# Costly Signaling and Prey Choice: The Signaling Value of Hunted Game

by

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ABSTRACT

For most of human history hunting has been the primary economic activity of men. Hunted animals are valued for their food energy and nutrients, however, hunting is associated with a high risk of failure. Additionally, large animals cannot be consumed entirely by the nuclear family, so much of the harvest may be shared to others. This has led some researchers to ask why men hunt large and difficult game. The "costly signaling" and "show-off" hypotheses propose that large prey are hunted because the difficulty of finding and killing them is a reliable costly signal of the phenotypic quality of the hunter.

These hypotheses were tested using original interview data from Aché (hunter gatherer; n=52, age range 50-76, 46% female) and Tsimané (horticulturalist; n=40, age range 15-77, 45% female) informants. Ranking tasks and paired comparison tasks were used to determine the association between the costs of killing an animal and its value as a signal of hunter phenotypic quality for attracting mates and allies. Additional tasks compared individual large animals to groups of smaller animals to determine whether assessments of hunters' phenotypes and preferred status were more impacted by the signal value of the species or by the weight and number of animals killed.

Aché informants perceived hunters who killed larger or harder to kill animals as having greater provisioning ability, strength, fighting ability, and disease susceptibility, and preferred them as mates and allies. Tsimané informants held a similar preference for hunters who killed large game, but not for hunters targeting hard to kill species. When total biomass harvested was controlled, both populations considered harvesting more animals in a given time period to be a better signal of preferred phenotypes than killing a

single large and impressive species. Male and female informants both preferred hunters who consistently brought back small game over hunters who sometimes killed large animals and sometimes killed nothing. No evidence was found that hunters should forgo overall food return rates in order to signal phenotypic qualities by specializing on large game. Nutrient provisioning rather than costly phenotypic signaling was the strategy preferred by potential mates and allies.

# DEDICATION

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# CHAPTER 1: Introduction

Humans possess many evolved traits that set them apart from other organisms. They have relatively large and complex brains, they cooperate extensively with kin and non-kin alike, and they have complex cumulative culture which makes them uniquely adaptable. Because of their large and slow growing brains, human babies are born less behaviorally capable than comparable mammal species. For nearly 2 decades of life, they are largely dependent on others for food, care, and instruction (Gurven & Walker, 2006). Their short inter-birth intervals relative to other great apes combined with a prolonged period of juvenile dependency mean that mothers often have more offspring than they can provision with food at any given time (Gurven & Walker, 2006)(for a discussion of human life history evolution see (Kaplan, Hill, Lancaster, & Hurtado, 2000)). They compensate for these shortfalls through an evolved cooperative breeding system whereby fathers contribute substantially to provisioning their mates and offspring, and where food sharing with both kin and non-kin is extensive (Hill & Hurtado, 2009). The nutritional importance of male contributions to diet in small-scale societies is rarely contested, however, the proximate motivation for male hunting and food sharing has been the subject of a longstanding debate (Gurven & Hill, 2009; Hawkes, O'Connell, & Blurton Jones, 2001b; Hawkes, O'Connell, & Coxworth, 2010; Hill, Kaplan, & Hawkes, 1993). Viewed through the lens of monogamous pair-bonding and cooperative breeding, it has traditionally been assumed that men target resources which are efficient for provisioning wives and offspring.

Human paternal provisioning occurs in the context of a sexual "division" of foraging labor (SDL) which is observed among all hunter-gatherer societies (Kelly, 2013;

Marlowe, 2007). Generally, men are more likely to hunt animals or collect honey (resources that are obtained in large packages and shared widely), and women are more likely to collect plant, insect, and other sessile small resources. Differences in male and female foraging strategies have been traditionally explained in terms of nutrient complementarity (protein and fats from animals to complement the carbohydrates and sugars from plants) and comparative advantage, with gathering viewed as the foraging activity most compatible with effective child care (Brown, 1970; Hurtado, Hill, Hurtado & Kaplan, 1992; Isaac, 1978; Lancaster, 1978). According to this argument, the demands associated with caring for an infant such as decreased mobility due to the need to carry offspring, the need to make frequent stops for breastfeeding, and the likelihood that a child's cries will scare away animals are all likely to make hunting less efficient for women with small dependent offspring. These constraints, combined with the long learning period needed to become an efficient hunter, may explain why women in small scale societies typically favor harvesting the suite of resources that they do.

The classic view of the SDL is that mothers and offspring receive fitness benefits from meat, honey, and other resources provided by fathers, while skilled hunters receive fitness benefits from provisioning. Potential benefits to skilled hunters include acquiring or retaining more and higher quality mates, achieving earlier age at first reproduction, experiencing improved offspring survival, achieving higher completed fertility, and producing higher quality offspring (i.e. offspring of higher reproductive value) (Smith, 2004). In most cases where it has been measured in foraging societies, being a good hunter and generous sharer is indeed correlated with increased reproductive success and higher social status (Alvard & Gillespie, 2004; Gurven, 2004a; Gurven & Rueden, 2006;

Hawkes, O'Connell, & Blurton Jones, 2001a; Hawkes et al., 2001b; Hurtado & Hill, 1996; Kaplan & Hill, 1985; Marlowe, 1999; Marlowe, 2003; Patton, 2005; Smith, 2004; Smith, Bird, & Bird, 2003; Wiessner, 1996).

Given the assumption that hunters are trying to efficiently provide resources to their families, models from Optimal Foraging Theory (OFT) have been used to make predictions about the resources a hunter should pursue or ignore when encountered during search. OFT models assume that a forager has a specific goal, such as maximizing their rate of nutrient acquisition, and then model the best way to achieve that goal given information about the distribution, abundance, costs, and benefits of pursuing different resources in the environment (Stephens & Krebs, 1986). OFT has been a useful tool for "predicting" which species should be included or excluded from the diet, under what conditions the diet breadth (the range of species included in the diet) should shrink or expand, and how a forager should allocate effort when foraging in a patchy environment.

Traditional assumptions about men's foraging goals, however, were called into question 28 years ago with the introduction of the "Show-Off" Hypothesis (SOH) (Hawkes, 1991). The SOH proposes that the goal of male foragers is to maximize the amount of positive social attention directed to a hunter by potential mates and allies, through providing public goods (large, widely shared game items). The SOH proposes that men consistently bypass resources that should be pursued if men's goal were to efficiently provision the hunter's nuclear family and close kin. According to the SOH bypassed resources should include plant foods and small game which are presumed to be more abundant, entail a lower daily risk of failed harvest, and are presumably shared less widely, thus contributing a greater percentage of the harvest directly to the hunter's

family. The SOH proposes that small game and plants are ignored by hunters in favor of searching for and pursuing large animals which will be widely shared outside the hunter's family, hence resulting in increased "social attention" from potential mates and allies. The SOH explicitly envisions male hunting and meat sharing as a mating strategy rather than a provisioning strategy: hunters kill large and hard to kill prey species to demonstrate their superior phenotypic traits to an audience even at the cost of providing less food for their own nuclear families (or providing food less consistently).

The goal of this dissertation is to examine the relative merits of provisioning vs. show-off-based explanations for male hunting patterns by employing experimental ethnographic evidence from two foraging populations. Specifically, this research aims to determine whether hunters intentionally ignore easy to acquire but profitable resources in favor of targeting less profitable hard to find or hard to kill prey, for the purpose of signaling their phenotypic quality to potential social interactants. In the first chapter of this dissertation explanations of the Family Provisioning Hypothesis (FPH), the "Show-Off" Hypothesis (SOH), and its modified variant the Costly Signaling Hypothesis (CSH) are provided. Then the specific research questions that guided the data collection in chapters 3 and 4 are outlined. In the second chapter the origins and criticisms of the costly signaling hypothesis are reviewed, followed by an examination of the ethnographic literature pertaining to both costly signaling and food sharing. In the third and fourth chapters, research methods and results from studies of the Aché hunter gatherers of Paraguay and the Tsimané hunter horticulturalists of Bolivia respectively are described. In the fifth and final chapter, the empirical results of these studies are synthesized and

their implications for understanding the roles of signaling in provisioning in male foraging strategies are discussed.

## Men's Foraging Goals: Provisioning, Showing Off, and Costly Signaling

Both provisioning and signaling hypotheses for men's foraging are based in evolutionary theory and hence propose the same ultimate goal for hunters: to hunt in a way that maximizes the inclusive fitness benefits of the individual making the foraging decisions. The main difference between them is their proposed mechanism for maximizing inclusive fitness. Provisioning hypotheses propose that the greatest fitness benefits accrue to hunters who maximize the nutrient utility of prey harvested, both as a food source for ego and kin and as a "trade" resource for direct or indirect reciprocity (Hawkes, 1991). Signaling hypotheses, on the other hand, propose that the greatest fitness benefits accrue to hunters who maximize various aspects of the signal value of prey harvested in order to advertise hunter quality and attract the attention of potential mates and allies, even at the cost of lower nutrient acquisition (Hawkes, 1991; Smith & Bird, 2000). A compromise alternative that is not tested here, is that some mix of nutrient and signaling fitness gains determines the favored hunter strategy. In any case, whether a hunter is attempting to provision or signal has implications for the types of prey a hunter should pursue and how prey items should be shared after the kill.

## The Family Provisioning Hypothesis

The Family Provisioning Hypothesis (FPH) proposes that a hunter will prioritize the efficient acquisition of prey with high nutrient utility for their own consumption, provisioning close kin, and for cooperative "trade" via direct and indirect reciprocity. Human children (and those in these study populations specifically) are recognized to be

dependent on adult provisioning, and reproducing females with multiple dependent children through much of their adult lives are frequently unable to meet offspring nutrient needs (Gurven & Walker, 2006; Hill & Hurtado, 2009). According to this hypothesis then, provisioning is primarily in the form of kin investment for unmarried men, and parental investment for married men. In both cases, hunters should prefer to acquire prey with high nutrient utility that compliments the nutrients generally acquired by reproductive women.

