hunter was perceived as having greater future provisioning in only 16% (0.16, S.E. = 0.026) of the comparisons, greater physical strength in 17% (0.17, S.E. = 0.024), greater fighting ability in 41% (0.41, S.E. = 0.012), and having lower disease susceptibility in 40% (0.40, S.E. = 0.011). Likewise, the Large-Game Hunter was selected as having higher mate value in only 25% percent of comparisons (0.25, S.E. = 0.024) and social partner value in 14% of comparisons (0.14, S.E. = 0.022). The results suggest that, when total biomass harvested is perceived to be about the same, informants strongly favor Small-Game Hunters, over Large-Game Hunters.

2.5. Task 4: large-prey specialist vs small-prey specialist comparison

2.5.1. Task 4: methods

Informants were next asked to compare and evaluate hunters who adopt either a Large-Prey Specialist or a Small-Prey Specialist strategy by killing different combinations of large or small prey species over a longer time frame (15-weeks). This task is designed to test the idea that informants might prefer hunters who kill large and impressive species even if their long term return rate is somewhat lower (Hawkes, 1991). The total estimated biomass of animals in the depicted Small-Prey Specialist set was approximately 279 Kg, or 28% greater than that the estimated biomass depicted for the Large-Prey Specialist set (217.3 Kg) (Table 6).

Informants were shown comparison sets of five note cards at a time, each containing images representing the prey animals that a hunter reportedly killed in a single week. Married men and women were asked which hunter they would prefer to have marry their daughter, while unmarried women were asked which hunter they would marry, and unmarried men were asked which prey-set they would prefer to kill. The comparison was repeated three times, representing 15 weeks of hunting results, in order to determine whether informant perceptions changed with increasing information about the hunter's long-term returns.

The Large-Prey Specialist set of cards (hunter A) depicted a total of 10 weeks in which the hunter killed one large, Hard-to-Find or Hard-to-Kill species and 5 weeks in which the hunter killed nothing at all. The Small-Prey Specialist set (hunter B) depicted 15 weeks of consistent successful harvests of small prey, with each week's harvest consisting of a variety of low body weight and low ranked (Hard-to-Find or Hard-to-Kill) species (see Fig. 4). The complete Large-Prey Specialist set depicted 10 animals: three brocket deer, four collared peccaries, and three white lipped peccaries killed over 15 weeks. The complete Small-Prey Specialist set depicted 75 animals: 15 coatimundi, 30 capuchin monkeys, 15 armadillo, and 15 paca killed over 15 weeks.

Table 6
Prey set characteristics.

	Large-Prey Specialist	Small-Prey Specialist
# Prey in Set	10	75
Total Weight (Kg) of Set	217.30	279.00
Mean Hard-to-Find	8.22	4.98
Mean Hard-to-Kill	9.57	6.42
Informant Preference	5	148

Note. - Characteristics of the Large-Prey Specialist and Small-Prey Specialist prey sets for interview task 4. The prey species in the Large-Prey Specialist set are larger, harder to kill, and harder to find. Informant preference tallies how many times each card type was chosen as preferred by participants.

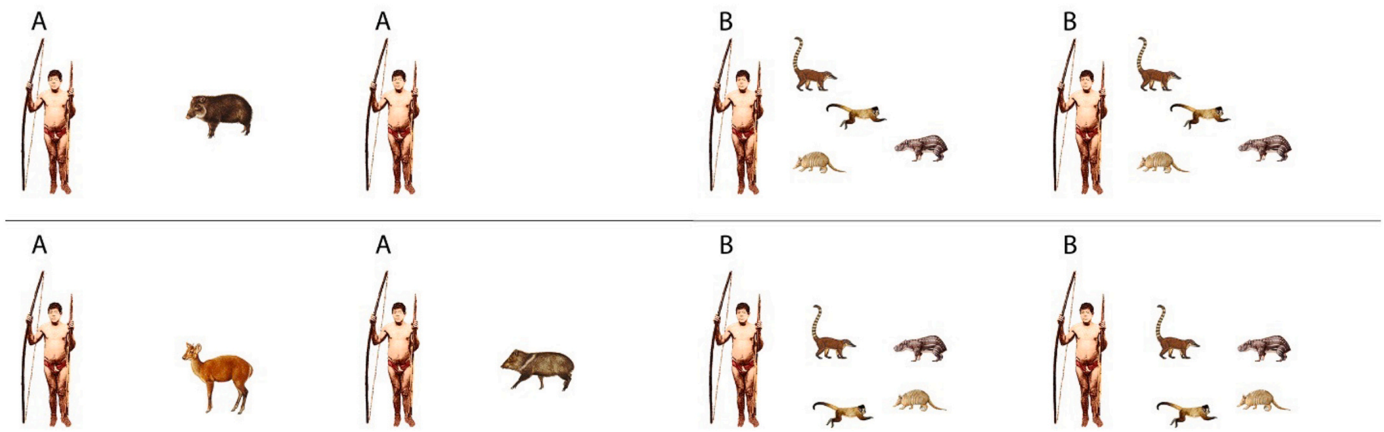

Fig. 4. Examples of cards depicting the Large-Game Specialist hunter (hunter A) and the Small-Game Specialist (hunter B) for interview task 4. Each card represents the harvest for 1 week.

2.5.2. *Task 4: analyses*

Informants selected the hunter with greater mate value three times (at 5 weeks, 10, and 15 weeks), and then we calculated the proportion of informants preferring the Small-Prey Specialist (more meat, but from easier to find and kill species).

2.5.3. *Task 4: results*

Informant responses also indicate a strong preference for hunters who follow the Small-Prey Specialist strategy. Informants ($n = 52$) were given three opportunities to choose between a Large-Prey Specialist set of five cards and a Small-Prey Specialist set of five cards. Of informants, 94% (49 of 52 informants) unanimously choose the Small-Prey Specialist set for all three five-card comparisons, 4% (2 of 52) choose the Small-Prey Specialist set two out of three times, and only 2% (1 of 52) preferred the Large-Prey Specialist set for all three comparisons. These results are consistent with valuing the greater total biomass harvested by the Small-Prey Specialist.

3. Discussion

Analyses of the relationships between prey traits and assessments of hunter phenotype showed that, in one-time scenarios, hunters who killed large and hard-to-kill prey species were perceived as having greater future provisioning, strength, fighting ability, and lower disease susceptibility, whereas hunters who killed hard-to-find prey species were perceived as having worse future provisioning, strength, fighting ability, and greater disease susceptibility (Table 3). In scenarios where the biomass of prey harvested was equalized (Task 3), hunters who killed many small animals were perceived as having superior phenotypes relative to hunters who killed a single large animal (Section 2.4.3).

In one-time scenarios, hunters who were rated as having greater future provisioning and strength were also chosen as more desirable mates and social partners (Table 5). In scenarios where the biomass of prey harvested was equalized, hunters who killed many small animals were rated as having greater mate value and social partner value over hunters who killed a single large animal (Section 2.4.3). Likewise, hunters who adopted a small-prey-specialist strategy and killed a greater total biomass in Task 4 were almost unanimously chosen as having greater mate value (Section 2.5.3). In other words, Aché men should not be expected to sacrifice higher hunting returns on small game in order to obtain a lower prey harvest that is mainly large game. Much like research among the Achuar, Quichua, and Zapara forager horticulturalists which found that hunters who share more meat (regardless of the size of prey acquired) receive greater coalitional support (Patton, 2005), our findings suggest that hunters can best enhance their mate and social partner value by bringing home more meat, regardless of the size of prey acquired.

3.1. *Question 1: prey traits and hunter phenotype*

The Costly Signaling Hypothesis of human hunting assumes that there is variability in the value of different prey harvested as honest signals of some hidden and desirable trait of the hunter who kills them (Bishop, 2019; Bliege Bird et al., 2001; Hawkes & Bird, 2002; Smith et al., 2003; Smith & Bird, 2000; Stibbard-Hawkes, 2019; Wood, 2006). Potential sources of variation in signal value include, but are not limited to, the size of the prey, how difficult it is to find or kill, and the breadth and depth of how it is distributed to others. The current research built upon prior work on the Costly Signaling Hypothesis by systematically analyzing the impacts of body size, number of animals killed, Rank Hard-to-Find, and Rank Hard-to-Kill on perceptions of hunters' phenotypes.