The FPH assumes that the purpose of men's hunting is to increase their fitness through multiple pathways: First, hunting directly increases men's inclusive fitness through the provisioning of valuable animal products (food, hides, etc.) to themselves, their nuclear family, and other closely related individuals in their group. This benefit accrues to hunters even if they don't directly control food distributions, or retain 100% of their kill, as long as some threshold minimal portion of acquired resources are reliably used to enhance the survival or reproduction of ego and kin (Gurven, 2004c; Trivers, 1971). Second, hunting additionally increases men's fitness if food and animal products shared with non-kin reliably result in return benefits of some kind for the hunter or his kin (reciprocal altruism) (Gurven & Rueden, 2006; E. A. Smith, 2004). Return benefits of food sharing do not have to come in the form of repaid meat but can come in any fitness enhancing currency such as care for a hunter's offspring, or increased attention to the wellbeing of the hunter's close kin (Gurven, Allen-Arave, Hill, & Hurtado, 2000). Third, benefits may come from sharing food to non-kin in a way that induces them and other observers to more frequently choose the hunter as a cooperative partner, when advantageous cooperative associations are freely chosen (indirect reciprocity) (Boyd &

Richerson, 1989; Gurven, 2004c; Trivers, 1971). Fourth, long term hunting success can enhance the fitness of unmarried men by serving as a cue of their provisioning ability, hence increasing their attractiveness to potential mates.

The third and fourth conditions parallel some aspects of the SOH, however, they differ in important ways. Both the CSH and the SOH specifically propose **inefficient** nutrient acquisition as a means to gain attention and signal information about the hunter. In the case of costly signaling, the inefficiency does not have to come in the form of realized costs and can include situations where the signaling behavior is efficient for high quality individuals, but not efficient for lower quality ones. The FPH specifies that hunters should choose the most efficient strategy for acquiring food nutrients and does not require any intent to signal on the part of the hunter. If the primary information transmitted is the future provisioning ability of the hunter, and if that information is transmitted to others by them watching the outcomes of the hunters foraging as he attempts to maximize nutrient production then the behavior may be better described as a cue than a signal. Signals and cues are distinct in that signals are traits or behaviors which evolved for the purpose of communicating information, while cues are traits or behaviors which can be used as sources of information but did not evolve for the purpose of communication.

The "Show-Off" Hypothesis

Hawkes et al. (1991) were the first to propose that the main goal of male hunting was to "show-off" hunter phenotypic traits. They suggested that male foraging behavior among the Aché hunter-gatherers of Paraguay was not optimal for provisioning a family because hunters were overly focused on the pursuit of large prey species, rather than on

small game and plant foods. Specifically, they argued that hunting large game was an inefficient way to provision families because large animals were shared widely with non-kin and (they claimed) no return benefits were provided by those who received shares. Small game, they suggested, were more abundant, easier to kill, and most importantly, not widely shared so that almost all the food acquired was retained by the family of the hunter (A claim which was contradicted through quantitative analyses of food sharing from the 1980s (Gurven, Hill, & Kaplan, 2002)). This led to the SOH: that Aché men hunted large game specifically in order to attract the favorable attention of potential copulation partners or allies, rather than to efficiently provide nutrients to their families.

The SOH argues that there is often a divergence between harvested prey species that provide more nutrients per unit time to the hunter's family (or provide nutrients more consistently (Codding, Bird, & Bird, 2011)), and prey that provide the most positive signals about desired characteristics (such as strength, skill, stamina, etc..) of the hunters who kill them. The SOH proposes that there are higher fitness payoffs to hunters by signaling phenotypic quality to potential mates and social partners than can be achieved via nutrient provisioning and transfer to close kin and allies (Hawkes, 1991). They propose that the preferential targeting of large and widely shared game species by men (but not women) provides evidence for this claim. Hence SOH proponents propose that hunters intentionally adopt hunting patterns that, after discounting meat shared with non-kin, decrease the amount of food provided to family and kin. In short, the SOH proposes that hunters will seek to maximize the "signal value" of the prey species they harvest rather than the provisioning value, when provisioning value is defined as the proportion of hunted game which is consumed by offspring and kin.

The conflict between showing off and provisioning arises partially because, according to the SOH, the realized nutrient value of hunted prey species must be discounted by the proportion consumed by non-kin. According to Hawkes (1991), meat sharing with non-kin in hunter gatherer groups is a form of tolerated theft (TT), as opposed to reciprocal sharing (Blurton Jones, 1984; Wilson, 1998). According to TT meat is yielded to the demander once the fitness utility of consuming more meat is outweighed by the fitness cost of defending access to it from a hungry bystander. Because food "shared" is simply taken away and not repaid, there is no fitness utility gained from that portion of meat which is shared outside the nuclear family. For this reason, according to the SOH, the food value of large game has to be discounted by the proportion eaten by non-kin, making large game hunting considerably less efficient for family provisioning (SOH often assumes that >50% of large game is lost via food sharing). Small game, on the other hand, are more abundant, easier to kill, and retained by the nuclear family in greater proportions. SOH proponents originally assumed that 100% of small game and plant foods are kept by the family of the acquirer. Thus, they argued, because of differences in the fraction consumed by the hunter's family, hunting for small game is actually a more efficient strategy for provisioning than is large game hunting, even when large game hunting yields more meat per foraging hour on average. They further suggest that large game hunting is a bad strategy for provisioning even when it yields more meat per foraging hour (after accounting for redistribution) because large game hunting is associated with a higher variance in daily acquisition (Hawkes et al., 2001b).

The proponents of the SOH have further argued that large game hunting, followed by redistribution via TT, creates a collective action problem in which each hunter benefits from the harvest of large game by others, but no hunter is incentivized to hunt large game themselves (and lose most of it). The proposed solution to this collective action problem is that large game hunting "attracts social attention" from potential extra-pair mates and allies, which hunters are able to convert into individual fitness even if their families do not benefit nutritionally (Boone, 1998; Hawkes, 1991).

The original authors of the “Show-Off Hypothesis” introduced several key propositions to the discussion of male hunting. These include: the idea that hunter-gatherer food sharing is primarily due to TT with no fitness payback from sharing; that hunting and sharing large animals creates a collective action problem; that signaling strategies result in different prey being targeted than provisioning strategies; that targeting large prey is good for signaling but not for provisioning; and that male hunting creates a conflict of interest between wives who would prefer that their husbands engage in provisioning activity, and husbands who would prefer to signal to obtain additional mates. Many subsequent studies of the role of signaling in foraging behavior have often explicitly or implicitly accepted these propositions about the nature of foraging and signaling, while other studies have challenged these assumptions (Gurven & Hill, 2009).

The original SOH did not explain how meat which was relinquished due to TT could accrue fitness benefits to the hunter. SOH proposed that provisioning of large game would result in "increased social attention" being directed to the hunter by non-kin, which the hunter could then convert into fitness primarily through extra-marital affairs. SOH did not, however, explain why women should want to reproduce with the successful

show-off. If meat sharing is simply TT, then a successful big game hunter could not preferentially direct meat to his wife and children. So why would any woman prefer to mate with a successful big game hunter? Smith et al. (2000) provided a possible solution to this problem by introducing Costly Signaling Theory to the discussion.

## The Costly Signaling Hypothesis

Costly Signaling Theory (CST) is a special case of honest signaling theory that specifies the conditions under which costly behaviors can evolve as reliable honest signals of hidden quality. According to the theory, signals must accurately demonstrate phenotypic quality in some domain in a way that results in audience preferences benefitting the signaler more than the cost of producing the signal. For this to work, individuals must produce a signal of variable strength which is broadcasted and received by an audience, and the audience must use the strength of the signal as a basis for judging a hunter's hidden qualities (Grafen, 1990). Behaviors which cannot be observed by an audience will not function as costly signals. A second critical feature of CST is that higher quality individuals must be more efficient at converting signal effort into fitness (Getty, 2006; Grafen, 1990). This condition, referred to as the increasing efficiency criterion, is met either when higher quality individuals pay a lower marginal fitness cost to signal, or higher quality individuals receive a higher marginal fitness benefit from signaling at any specific level. Because the fitness cost paid and benefits received are based on the quality of the signaler, lower quality individuals achieve their fitness optima either by not signaling or by signaling at lower levels, and hence, the level of a signal produced is an honest indicator of the phenotypic quality of the signaler. Importantly, later analyses have shown conditions under which the mechanisms associated with costly

signaling can sustain signal honesty when few or no realized costs are paid to signal, meaning that the presence or absence of signal costs are not sufficient for determining whether a behavior is explained by costly signaling (Hurd, 1995, 1997; Lachmann, Számadó, & Bergstrom, 2001; Számadó, 2011).

Some examples of potential costly signals include the ornate plumage of male peacocks and other birds (Hamilton & Zuk, 1982; Amotz Zahavi, 1975), bright colors on male guppies (Endler, 1980; Lozano, 1994), stotting by Thompson's Gazelles (FitzGibbon & Fanshawe, 1988; J. M. Smith & Harper, 2003), begging by baby birds (Godfray, 1991), and alarm calls by Eurasian Jays (Bergstrom & Lachmann, 2001). CST has been especially useful in studying the relationships between signaling and immuno-competence (Folstad & Karter, 1992a; Hamilton & Zuk, 1982; Tybur Joshua M. & Gangestad Steven W., 2011).

Hunting is a plausible domain to test for costly signaling because different hunting behaviors are associated with different measurable proxies for fitness costs and benefits, and those costs and benefits are likely to be honestly linked to the phenotypic qualities of the forager. Hunting and fishing require physical strength, fitness, coordination, and expertise that is primarily acquired through experience(Gurven, Kaplan, & Gutierrez, 2006), making it hard to fake hunting ability. Furthermore, the phenotypic qualities which are likely to be associated with successful hunting (strength, health, ability, local knowledge of plants and animals, leadership) are also likely to be of interest to an audience.