The results of Task 2 (section 2.3.3) demonstrated the positive impact of killing large and hard-to-kill prey on perceptions of hunter phenotype in a one-time scenario, and the negative impacts of killing hard-to-find species (Table 3). This might explain why large animals are often listed as preferred prey. In most small-scale societies, however, assessments of hunter quality are likely to be based on repeated observations of hunting returns over longer time periods. In Task 3 (section 2.4), the total biomass harvested between large and small game was equalized across a hypothetical week, and in Task 4 (section 2.5) hunting returns were considered across 15 weeks. Whether evaluated as a one-shot event (Task 3), or over a hypothetical duration of 5 to 15 weeks (Task 4), participants overwhelmingly prefer the hunter who killed a greater number of small animals over the hunter who killed a single large animal of equivalent biomass or multiple large animals with slightly lower total biomass. This preference demonstrates the viability of successful small game hunting as a potential vector for signaling among the Aché. Furthermore, these findings highlight the importance of examining how the number and biomass of prey being harvested impact informant rankings of preferred prey in future research. It is not sufficient to compare a single individual of each species.

One possible explanation for the strong preference for hunters who killed many small animals in Task 3 is that such hunters may be considered more *reliable* providers due to their demonstrated ability to repeatedly and successfully hunt small game. Alternatively, Small-Game Hunters may be viewed as more active or harder working because they continue to hunt after successfully harvesting small prey. These two possibilities are supported by the finding that large-game hunters were chosen as having greater future provisioning and Strength in only 16% and 17% of cases, respectively (Section 2.4.3). The difference in perceptions of fighting ability and disease susceptibility between Large-

Game and Small-Game Hunters were smaller, but still favored the Small-Game Hunters.

3.2. Question 2: hunter phenotype and desirability as mate or ally

Advertising phenotypic qualities serves little purpose if it does not result in a change in behavior among those observing the signal. Advocates of the Costly Signaling Hypothesis have proposed that hunting may serve a variety of purposes, such as attracting potential mates and cooperative partners as well as deterring potential competitors (Hawkes, 1991; Hawkes & Bird, 2002; Smith et al., 2003; Smith & Bird, 2000).

The results of Task 2 and Task 3 both showed that, in a hypothetical scenario, differences in prey harvest composition indeed predicted assessments of a hunter's mate value or social partner value (Table 4, and Section 2.4.3): both future provisioning and physical strength were significant and positive predictors of having higher mate value or social partner value (Table 5).

The results of dyadic prey comparisons in Task 2 support the existing literature suggesting that better hunters are preferred as mates (Alvard & Gillespie, 2004; Gurven & von Rueden, 2006; Kaplan & Hill, 1985; Marlowe, 2004; Smith, 2004). One key finding of the present study, however, is the importance of successful small-game hunting (Task 3) as an avenue for attracting mates and social partners even when total biomass harvested is no greater, and even though in the current study, small-game were frequently viewed as somewhat less difficult to find or kill (Table 1). Our findings are not consistent with the notion that some aspect of successful large game hunting, apart from the meat it provides, makes it inherently more valuable for signaling phenotypic qualities or for attracting mates and allies than successful small game hunting. It is more likely, given our findings, that the value of large game hunting derives primarily from the higher caloric return rates with which it is often associated. Future research arguing for the inherent value of large game as signals should first strive to demonstrate that there are not easier alternative means by which the same quantity of food could be acquired.

3.3. Question 3: implications for family provisioning and costly signaling hypotheses

Two key findings have important implications for the Family Provisioning Hypothesis and the Costly Signaling Hypothesis. First, there is little evidence among the Aché for a conflict or tradeoff between costly signaling and family provisioning. Second, among the Aché, targeting small-game may be an important avenue for signaling long-term consistent provisioning potential as well as phenotypic quality.