Smith et al. (Smith & Bird, 2000) applied CST as an explanation for the costly and difficult pelagic turtle hunts that are used to supply feasts among the Meriam

Islanders (Bliege-Bird, Smith, & Bird, 2001; Bliege-Bird & Bird, 1997; Smith et al., 2003; Smith & Bird, 2000). Turtle hunting at sea requires a boat, expensive fuel, and it involves recruiting and coordinating a group of fishermen. They argued that hunting large turtles at sea was so difficult and inefficient as a foraging method and that the hunters retained such a small proportion of the kill, which was shared with guests during a communal feast, that provisioning kin could not be the explanation for sea turtle hunts. Instead, they argued that the turtle hunt and subsequent sharing served as a costly signal of the lead hunter's wealth and leadership ability.

According to Smith and Bliege-Bird's (2000) application of CST, a hunter could reap fitness benefits from killing a large animal and giving away meat, even if the meat was relinquished due to TT, as long as the cost (or difficulty) of hunting the animal served as an honest signal of a hidden and desirable phenotypic traits of the hunter, resulting in that hunter being preferred as a mate or ally. Generalizing from this, they suggested that hunting a specific prey species could serve as a costly signal as long as killing that species was difficult or costly in a way that revealed hidden characteristics about the hunter, and those characteristics, once revealed, led to the hunter receiving fitness benefits from potential mates and allies, or deference from potential competitors. This could be true, for example, if the species was difficult or dangerous to find or kill. Successfully hunting such animals might cause observers to believe that a hunter was particularly strong, skilled, or healthy, or if the hunt required coordinating many individuals it might cause observers to believe that the hunter is wealthy or has influence.

It should be noted that in some contexts it has been argued that generous sharing can serve as a costly signal of prosocial intent (Bliege-Bird & Power, 2015; Gurven et al.,

2000; Smith & Bird, 2000). These arguments are touched on in the literature review section. While it is certainly true that hunting and generous food sharing can serve as costly signals of cooperative intent, these cases are arguably different in nature than the SOH. Costly signals of cooperative intent are related to the concept of indirect reciprocity and can be used to explain the provisioning of public goods as a means to maintain access to food sharing networks. These types of signals are not competitive in the sense implied by the show-off hypothesis, and therefore, are not the focus of this dissertation.

CST has provided a more explicit and theoretically sound basis for studies of the role of signaling in human foraging than the original "Show-Off Hypothesis". For this reason, the original form of the SOH has largely been reframed in terms of costly signaling. It should be noted, however, that CST has been the subject of considerable debate and criticism amongst biologists studying honest signaling theory (a review of the origins, theory, and criticism of CST is presented in the next chapter).

Drawbacks of Costly Signaling Hypothesis for Studying Human Hunting Choices

Although it is clear that the SOH is theoretically subsumed by CST, there are problems with framing the discussion of human hunting in terms of costly signaling. One problem is that total fitness benefits of a behavior may come from more than one source. If most of the fitness benefit of a behavior comes from its useful, non-signaling contribution, with a small benefit derived from signaling as well, it doesn't make sense to say that the behavior evolved because of its signaling value. Under those conditions, it could be the case that the behaviors being referred to as signals are actually cues.

It is easy to hypothesize that costly signaling is the explanation for almost any successful or useful behavior, but it is extremely difficult to demonstrate that a useful

behavior is adopted mainly for the purpose of signaling. The fact that a behavior is costly and that the increasing efficiency criterion is met does not indicate that the behavior is adopted because of its signaling value. Most behaviors are costly in some way, and positive phenotypic correlations are common in nature, making it easy to find cases where the increasing efficiency criterion is met. Two important questions that must be answered before hunting behavior can be definitively identified as costly signaling are whether men actively ignore more effective ways to supply nutrients to kin, and whether the signaling component of hunting provides a greater fitness benefit than the non-signaling component of nutrient provisioning.

No ethnographic study thus far, has been able to quantitatively demonstrate that a specific phenotypic quality is signaled by successfully hunting a specified prey type. Experimental studies of costly signaling in non-humans have occasionally been able to measure the fitness costs and payoffs of specific signaling behavior and signal values using experimental interventions (Barbosa & Møller, 1999; Cotton, Fowler, & Pomiankowski, 2004; McGraw & Hill, 2000; Møller et al., 1998; Roberts, Buchanan, & Evans, 2004); however, practical and ethical considerations have made such research difficult for humans. For this reason, quantitative studies of costly signaling in humans are usually limited to cases wherein realized and measurable signaling costs (as opposed to potential costs from over signaling) maintain signal honesty. This problem is further compounded by phenotypic correlations, because individuals who are high quality in one domain are often high quality in many domains, potentially decreasing the measurable costs of their signaling behavior (Nur & Hasson, 1984). Given these limitations, much of the human hunting literature that invokes costly signaling focusses on the pursuit of prey

that are apparently less efficient from an optimal foraging perspective than presumed available alternatives. Likewise tests of predictions based on CST among humans typically rely on verbal arguments that the increasing efficiency criterion is met, rather than empirical demonstrations that this is true.

Although these limitations make it difficult to study costly signaling in the context of human hunting, it is not impossible. Creative methodologies have been used to quantitatively test aspects of the hypothesis. One example of this is a study examining the hormonal responses to hunting success among Tsimané men (Trumble, Smith, O'Connor, Kaplan, & Gurven, 2014). This study showed that neither the size of animal killed, nor the presence of an audience were associated with increased levels of cortisol or testosterone among successful Tsimané hunters, as would be expected if men were excited to show off their kills.

Summary and Research Questions

In the proceeding sections two alternative explanations for the purpose of male hunting and subsequent food sharing have been presented. These include the family provisioning hypothesis, which proposes that the goal of foragers is to maximize the utility of prey harvested both directly as a source of nutrition, and indirectly as a trade good (reciprocal altruism), or inducement for future cooperation (indirect reciprocity). The family provisioning hypothesis proposes that men forage primarily to attract long term mates, to provision close kin, and once married, to provision wives, offspring, and other relatives. The second explanation is that male hunting is a form of advertising. That hypothesis has been developed in two closely related forms. The "show-off" hypothesis proposes that the goal of foragers is to maximize the social attention directed

at them by targeting large game which is shared as a public good. The SOH proposes that the primary payoff to men's foraging come in the form of increased status and access to extra-pair mates. A related variant of the advertising hypothesis is that male hunting is a form of "costly signaling" in which males preferentially target rare or hard to kill prey in order to signal their hidden phenotypic qualities to potential mates and cooperative partners. The CSH proposes that the inefficiency or difficulty of hunting certain species is an honest signal of the phenotypic quality of the hunter and that certain prey are thus preferred because of the difficulty of acquiring them.

In chapter two of this dissertation a literature review examining debates surrounding the FPH versus SOH and CSH is presented. This chapter begins with a brief review of the animal behavior literature related to the origins and criticisms of the CSH. Next, ethnographic evidence and debates pertaining to the presence of costly signaling among the Meriam and Ifaluk Islanders, as well as the Kubo, Hadza, Aché, Martu, and Tsimané is reviewed. Finally, evidence relevant to the food sharing patterns of people in these small-scale societies is examined.

Given the current state of the debate, in chapters three and four informant-based interview research is presented that will advance the debate by addressing 5 lines of questioning using quantitative evidence from two small-scale societies:

1) Prey provide nutrient biomass to consumers, and hunters who bring in more total biomass inadvertently "signal" their ability to provide food. But some prey might also be exceptionally hard to find or kill, indicating exceptional skill and strength of hunters who kill them. **Are there clear examples of prey whose value as a signal of hunter-phenotype is associated with the costs of acquiring them (HtF, HtK), and not**

**simply a function of how much food value they contain?** In other words, are there smaller but hard to find or kill prey that signal to an audience greater hunter skill and strength, and are there larger prey that provide no real signal of hunter strength or skill because they are easy to find or kill? Do all same size prey carry approximately the same signal value about hunter characteristics?

2) Harvesting specific types of prey could potentially provide signals of hunter phenotype. **Is it true that killing different prey lead informants to infer variation in hunter phenotype on dimensions of a) Expected Future Provisioning; b) Hunter Strength; c) likelihood to win physical contests with other men; d) hunter health - disease resistance?**

3) Some hunting strategies and prey sets may be better than others for signaling specific aspects of hunter phenotype. **Which aspect of perceived hunter phenotype have the greatest influence on whether that hunter will be preferred as a mate or ally?**

4) There could be a divergence between prey that provide high food biomass and prey that signal positive hunter phenotypes. **Are a hunter's perceived phenotypic quality and preferred status influenced more by their long-term hunting return rate or by the prey species they kill?**

5) Both the SOH and CS claim that there is a difference between the hunting strategies which are best for provisioning families, and the strategies which are best for signaling phenotypic quality. **Is there a tradeoff between hunting for maximum food value vs. hunting for maximum signal value? Which strategy would lead to better mating opportunities or more social partners as judged by informant preference?**

These questions are addressed in the following chapters through a series of ethnographic interviews in which informants are asked to compare prey by size, difficulty to kill, and difficulty to find, as well as hypothetical hunters based on the prey species they are reported to have killed. In the final chapter of this dissertation, these questions are systematically examined in light of the evidence presented in chapters three and four, and the implications of these findings for understanding of the provisioning versus signaling debate are discussed.

# CHAPTER 2: Literature Review

In this chapter the ongoing debate about the evolutionary purpose of men's hunting behaviors is contextualized. In order to understand whether men's hunting should be viewed as costly signaling, it is necessary to understand the origins and theory of the costly signaling hypothesis in evolutionary biology. The first section of this chapter contains a review and critique of Costly Signaling Theory (CST) followed by a review of ethnographic evidence pertaining to CST as an explanation for male hunting. Rather than reviewing the Costly Signaling vs Family Provisioning debate chronologically, each of the small-scale societies which have been important to this debate are examined as individual case studies. A central theme in the CST vs FPH debate is the question of how food is shared. There are substantial disagreements about whether food sharing should be viewed as a form of reciprocal exchange or tolerated theft, and how this impacts the value of large and small game from both a signaling and a family provisioning perspective. For this reason, the third section of this chapter contains a brief review of literature pertaining to food sharing in these and other small-scale societies.

## Costly Signaling: Theory, Background, and Criticisms

In this section the history, theory, and criticisms of CST in general are reviewed. This chapter begins with a discussion of its history and origins from Zahavi's (1975; 1977; 1999) "handicap principle" all the way through its formal description by Grafen (1990). This is followed by a look at criticisms of Grafen's model, before leading into the next section of this chapter, where the ethnographic evidence pertaining to CST and its alternatives as explanations of human hunting patterns is reviewed. For a recent

summary of the literature related to costly signaling in the context of human hunting, see Stibbard-Hawkes (2019).

## History and Background of Costly Signaling Theory

CST has a dual origin in economics and biology. Early applications of signaling theory to economics came in the form of a model of employer hiring decisions (Spence, 1973). A scenario was described in which employers needed to discriminate between the quality of job applicants. In order for signals of quality to be useful in distinguishing between job candidates, it was determined that the cost of producing the signal needed to be negatively correlated with the quality of the potential employee, such that producing the signal was less costly for high quality job applicants. CST entered the biological literature as the "handicap principle", a verbal model based on a sports metaphor (A. Zahavi, 1977; Amotz Zahavi, 1975; Amotz Zahavi & Zahavi, 1999). In horse racing, the fastest horses would be given handicaps in the form of weights carried under their saddles to make the race more competitive. The quantity of weight a horse could carry while still retaining a competitive advantage (the signal) was an honest indicator of their hidden quality (strength and speed). Since the best horse wore the heaviest handicap and yet remained competitive, one could always tell which horse was best.

The handicap principle was not well received initially because of the vagueness of the verbal model and because it was argued that handicap signaling would lead to a Fisherian runaway process in diploid species (Pomiankowski & Iwasa, 1998), wherein female selection for handicap signals would cause those traits to become exaggerated to the point of becoming a net fitness cost (Fisher, 1930). Furthermore, analyses of the

Philip Sidney game, a simple model of costly signaling, showed that costs were not needed to maintain signal honesty when the signaler and audience had coinciding interests (John M. Smith, 1991). Later work by Smith (1994) described a variety of conditions under which costs would or would not be needed to maintain signal honesty.

The handicap principle was later formalized into "Costly Signaling Theory" (CST). Life history modeling by Nur and Hasson (1984), and formal analytical modeling by Grafen (1990) and Godfray (1991) demonstrated how, under a robust set of assumptions, costly signaling can be an adaptive strategy that increases the net fitness of high quality signalers without leading to a Fisherian runaway process. Nur and Hasson (1984:284) portrayed costly signaling as a logical outcome of the Fisherian runaway process rather than a replacement for it. Nur and Hasson further differentiated costly signaling into additive and multiplicative models. The multiplicative model describes situations in which one aspect of fitness is traded off for another, such as lowering survival to increase reproductive success. The model is multiplicative because the fitness payoff to the signaler is the product of two currencies (in this case survival and reproduction). Mathematical modelling by Kokko (1998) has shown that multiplicative models may involve tradeoffs between various components of fitness, but that these tradeoffs occur within, rather than between, individuals. Because tradeoffs between fitness components occur within individuals who may vary in overall quality, some individuals will be better on all measures than others.

Multiplicative models are common in the context of sexual selection and competition for access to mates. Males engage in dangerous and costly displays such as

fighting and developing costly ornamentation which decrease survival but enhance reproduction. In Nur and Hasson's models (1984), higher quality males had higher survival and higher reproduction in spite of paying higher signal costs. They showed that as signaling becomes more costly relative to its fitness benefit, the difference in level of signaling between high-quality and low-quality signalers would decrease. Some examples of potential costly signals include the ornate plumage of male peacocks and other birds (Hamilton & Zuk, 1982; Amotz Zahavi, 1975), bright colors on male guppies (Endler, 1980; Lozano, 1994), stotting by Thompsons Gazelles (FitzGibbon & Fanshawe, 1988; J. M. Smith & Harper, 2003), begging by baby birds (Godfray, 1991), and alarm calls by Eurasian Jays (Bergstrom & Lachmann, 2001). CST has been especially useful in studying the relationships between signaling and immuno-competence (Folstad & Karter, 1992a; Hamilton & Zuk, 1982).

The additive costly signaling model describes the situation in which the fitness benefits and costs are additive rather than multiplicative, usually because they involve only one fitness currency. The sports handicap metaphor was critiqued on the basis that it described an additive outcome (decreasing your chances to win, in order to demonstrate that you could still win), while many signaling systems are better described by a multiplicative model (Getty, 2006). A stotting gazelle, for example, is hypothesized to pay a survival cost in order to reap a survival benefit. By spending time and energy signaling its ability to escape a predator rather than actually fleeing, the gazelle is decreasing the likelihood that it will successfully escape if pursued but is also decreasing the likelihood that it will be pursued. This is true because stotting provides a means by which predators can distinguish the condition of gazelles, allowing them to target

gazelles in poor condition. As long as the gazelles which signal the strongest are still able to escape the best, stotting for this purpose would be an evolutionary stable strategy (ESS). The conditions for an additive model to be an ESS are more restrictive than for the multiplicative model (Nur & Hasson, 1984).

### Grafen's Costly Signaling Model

Grafen (1990) modeled a signaling system with the following characteristics: 1) Signalers have a hidden quality of interest to receivers; 2) Signaler quality varies between individuals and cannot be altered by the signaler; 3) Signalers can pay a cost to produce a signal of varying strength, and receivers use the strength of the signal to assess the hidden quality of the signaler; 4) Receivers respond to the signal in a way that enhances the fitness of the signaler, with higher signalers receiving greater net benefits. Signalers will continue to increase their level of signaling until the marginal net fitness gain of a higher level of signaling drops to zero (this maximizes the ratio of signal fitness gains to signal costs).

According to CST, all individuals will continue to increase their level of signaling until the net fitness benefit of signaling at a higher level becomes zero. For costly signaling to be an ESS, higher quality signalers must receive their maximum net fitness gain from signaling at a higher level than lower quality signalers. This condition is satisfied when the ratio of the marginal costs of signaling to the marginal benefits resulting from signaling is an increasing function of quality (Grafen, 1990:520), meaning that higher quality individuals pay a lower marginal fitness cost to signal, gain a higher marginal fitness benefit from a given level of signaling, or both (Getty, 1998; Godfray,

1991; Johnstone, 1997; Smith, J.M., 1991). This condition protects against false or over-signaling and is analogous to Getty's (2006) "increasing efficiency" criterion.

### Critiques of Grafen's Model

Some have critiqued Grafen's models, arguing that potential costs for over-signaling (signaling dishonestly) are sufficient to maintain honesty without any realized costs being paid (Hurd, 1995, 1997; Lachmann et al., 2001; Számadó, 2011). These critiques are directed at the model assumption that all signalers must pay a realized cost to signal according to CST. However, formal Costly Signaling models do not, explicitly require that signalers pay a fitness cost when honestly signaling, only that there is a fitness cost to dishonest (over-) signaling. The view that honest signaling can be maintained by the potential fitness costs of dishonest signaling is consistent with Grafen's model, which shows that the partial derivative of fitness as a function of signaling (holding quality constant) must be negative, but does not explicitly require that any realized costs be paid for signaling at equilibrium (Grafen, 1990, section 2.2 & appendix 3). The conclusion that honest communication can be sustained without realized fitness costs to signalers has been repeatedly demonstrated (Bergstrom, Számadó, & Lachmann, 2002; Hurd, 1995, 1997; Lachmann & Bergstrom, 1998; Lachmann et al., 2001; Számadó, 1999, 2000, 2011).

Although Grafen's models of costly signaling address many of the potential criticisms of CST, the original sports handicap metaphor on which they were based failed to do so. Research guided only by the sports metaphor can easily lead to mistaken conclusions regarding the applicability of CST, which has led some researchers to

question its usefulness and even call for its retirement (Getty, 2002, 2006; Számadó, 2011). CST has also been criticized on the basis that other mechanisms, such as phenotypic "indices" (Hurd & Enquist, 2005; Searcy & Nowicki, 2005; Veherencamp, 2000), and very low-cost signals (Bergstrom & Lachmann, 1997; Bergstrom et al., 2002; Lachmann & Bergstrom, 1998; Lachmann et al., 2001; Számadó, 1999, 2000, 2011) can also produce honest communication in the face of conflicting interests; that other models can also account for the evolution of honest signaling (Kane & Zollman, 2015); and that, when reliable honest signals are too costly, low cost dishonest communication is also a likely outcome (Dawkins & Guilford, 1991; Számadó, 2000).

## Ethnographic Evidence of Costly Signaling

In this section, ethnographic evidence pertinent to discussions of CST and the SOH as explanations for patterns in human hunting is examined. Specifically, attention is given to evidence suggesting that hunters engage in the pursuit of inefficient prey types in order to signal phenotypic quality. While some of the studies examined large but low ranked (low return rate upon encounter) animal species, the majority examined large and highly ranked prey (prey which are efficient from an OFT perspective), however, the SOH proposes that meat shared from large game isn't repaid, and that its value should be discounted accordingly, potentially changing the rank of prey from an OFT perspective. Readers should keep in mind the question of whether hunters are attempting to maximize the nutrient utility or signal value of prey they harvest, and whether the evidence is more consistent with the goal of provisioning families or with the goal of attracting extrapair mates and allies.