In the literature and debate surrounding the Costly Signaling Hypothesis and Family Provisioning Hypothesis, considerable emphasis has been placed on successful harvests of large game as potential costly signals that lead to suboptimal outcomes for a hunter's family. This is due to the belief that the nuclear family of a hunter retains a much larger share of small game than large game in many societies (Bliege Bird & Bird, 2008; Hawkes et al., 2001a; Smith & Bird, 2000; but see Wood & Marlowe, 2014). Thus, it has been argued that men might more effectively provision their families by adopting a small-game-specialist strategy (Hawkes et al., 2001b). The Costly Signaling Hypothesis has frequently been proposed as the explanation for why men would choose to hunt animals which are believed to be less efficient for provisioning. Large game might be valued because the difficulty in hunting them signals the phenotypic qualities of a hunter (Bliege Bird et al., 2001; Bliege Bird & Smith, 2005; Smith, 2004; Smith et al., 2003; Smith & Bird, 2000; Stibbard-Hawkes, 2019), they might be valued because the sacrificial nature of provisioning the group is an honest signal of generosity or cooperative intent (Gurven et al., 2000; Smith & Bird, 2000), or they might be preferred because large game is distributed to a broader audience of recipients, potentially amplifying the "broadcast efficiency" of the signal (Hawkes & Bird, 2002; Smith & Bird, 2000).

But no tradeoff between signaling and provisioning was observed among the Aché. The prey harvest compositions which resulted in the most positive assessment of phenotype among the Aché were those which resulted in greater biomass harvested (Task 2) and which implied more consistent prey harvests (Task 3). Furthermore, the hunters who were chosen as having greater mate value and social partner value were those who harvested a greater biomass (Task 2 and 4), or those who whose harvests implied or demonstrated (Task 3, 4) greater harvest consistency. This is consistent with the finding that Achuar, Quichua, and Zapara forager horticulturalists gained greater coalitional support by sharing more meat regardless of prey size (Patton, 2005). The emphasis on provisioning observed in our study echoes the finding that Aché hunters generally preferred to be in camps where there is greater food abundance over camps where they have more opportunities to highlight their own skill (Wood & Hill, 2000). These results call into question applications of the Costly Signaling Hypothesis which argue that hunters will consistently show-off at the expense of overall foraging return rate, as has been argued by some archaeologists (Hildebrandt & McGuire, 2003; McGuire & Hildebrandt, 2005).

While killing a single large game item did result in a greater positive assessment of hunter phenotype than killing a single small game item (Task 2), this preference was reversed when the total biomass harvested was equalized through harvesting multiple prey items (Task 3). These findings do not support the speculation that Aché hunters who wish to advertise their phenotypes should preferentially target larger animals. Rather, they should pursue prey according to a strategy which maximizes their overall long-term biomass harvest rate. This is consistent with the observation that the Aché generally pursue prey which fall within the optimal diet according to the prey choice model of Optimal Foraging Theory (Hill et al., 1987).

Although our findings do not support the presumption that there is a tradeoff between provisioning and signaling among the Aché, or that harvesting large game provides an inherently superior signal than does the harvest of small game, we acknowledge that different cultural contexts may result in different findings in other populations. The fact that the Aché share both large and small prey equally with all group members while in the forest (Gurven et al., 2002; Kaplan, Hill, Hawkes, & Hurtado, 1984) might explain the particular alignment between signaling and provisioning in this study population. It should be noted, however, that the alignment between provisioning and signaling persists in modern contexts even though large game are shared more widely than small game on current Aché reservations where decisions about marriage, social partners, etc. are being made (Gurven et al., 2002). Whether such an alignment between signaling and provisioning exists in other populations where large game are shared more widely and in greater proportion, as has been argued among the Hadza (Hawkes et al., 2001a; Wood & Marlowe, 2013, 2014), remains an open question. However, currently available Hadza data show frequent small-game hunting and also suggest that the importance of large game hunting can best be understood as a biomass harvest rate maximizing strategy by hunters (Wood & Marlowe, 2014), although some sources disagree (Jones, 2016).