Attempts have been made to quantitatively test costly signaling and show-off explanations for male hunting patterns among the Meriam (Bliege-Bird, Smith, & Bird, 2001; Bliege-Bird & Bird, 1997; Smith, Bird, & Bird, 2003; E. A. Smith & Bird, 2000), and Ifaluk islanders (Sosis, 2000, 2002), the Kubo (Dwyer & Minnegal, 1993), the Aché (Hawkes, 1991; Hill, Kaplan, & Hawkes, 1993; Wood & Hill, 2000), the Hadza (Hawkes, O'Connell, & Blurton Jones, 2001a, 2001b; Hawkes & Bird, 2002; Hawkes, O'Connell, & Blurton Jones, 2014; Hawkes, O'Connell, & Coxworth, 2010; Wood, 2006; Wood & Marlowe, 2013, 2014), and the Martu (Bliege-Bird, Codding, & Bird, 2009; Bliege-Bird & Bird, 2008). Here evidence is examined which pertains to whether hunters ignore more efficient food sources to exploit resources with potential signal value, and whether informants gain fitness benefits from doing so. In each of these cases certain assumptions of signaling models of human foraging have been tested and observed patterns of behavior compared with expected behavior if the goal of foraging is to signal quality in some domain. However, despite 25 years since the initial proposal of the SOH, none of its proponents has ever attempted to measure the signal value of any food resource obtained, nor tested whether signal value per unit time foraged is maximized rather than nutrient gain per unit time foraging. Most "tests" of the hypothesis that are claimed to support it are not tests, but simply "predictions" about things that would supposedly be true if the SOH were true. However, many of those "predictions" do not necessarily flow uniquely from the show-off model of men's hunting. Instead they are often predictions that are equally expected from other models about men's foraging goals.

## The Meriam Islanders

The most convincing case study of the CSH in male foraging practices comes from the Meriam Islanders (Torres Straights, Australia), wherein a subset of men regularly engage in costly and difficult attempts to capture turtles at sea, in order to provision large public feasts in which neither they nor their families get a larger than average share of the meat (Bliege-Bird & Bird, 1997). Turtle hunting occurs during both the nesting and feasting seasons. During the nesting season turtles can be pursued at sea or captured on the beach. Because of differences in turtle behavior during different times of year, turtle collecting and pelagic turtle hunting during the nesting season provides higher returns than pelagic turtle hunting during the feasting season (Bliege-Bird et al., 2001). Smith et al. (Smith & Bird, 2000) make a case that turtle hunting during the feasting season is costly signaling by arguing that only a subset of (presumably high quality) men engage in turtle hunting because of the great difficulty and cost in terms of time and gasoline. They argued that turtle hunting should be considered a signaling activity rather than a provisioning activity because shared meat is a public good, distributed to a large audience, and not counterbalanced by trade. They posit that different roles in the hunt signal different qualities, with "public spirit" being advertised by young hunters, and wealth, leadership, and knowledge being advertised by hunt leaders. And they argued that younger men received benefits in the form of enhanced political standing, and potentially enhanced desirability to future in-laws, while hunt leaders gained increased reproductive success and political power (Smith et al., 2003; Smith & Bird, 2000).

Bliege-Bird et al. (2001) make the argument that the purpose of Meriam turtle hunters is to signal by provisioning feasts, since, after calculating the man hours and fuel costs involved, pelagic turtle hunting yields fewer calories per man hour of effort (4,653 Kcal/man hr overall return rate during hunting season, n = 10 hunts) relative to other provisioning methods such as sardine net fishing (11,008 Kcal/ man hr overall return rate, n = 28 hunts), and families of turtle feast hunters do not receive a special share. In some ways this sounds like a nice example of the SOH, which proposes that men pursue large food packages for the purpose of sharing meat widely and attracting positive social attention.

There are two potential criticisms of this this study. First, it isn't clear that any alternative food source could be used to provision a feast, so it is not obvious that turtles are selected as prey due to the cost associated with hunting them as opposed to being selected because they provide the large package size needed for a village feast. Of the 54 feasts observed by Bliege-Bird et al. (2001) the average attendance was 174.9 people, indicating that feasts require very large quantities of food harvested in a very short time period. Alternative strategies may yield higher returns per unit time, but they do so with lower variance and over a shorter foraging period, meaning that there are fewer failed hunts, but also fewer hunts that return large bonanzas of food. The very act of choosing to provision a public feast may be a case of costly signaling, but little evidence was found that hunters are intentionally choosing inefficient prey as a method of signaling, as suggested by the SOH and CSH. The second potential criticism is that, while organizing and providing for a feast may indeed be a case of costly signaling, turtle hunting does not represent a significant fraction of the total foraging effort of Meriam Islander men. The

show-off versus provisioning debate is primarily about general daily foraging patterns, not about special cases such as provisioning feasts.

Bliege-Bird et al. (2001) present data on spear fishing which is more directly relevant to discussions of daily foraging practices and the SOH. While men engage in both spear fishing and reef collecting, they spend twice as much time spear fishing as reef collecting on average (63% of reef foraging time was spent spear fishing and 31% was spent shellfish collecting). Based on their sample of observations, they show that men gain an average of 1,492 Kcal/hr of foraging for shellfish on the reef, but only 292 Kcal/hr while spear fishing in the same habitat during the same low tides. They note that many men ignore shellfish encountered while spear fishing, even when OFT predicts that they should be included.

In a sample of 33 interviews conducted with Meriam men and women, Bliege-Bird et al. (2001) report that none of the informants would nominate anyone as a good shellfish collector because they viewed success at shellfish collecting as being a byproduct of foraging effort, not skill. Supporting this claim, Bliege-Bird et al. showed that time spent foraging was a significant positive predictor of harvest size among shellfish collectors but not among spear fishermen, however, this conclusion appears to be drawn from a sample of only 26 spear fishing events, and the significance of the trend might change with increasing sample size. Informants were willing to nominate 15 men as being the best spear fishermen. Of these, one man was a far outlier both in terms of frequency of spear fishing, overall return rate from spear fishing and in reputation. However, even this man still gained a lower overall energetic return rate from spear

fishing than the mean from shellfish collecting. It is not clear what benefits this man received for his reputation apart from being recognized as the best fishermen (he received 1/3 of all nominations for best living spearfisherman). Bliege-Bird et al. (2001) suggest that the spearfisherman may be attempting to intimidate potential competitors (in the past, the spear was a common weapon for ambushing competitors), as opposed to attempting to attract mates, since they propose that wives should be more interested in men who collect shellfish.

Ifaluk Islanders

In a similar ethnographic context, Sosis (2000) looked for evidence of show-off behavior on Ifaluk Atoll (South Pacific). He argued that torch fishing was a costly signal of work ethic and the productivity of a matriline. Sosis observed that torch fishing was a widely observable practice and that women took note of who participated, unlike in their highly segregated work in other contexts. Sosis argued that torch fishing was costly because of the physical difficulty and long duration of foraging bouts relative to other foraging activities, and because the ritual nature of torch fishing imposed a large number of preparation costs which weren't directly related to foraging efficiency. Sosis did not, however, provide clear evidence that the "costs" of torch fishing impose actual fitness costs on participants. Since torch fishing takes place at night, no indication is given that torch fishing trades off against other, more productive forms of fishing. Although Sosis reports that torch fishing is less efficient than types of fishing done during the daytime (for example, Sosis (2002) reports that fishing in the lagoon provided a mean per capita return rate of 0.79 – 0.82 kg/hr vs the 0.43 kg/hr achieved by torch fishing), he also reports that, when asked about the low returns, torch fisherman stated that they had

expected to capture more fish than they did. This suggests that the small sample of observed torch fishing events may have been less successful than normal. After controlling for age, education, marital status, and clan affiliation, Sosis found that participating in torch fishing was a reliable indicator of greater frequency and success of fishing overall, and thus could serve as a reliable indicator of both work ethic and fishing ability. Although no data were collected to assess the fitness consequences of torch fishing, Sosis did find that most torch fishermen were unmarried, implying that their goal could be to attract the attention of future mates.

As with turtle hunting among the Meriam, torch fishing takes place in a ritualized context and isn't representative of the general foraging pattern of the Ifaluk Islanders. Since no alternative foraging strategies can be done at night, any signal value associated with torch fishing should derive from the choice to participate (foraging effort) rather than from the species being targeted (prey choice). Likewise, because torch fishing is a group activity and because women are not present on the trip, it is not likely that men use their individual performance as a means to attract mates. It is plausible, however, that choosing to participate in a torch fishing bout is a signal of work ethic or group productivity.

### Kubo Hunter-Horticulturalists

Although they didn't directly test the "show-off" hypothesis, Dwyer & Minnegal (1993) looked for evidence of showing off among the Kubo hunter-horticulturalists (Papua New Guinea). Kubo men hunt small game and tend to be individually specialized in the species they pursue. They found that there were individuals who produced

substantially more meat than others, and that these individuals produced more meat while resident in camps than when out in the surrounding countryside, as would be expected if they were attempting to show-off for an audience. However, there are many non-signaling reasons why hunters might produce more when in resident camps (e.g. provisioning kin), so this observation is not very informative. The authors did not find differences in reproductive success between high and low producing males. They argued that Kubo hunting represents a specialization of labor wherein different men specialize in particular game animals for provisioning rather than signaling purposes. They concluded that men were not intentionally targeting inefficient prey for the purpose of signaling.

Hadza Hunter-Gatherers

Among the Hadza, evidence for "show-off" hunting is mixed. One group of ethnographers concluded that Hadza big game hunting could only be explained by "showing off" (Hawkes et al., 2001a, 2001b; Hawkes & Bird, 2002; Hawkes et al., 2014, 2010). But a second group of ethnographers concluded that Hadza foraging was aimed at provisioning kin, not signaling hunter quality (Wood & Marlowe, 2013, 2014). Based on data collected with the Hadza hunter gatherers of Tanzania between 1985-1989, Hawkes and colleagues argued that Hadza men were targeting large game and frequently bypassing smaller animals, plants, and other resources, which they shouldn't ignore if their goal was to provision families. In a sample of 2,076 hunter days collected between 1985-89, Hadza men killed 71 large animals yielding approximately 10,115 kg or 4.9 kg per hunter/day. Data on small game hunting returns were limited in their data set to a sample of 75 hunter/days, during which time, hunters brought in 0.062 kg per hunter/day on average. Extrapolating from this, they estimated that small game constituted less than

1% of the biomass harvested by hunters (Hawkes et al., 1991). Based on a sample of household sharing events, Hawkes et al. (2001a) reported that the families of a successful hunter keep on average 5% of the edible body weight of animals weighing between 40 - 180 kg, and 10% for animals weighing more than 180 kg. By assuming that the nuclear family of the hunter gets to keep 10% of the meat from large game, and 100% of the meat from small game ( < 40 kg), and using the return rates from daytime large game encounter hunting (0.78 kg/hr) versus from small game hunting and snaring experiments, they estimated that a hunter could gain 0.08 kg/hr of meat for his family by specializing in only searching for and pursuing large game, and 0.04 kg/hr of meat by specializing in only hunting small game (Hawkes et al., 2001b).

Hawkes and colleagues admit that men would achieve a lower overall mean return rate by focusing exclusively on small game hunting, however, they propose that this should still be more desirable to mates because it would result in lower daily acquisition variance. Furthermore, Hawkes et al reported that the Hadza regularly ignored small game in favor of continuing to search for large game whereas they assert that the best strategy for provisioning would be to pursue small game whenever it was encountered in addition to pursuing large game.

They further argue that even with its lower mean return rate, small game should be the preferred prey from the perspective of family provisioning because it results in returns to the family consistently, whereas large game is highly inconsistent in its day to day yields. The observed pattern of focusing exclusively on high variance big game hunting is designed for signaling, they suggest. They propose that signaling is

maximized by pursuing large game which is rare, hard to kill, and shared widely so that everybody forms a favorable opinion of the men who are successful big game hunters even if the families of those men eat less meat than they would if small game were hunted. No specific claims were made about what phenotypic quality was being signaled by pursuing large game although they claimed that hunters who killed large game would be preferred as mates and allies (Hawkes et al., 2001b).

In contrast, another group of later ethnographers contested the claim that the Hadza are big game specialists (Wood, 2006; Wood & Marlowe, 2013, 2014). These researchers found that, rather than specialize on big game, Hadza men frequently harvested small game, honey, and fruit, bringing food every 1.8 and 3.6 days for wet and dry seasons (Wood & Marlowe, 2013). Based on 2,297 person days of observation collected between 2005 - 2009, they found that Hadza men brought back small game, fruit, and honey 853 times. Looking only at meat, men brought animals back to camp 229 times (when multiple small animals were brought back by a single hunter, this was counted as a single event). In 79% (180/229) of the cases where animals were brought back to camp, the animal(s) weighed less than 10 kg (Wood & Marlowe, 2014). They argued that Hadza hunting decisions were primarily motivated by the goal of provisioning family through the pursuit of both large and small game as well as honey and fruit.

Wood and colleagues also contest estimates made by Hawkes and colleagues that Hadza men can keep 100% of the meat from small game they capture and only 10% of the meat from large game. They report that the families of successful hunters retained

about 42% of the total carcass weight of large game killed, including the animal's skin. The successful hunter's household consumed 18% of the carcass weight from large game and 47% from small game (Wood & Marlowe, 2014). In their sample, hunters kept twice as much of the meat from large game kills as was observed by Hawkes and colleagues, and hunters only retained half of what Hawke's group estimated for small game. Furthermore, Wood and Marlowe suggest revised rates for the on-encounter profitability of hunting large game (2,058 Kcal/hr) and small game (1,121 Kcal/hr) respectively which implies that men should pursue both classes of game based simply on optimal foraging principles (not costly signaling).

The Wood and Marlowe estimates were made using three assumptions. 1) The proportion of hunting time spent handling large game and small game during 40 hunter focal follows (handling time is the time spent actually pursuing, killing, and butchering prey) is representative of their proportions in the broader 2,297 hunter day data set. 2) The proportion of large and small game kept by a hunter's nuclear family during meat sharing experiments is representative of the proportion kept overall. 3) Each of the hunters in the sample hunted for a mean of 4.1 hours per day (based on Hawkes et al measured hunt times). They then divided the fraction of the edible weight that would be kept by the hunter's family for all large and small game from the 2,297 hunter/day sample by the total estimated time spent handling large and small game respectively and then converted the resulting Kg of meat into Kcal. Wood and Marlowe's estimates showed that pursuing large game yielded roughly twice the on encounter return rate as pursuing small game, even after adjusting for differences in the proportion kept by the nuclear family.

The show-off proponents presumed that Hadza men had no control over how meat was redistributed (assuming that meat is transferred due to tolerated theft and hence no return payoff is expected), and that men simply reacted to the constraint that large game were mainly going to provision non-family members. The possibility that males were engaging in a strategy of generalized reciprocity in order to reduce the risk of food shortfall was discounted on the basis that men did not control distributions of game they killed. Likewise, they argued that the lack of producer control of meat distributions meant that hunters could not be sharing meat for the purpose of receiving reciprocal fitness enhancing benefits (trade). However, later analyses by Gurven et al. (2004) showed that Hadza men who shared more meat also received more meat (correlation between meat given and meat received $r = 0.46$), implying some degree of producer control and fitness payback to good hunters.

In support of the family provisioning view, there is evidence that Hadza men increase foraging effort when they have dependent offspring (Marlowe, 2003; Wood & Marlowe, 2013) and that Hadza wives and offspring gain weight when their husbands are successful hunters (Hill et al., 1993). As evidence that men increase foraging effort in response to dependent offspring, Wood and Marlowe (Wood & Marlowe, 2013) report that on a given day 28% of single men and 31% of married men with no dependent offspring brought food to camp, while married men with dependent offspring brought food back to camp on 42% of days. Furthermore, they report that married men bring back greater quantities of fruit and honey (resources that are shared less widely) when they have dependent offspring (Marlowe, 2003). This finding is consistent with the hypothesis

that the purpose of male foraging and the gendered division of labor is to provision nuclear families (Marlowe, 1999; Marlowe, 2007).

In contrast to this, Blurton Jones (Jones, 2016) finds no significant effect of father absence or reputation on measures of child growth up to age five, nor do they find a significant effect of father presence on the weight of children under the age of 3. Furthermore, having a father who was nominated as a good hunter was shown to increase the probability of child death. Nevertheless, children ages 5-13 were observed to be heavier and taller if their father was present, although multilevel analyses have shown that it is the father's presence, not his identity which matters for child weight and height.

Among the Hadza, a vignette study (Wood, 2006) revealed that the majority of men sampled (26/34) preferred to be in a camp with good hunters rather than a camp where their own relative contribution would be higher (hence facilitating "showing off"), but that preference was not predicted by marital status or the presence of dependent offspring. Virtually all women preferred to reside in a camp with good hunters. This indicated that the majority of males were principally concerned with family access to food, while a minority of males may have preferred the opportunity to signal in order to gain increased mate access.

### Aché Hunter-Gatherers

Among the Aché, different studies have provided evidence consistent with signaling hypotheses about hunting, and evidence that contradicts the hypothesis that men hunt mainly to signal quality and gain mating opportunities. Kaplan and Hill (1985) found that better hunters among the Aché did not have significantly more offspring, but

that they were characterized by higher offspring survival despite the fact that the nuclear family of the hunter received no greater share of his prey in measured foraging redistributions than did any other band member. Hawkes (1991) observed that males tended to target meat and honey which was shared more widely then the plant foods targeted by women (consistent with signaling goals), whereas Hill (personal communication) pointed out that men were encouraged and even pressured by wives to hunt meat rather than collect plant foods, presumably because of the critical nutrient contributions from meat. If the goal of hunting is to gain reproductive access to females rather than to provision families, it seems unlikely that wives would encourage their husbands to pursue meat and honey rather than plant foods. If, however, the goal of foraging is to signal generosity or cooperative intent in order to maintain access to food sharing networks and increase the likelihood of being cared for while sick or incapacitated (Gurven, 2004c; Gurven, Allen-Arave, et al., 2000) then a strategy which maximizes long term return rates and encourages widespread sharing might be favored by both men and women. Indeed, Gurven and colleagues (Gurven, Allen-Arave, et al., 2000) showed that hunters who were more generous (shared a greater proportion of their kills than average) as well as hunters who were more productive (brought back more meat than average) received more food when sick, injured, or otherwise unable to hunt than did those who produced or gave less than average. In this case, the optimal strategy for signaling cooperative intent aligns well with the optimal strategy for provisioning families (who also benefit from shares given to the incapacitated hunter).

Wood and Hill (2000) found in a vignette study that married Aché men with dependent offspring expressed a desire to co-reside in bands with better hunters, whereas

unmarried men and men with no dependent offspring preferred to join bands with poor hunters, where they might have more opportunity to "show-off". They concluded this based on the results of a structured interview which showed drawn images of identical foraging bands containing a few eligible women, with the only difference between the bands being the number of dead animals that hunters in the picture had brought back to camp. They asked informants to select the band they would prefer to join based on the content of the picture presented (abundant game hunted vs. little game hunted by camp members). The result is consistent with the possibility that single males seek to signal their provisioning ability in order to acquire better mates, but once married prefer to obtain more food for dependent offspring (as recipients of food sharing) rather than seeking additional mating opportunities.

Hawkes (1991) observed that Aché men are not maximizing their energy gain rate because they regularly bypass edible palms, which were estimated to yield a very high caloric return rate, in order to hunt. They argued that if the goal of men is not to maximize energy gain rate, then it must be to signal. More recent experiments have shown that only 1 in 35 palms are suitable for starch extraction, and that less of the starch is digestible than previously thought; however, these differences don't change the conclusion that palm starch extraction is at least as efficient as hunting for producing calories (Gurven & Hill, 2009). Regardless, Hill and colleagues have pointed out that energy maximization is unlikely to be the only goal of Aché foraging, and that a sexual division of labor allowed men to harvest resources which produced valuable proteins and lipids whereas women provided complimentary carbohydrates (Hill et al., 1993). Indeed, the systematic exchange of meat for much greater caloric values of starch crops (corn,

rice, wheat, etc.) in several small-scale societies demonstrates via price ratios that protein and lipids have relatively higher nutritional value (consumer utility) than energetically equivalent carbohydrates that come from starchy foods (Hart, 1978; J. T. Peterson, 1981).