3.4. Study limitations

Despite the strong connections observed between prey-harvest composition and perceptions of hypothetical hunters' phenotypes, and the high degree of cultural consensus surrounding prey rankings and assessments of hunter quality, our study did not directly test for a link between killing these species and actually possessing the superior phenotypic qualities such as greater future provisioning, strength, fighting ability, disease resistance. Further research is needed to evaluate such a link.

Furthermore, our findings cannot conclusively rule out the possibility of halo effects in which better hunters are simply presumed to have better phenotypic qualities in general. It is noteworthy that informants tended to assign higher quality on all four dimensions to the same hunter, suggesting the possibility that participants may simply view hunters as generally good or generally bad, without making fine distinctions between the four aspects of hunter quality examined in this study. When asked which hunter would be better on a given trait, some informants simply replied, "the good hunter", before being prompted to select hunter A or B. However, our results do suggest that informants were able to distinguish certain traits based on differences in prey harvest composition because both fighting ability and disease susceptibility were not predictive of being a preferred mate or social partner in task 2 (Section 2.3.3, Table 5), and in Task 3 the attribution of provisioning ability and strength to small-game hunters was more consistent than the attribution of fighting ability or disease susceptibility. In Task 2 and Task 3 informants should have been explicitly presented with the option to state that hunting outcomes were not informative about the aspect of hunter phenotype being examined.

4. Conclusions

There were two key findings of this study which have implications for the Costly Signaling vs Family Provisioning debate. First, no evidence was found for a tradeoff between signaling and provisioning among the Aché. The hunters who killed a greater total biomass were attributed greater phenotypic quality (Task 2), and desirability as both mates (Task 2 and 4), and social partners (Task 2). When the biomass of prey harvested was equalized, hunters who killed many small prey were attributed greater phenotypic quality, and desirability as both mates and allies. Second, any apparent differences in signal value between large and small game were eliminated once acquired biomass was equalized across large and small game scenarios. These two findings highlight the importance of reconsidering the Costly Signaling vs Family Provisioning dichotomy, and reconsidering the role of small game hunting in discussions of costly signaling. It is no longer fair to assume that large game hunting is inherently superior to small game hunting for signaling phenotype or attracting mates and allies. When large game hunting is more highly valued as a source of prestige, researchers must consider whether that value comes from the food value of the animal or from some other characteristic it possesses.

The "showoff hypothesis" as an alternative explanation for the "sexual division of labor" in hunter-gatherers is a logical extension of signaling theory. However, when food is limited in supply, and survival and fertility are strongly affected by food intake, fitness enhancing signaling may be heavily constrained by demands of food consumption. Our study suggests that hunter-gatherer men may often find an optimal compromise in adopting strategies that both maximize prey harvest rates, and also signal to a social audience that the hunter is likely to provide resources more reliably than other conspecifics in the future.

The larger theoretical goal of this research project is to increase general understanding of the role of costly signaling in human behavior. Among anthropologists, Costly Signaling Theory has generally been applied to explain three types of behaviors: 1) contributions to public goods; 2) costly religious behaviors which primarily serve spiritual purposes; and 3) the pursuit of risky resources, especially when they are widely shared (Barker et al., 2019). The first two categories often entail conspicuous costs which lack a practical justification. Massive expenditures of resources designed to change the perceptions and behaviors of a social audience, such as the Potlatch Festivals of NW Coastal Tribes (Boone, 1998) or the construction of pyramids (Neiman, 2008), seem to be a common feature of human social behavior (Boone, 1998). The American obsession with sending a man to the moon in the mid-20th century might even be a form of costly signaling. However, not all honest signals entail conspicuous costs without an obvious practical justification. Aché hunters seem to vary little in the costs they pay to signal (in terms of time or effort), but vary greatly in their ability to convert those costs into signals (harvested biomass). Because production of the signal provides direct fitness benefits to justify its costs apart from the benefits received from an audience, and because lesser skilled hunters are unable to fake hunting success, hunting among the Aché might best be described as an index (Maynard-Smith et al., 2003) of hunter quality rather than a costly signal.

Data availability

The data associated with this research are available in the supplement.

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Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2022.10.001.

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