Martu Hunter Gatherers

One group of researchers has argued that the Martu hunter gatherers of Western Australia are typical "show-off" hunters (Bliege-Bird et al., 2009; Bliege-Bird & Bird, 2008). Among the Martu both sexes will occasionally hunt all prey; however, men prefer to hunt bustard and kangaroo, and women prefer to hunt goanna, cats, and snakes. As in previous cases, the larger prey which are preferred by men generate a higher mean caloric return rate for time spent hunting, but are associated with a greater risk of failed pursuits.

Bird and colleagues examine the variance in daily contribution to diet of men and women in mixed-sex Martu foraging groups, showing that women produce a greater proportion of the calories on any given day (60-70%) and the majority of calories overall due to the higher numbers of women than men in the observed foraging groups, but that men contribute more per capita (Bliege-Bird et al., 2009). Percent contribution data for their analyses are based on outcomes of mixed sex foraging groups where the majority of foragers were women. They are not mean daily contributions per individual (where males obtained considerably more per forager per hour), which are the typical criteria for deciding the optimal foraging pattern. Bliege-Bird et al. (2009) subsequently argue that the more consistent daily caloric returns associated with women's foraging might be of greater overall value to the health of foragers than the bonanzas provided by men, because meat consumption should be subject to diminishing returns such that there is

little value in eating past satiation. However, band wide food sharing ameliorates the disadvantage of harvest variance and no nutritional data are cited to back the assertion that diminishing nutrient utility should be assumed to discount men's but not women's contributions.

In addition to having higher daily acquisition variance, Bliege-Bird et al. (2008) claim that Kangaroo hunters were providing a public good at a personal cost. Goanna hunting success is more common and goanna hunters keep a larger percentage of their kill on average than kangaroo hunters. In their data set of sharing based on observations of distributions of 11 kangaroos and 19 goanna they that found that kangaroo hunters consumed an average of 2,480 Kcal from the animal they killed, while goanna hunters consumed 1,720 Kcal from animals they killed (where consumption portion equals the portion of a kill directly retained by the hunter plus any secondary meat redistributions to a hunter from their own kill). Although Kangaroo hunters consumed more meat than goanna hunters on days when they were successful, 75% of days spent Kangaroo hunting resulted in failure, while only 9% of goanna hunt days were unsuccessful. Based on these differential success rates, they calculate that goanna hunters would consume an average of 1,548 Kcal/day from their own kills, while kangaroo hunters will average just 620 Kcal/day (Bliege-Bird & Bird, 2008). They point out that the average of 620 Kcal/day consumed by kangaroo hunters from their own kills is lower than the average portion received by non-hunters from a kangaroo hunter's kill (740 Kcal per distribution), and they thus make the argument that hunters are providing a public good at a personal cost, since they could get more Kcal/day by receiving shares of another's kill than they

make by hunting for themselves. This, however, assumes that they will continue to receive shares regardless of their own foraging effort.

Bird et al suggest that men tend to target prey which is shared widely, and they report that men do this for the purpose of increasing their ritual status. It should be noted that in another study examining the same populations, Bird et al (Bird, Codding, Bliege-Bird, Zeanah, & Taylor, 2013) report that feral camels (an introduced species) can be hunted relatively easily and for much higher return rates than kangaroo or bustard, but that men regularly forgo opportunities to kill camels in favor pursuing kangaroo or bustard. They hypothesize that men could be ignoring the camels because they are too large and therefore the labor and fuel cost of butchering and sharing the camel are too high. Gaining high ritual status is associated with, among other things, being a proficient hunter, sharing meat widely, and prioritizing relationships (through sharing) while avoiding wealth accumulation or selfishness. Bliege Bird and colleagues (2009) assert that men target large game expressly for the purpose of sharing with the whole group, rather than hunting for the purpose of providing the most nutrients for their families. Additionally, they report that Men aren't the only ones who feel pressure to kill animals which are large enough to share widely. Even one of the female informants was quoted as not wanting to hunt goanna (a small reptile) on a day when there were many people in camp for fear that she would be accused of selfishness. She stated that it was better to hunt large game even if you got nothing, because at least everyone would be hungry together.

Although they conclude that men's preference for hunting large game is motivated by a desire to achieve ritual status, they later provide evidence that women's small game hunting serves a similar purpose. In a later analysis of food sharing behavior and cooperative network centrality in the context of mixed-sex foraging groups (Bliege-Bird & Power, 2015), they show that generosity (rather than overall productivity) predicts centrality in cooperative networks. They use these data to suggest that generous food sharing serves as a costly signal of prosocial intent, rather than being competitive and self-aggrandizing signal.

The pursuit of ritual status seems to fall squarely within the realm of "show-off" behavior, however, the strong social enforcement of norms requiring hunters to pursue prey which is large enough to feed the group (and incidentally, prey with higher mean caloric return rates per unit of pursuit time) is also consistent with the goal of provisioning in a society that emphasizes reciprocal sharing. Social norms about what to hunt and the opportunity costs of hunting small game (in the form of lost ritual status) can be viewed as norms and punishments used to stabilize a sharing system based on indirect reciprocity. The fact that both men and women experience social norms and pressure to share their returns generously undercuts the idea that hunting is a form of self-aggrandizement among the Martu. The ultimate question of the "show-off" hypothesis is whether men intentionally target prey which is hard to acquire and suboptimal for provisioning in order to advertise their individual quality, however, this conclusion is contradicted by three facts. First, norms of generous sharing apply to all game, large and small. Second, it is generosity rather than productivity that provides the key pathway by

which information is being signaled. Third, these norms and expectations apply to both sexes.

Ultimately, Bird and colleagues assert that the explanation for differences in male and female hunting strategies are not due to cooperative specialization, but rather by differences in risk sensitivity, and that men preferred large game primarily because its large package sizes allow for greater sharing breadth, while women prefer small game due to the lower associated risk of failure. Differences in risk sensitivity alone are not enough to demonstrate that a foraging behavior is costly signaling in the sense proposed by the show-off hypothesis. If risky foraging produces higher returns per unit time on average and if mechanisms can be developed to reduce problems associated with bonanzas and shortfalls, then risky, high return foraging can still be consistent with the goal of provisioning.

### Tsimané Forager Horticulturalists

Researchers studying the Tsimané horticulturalists of Bolivia have also explored several unique but more indirect pieces of evidence pertaining to the debate about whether male hunters are mainly motivated to provision families or to acquire extra pair matings. One research group examined hormonal reactions to hunting success (Trumble, Smith, O'Connor, Kaplan, & Gurven, 2014). They proposed that if men are primarily interested in "showing-off" by hunting large game then they should show higher levels of testosterone and cortisol (indicating excitement) when they successfully kill large game (vs small game) or when they are observed by an audience while returning from a hunt (vs no audience). Contrary to these predictions, Tsimané hunters did not show relatively

greater increases in cortisol or testosterone in response to making larger kills or in response to encountering an audience while returning with a kill.

Another group of researchers explored the contexts in which Tsimané men cheat on their spouses in order to unpack the motivations for male-female pair bonding (Winking et al., 2007). They argue that if the purpose of marriage is primarily to control reproductive access to mates (the mating access model), men should be more likely to cheat as spousal reproductive value declines, whereas, if the purpose of marriage is primarily to ensure the effective provisioning of offspring, men should be more likely to cheat when they have fewer dependent offspring. They found that being older and having more dependent offspring were both associated with a decrease in the frequency of cheating. The same PI found that Tsimané men were more likely to engage in direct childcare behaviors when the mother was physically absent than when present, indicating that fathers engaged in the behavior as a form of parental investment (compensating for mother's absence) rather than as a form of signaling (since mothers were not present to observe the behavior) (Winking, 2005).

Contrary to the provisioning hypothesis, however, the same researchers examined the impact of father's death on the success of adult offspring using the metrics of BMI, height, age at first reproduction, completed fertility for age, and number of surviving offspring for age (Winking, Gurven, & Kaplan, 2011). They found that father presence did not have a significant impact on these measures except that adult daughters with present fathers had a greater BMI. Their findings are consistent with the evidence summarized by Sear and Mace (2008) showing that father death has a variable (and

sometimes negligible) impact on child survival in a sample of subsistence populations. This is presumably because other close kin provide substitute investment when the father of a particular offspring dies. Sear and Mace show that in 8 out of 15 societies studied (this sample is not limited to small-scale societies or natural fertility populations) using appropriate statistical techniques, father death does not predict child death. This finding may appear hard to reconcile with evidence that good hunters have improved fertility, however, hunters can improve their fitness and that of their spouses without enhancing the survival of individual offspring if their contributions allow the wives to have more children while holding survival rates constant (Gurven & Rueden, 2006).

## Ethnographic Summary

Because quantitative ethnographic evidence related to the role of signaling (costly or otherwise) in male foraging decisions has been collected in just a few societies, it is difficult to draw general conclusions. Most studies have speculated on whether signaling and provisioning strategies would result in different patterns of observed behavior, and if so, whether observed male hunting was more consistent with provisioning or signaling. In many cases, claims of a specific "prediction" from costly signaling behavior are themselves based on untested assumptions about foraging or sharing patterns. The small ethnographic sample combined with a lack of systematic methods for testing predictions based on CST has made cross-cultural comparisons difficult. Here the ethnographic evidence presented above is summarized. Evidence pertaining to how food is shared will be addressed in the next section of this chapter.

Current ethnographic evidence supports the possibility that men sometimes engage in ritualized foraging activities for signaling purposes. Among the Meriam islanders, some men choose to provision public feasts via costly and difficult turtle hunting, presumably for the purpose of signaling public spirit, generosity, or leadership ability (Smith & Bird, 2000). Among the Ifaluk Islanders, men sometimes engage in communal nighttime torch fishing, which is less productive on average than daytime fishing. Ethnographers suggest that torch fishing results may serve the purpose of signaling the productivity of a matriline by indexing their productive ability, however, the ethnographers also note that torch fishermen had expected to catch more, so it may be the case that a larger sample of torch fishing events would show that it is a more productive activity than previously thought (Sosis, 2000).

The evidence does not support the conclusion that signaling is the explanation for the majority of men's foraging activities (both torch fishing and turtle fishing are ritualized activities). Among the Aché (Gurven, 2004c; Gurven, Allen-Arave, et al., 2000) and Hadza (Wood & Marlowe, 2013, 2014), male foraging patterns appear consistent with the goal of provisioning families in the context of generalized reciprocity norms wherein all individuals share food. In both cases, men prefer prey which yield the highest average returns, even after controlling for portion retained by the hunter's family. For both the Aché and Hadza, large game (with higher average food returns) are preferred resources and may be the "focus" of search (this is not demonstrated directly), however, small game and other resources such as fruit and honey are also regularly harvested upon encounter. The Hadza have been shown to increase foraging effort when they have more dependent offspring (Marlowe, 2003; Wood & Marlowe, 2013). Among

the Aché, good hunters and generous sharers have better offspring survival (Kaplan & Hill, 1985). There is evidence from vignette studies that unmarried Aché men and both unmarried and polygynously married Hadza men might be motivated by "showing off" (Wood & Hill, 2000; Wood, 2006), but whether they do so at the expense of provisioning is hotly debated (Hawkes et al., 2001a, 2001b; Hawkes & Bird, 2002; Hawkes et al., 2014, 2010; Wood, 2006; Wood & Marlowe, 2013, 2014).

The Martu provide a potential case study for costly signaling as the driver for men's foraging decisions. Among the Martu, men spend the majority of their foraging effort on large prey items which are shared as a way of achieving ritual status. The pursuit of ritual status seems like a probable case of signaling behavior, however, it can also be interpreted as a case of enforced sharing norms. Martu men pursue the prey which are most efficient for provisioning (yield the most calories per unit foraging time on average), However, if the value of food is discounted by the proportion shared with non-kin and a non-reciprocal exchange system is assumed, then men may be foraging in a way that maximizes their public contribution at the expense of their direct family provisioning (Bliege-Bird et al., 2009).

In order for general conclusions about the role of signaling in male foraging decisions to be drawn, it is important for future studies to explicitly identify: who is supposedly signaling, what they are trying to communicate, who their intended audience is, and how the signal is honestly linked to the quality being signaled.

Food Sharing: Kin Selection, Reciprocal Altruism, Indirect Reciprocity, Social Norms, and Tolerated Theft

The question of why meat is shared in hunter gatherer societies is a recurring theme in debates about costly signaling vs family provisioning. The Hadza, Aché, Martu, and Meriam islanders all hunt prey larger than what a hunter's nuclear family can consume before it spoils. Of these, only the Martu and Meriam Islanders have reasonably convenient access to freezers for storing meat. Even if large game hunting yields higher average returns than pursuing small game or plant foods, if the excess meat cannot be converted into utility then it has no value to the hunter. In each of these societies, meat is transferred to individuals outside the hunter's nuclear family. In some cases, the hunter's family may keep less than they could consume.

There is little agreement about how generalized patterns of sharing are structured or maintained in the context of human food sharing. Both theoretical models (Smith, 1988; Winterhalder, 1986) and empirical examination (Kaplan & Hill, 1985) have strongly suggested that widespread food sharing is beneficial for most or all group members, however, it has been noted that egalitarian food sharing creates a collective action problem wherein all members of the group want access to shared food resources, but should not want to pay the costs of contributing their own food to the resource pool (Hawkes, 1991).

In addition to costly signaling discussed above, there are four other cooperative mechanisms and one non-cooperative mechanism that could potentially explain why hunter-gatherers frequently transfer food to band co-residents (Henrich & Henrich, 2007).

These are kin selection, reciprocity, indirect reciprocity, social norms with cultural group selection, and tolerated theft. These mechanisms are briefly discussed in the following paragraphs. Genetic group selection provides an additional potential mechanism for explaining the evolution of cooperation, however, this mechanism seems very unlikely since group composition changes rapidly, and within and between-group (band) genetic variation is probably equal within hunter-gatherer societies.

Kin selection (KS) is a common nickname referring to inclusive fitness theory. Inclusive fitness theory attempts to explain altruistic behaviors (paying a cost in order to provide a benefit to someone else) by calculating how genes can affect copies of themselves in the bodies of kin who are likely to share the same alleles via common descent (Hamilton, 1964). According to IFT, altruistic behaviors can evolve when the benefit (B) to the recipient (in the form of increased fitness) discounted by the probability (r) that the recipient shares a rare allele via common descent, is greater than the cost (C) to the donor (in the form of decreased fitness). This condition, expressed as $rB > C$, is commonly referred to as Hamilton's Rule. When relatedness is very high, these conditions are more likely to be satisfied, thus, greater levels of altruistic behavior are expected between more closely related individuals. Relatedness decreases very quickly with greater kinship distance, thus much lower levels of altruistic behavior are expected between cousins, aunts, uncles, etc. than between parents and children, or among siblings. Furthermore, because KS is concerned with increases and decreases in components of fitness, there should be sensitivity to the reproductive value of the recipient of benefits when altruistic behavior affects survival, with flows of benefits more likely to be directed toward individuals with higher reproductive value.

Reciprocal Altruism (RA) refers to a theory within evolutionary biology, which proposes that a donor will pay a fitness cost to provide a fitness benefit (goods or services) to a recipient based on the probabilistic expectation that the recipient will provide a return fitness benefit (in goods or services) to the donor at a future date (Trivers 1971). RA requires that the net fitness benefit to both donors and recipients is positive on average over a reasonable time scale. When receiving food from a donor is predicated on having given to that donor in the past, food sharing is said to be contingent. Return benefits received for RA do not have to be certain, only statistically probable. The return benefits do not have to come in the same currency as benefits provided, nor do amounts transferred have to be the same as long as the cost paid by the donor is less than the fitness benefits statistically expected to be returned by recipients.

The ability of reciprocity to sustain cooperation is very sensitive to rates of defection, wherein recipients do not provide return benefits. A number of mechanisms can help reduce probability of defection, such as punishment of defectors, reputation monitoring, and repeated interactions between individuals (Boyd & Richerson, 1992). Relatedness may also facilitate RA because related individuals are more likely to have repeat interactions and because inclusive fitness benefits decrease the cost of cooperation and increases the cost of defection among family (Kaplan & Hill, 1985). Additionally, relatedness may facilitate RA if there are greater reputational consequences or punishment for those who defect on kin, especially punishment from people who are more closely related to either party than the two parties are to each other.

Indirect reciprocity (IR) refers to an extension of RA in which donors pay a cost (in goods or services) in order to signal their proclivity to cooperate, thereby enhancing their reputation and making them more desirable as cooperative partners. IR is likely to be important when 1) opportunities for dyadic cooperation are abundant and fitness enhancing; 2) potential cooperative partners chose a smaller subset of partners from among a larger pool of willing interactants. Competition to be chosen as a partner drives IR. Indirect reciprocity does not require the recipient of a benefit (or anyone else) to repay the donor directly, hence donors may share without obvious repayment of an equal amount from anyone. The donor benefits because third party observers of the behavior gain reliable information about the cooperative nature of the donor and are thus more likely to prefer the donor as a cooperative partner.

Costly signaling theory (CST) and IR share some features and can be integrated to predict behaviors likely to be part of the food sharing pattern. For example, CST can help explain why an individual might behave prosocially toward a recipient, even if the recipient is a known non-cooperator. Likewise, both CST and IR can be invoked to explain why a donor might provide a public good or other benefit which is likely to be consumed by many non-cooperators (Engelmann & FischbAchér, 2003; Panchanathan & Boyd, 2003). In both cases, the donor is willing to provide the benefits to a large group of non-reciprocators, as long as the reputational benefits are high enough to result in the donor gaining sufficient future cooperation to account for the cost. Such behaviors can be described as costly signals of cooperative intent. They are not theoretically distinguishable from other types of costly signaling referred to thus far in the paper, however, they are meaningfully different from costly signaling in the context of the

"show-off: hypothesis because the signal is designed to communicate cooperative intent, rather than to advertise phenotypic quality and attract mates or intimidate competitors.

Social norms spread by cultural group selection can provide a fourth mechanism which has potential to explain prosocial food transfers. Norms refer to shared patterns of beliefs, behaviors, and practices which are acquired via social learning. They can be identified by three traits. Norms are shared, norms proscribe proper behavior (or prohibit improper behavior), and failure to follow norms will anger those holding the norm, even when the failure doesn't impact them directly (Henrich & Henrich, 2007). Some norms are costly to the individual practicing them, such as cooperative norms requiring contributions to public goods. Henrich and Boyd (2001) showed how punishment and conformist biased cultural transmission provide a solution to the free rider problems associated with cooperative prosocial norms. Specifically, they showed that even costly norms can be stable if the cost of following the norm is lower than the cost of being punished for violating the norm. However, punishment of defectors is likely to be costly to the punisher, while the benefits of having defectors be punished go to all, thus creating a second-order free rider problem. This second-order free rider problem can be solved if there are norms requiring the punishment of those who fail to punish defectors. If the costs of punishing those who fail to punish are diffused across the group, they can be small enough to be stabilized by conformist transmission.

Panchanathan and Boyd (2003) showed conditions under which indirect reciprocity can also be used to enforce norms without direct punishment of defectors. If norms only require that individuals cooperate with others who maintain good standing,

and if standing is determined by a past history of cooperating with others who are also in good standing (indirect reciprocity), then a cooperative system is able to exclude non-cooperators.

Henrich and Boyd (2001) show that norms of punishment, and of punishing non-punishers can stabilize almost any costly normative behavior (not just cooperative norms). Thus, they propose cultural group selection as a mechanism for explaining the prevalence of cooperative norms stabilized by punishment. According to this view, groups with prosocial sharing norms do better and ultimately either replace or are copied by less cooperative groups.

In addition to these four mechanisms for explaining cooperative food sharing, tolerated theft (TT) provides a fifth, non-cooperative mechanism for explaining food sharing (Blurton Jones, 1984). According to TT, as an organism becomes satiated, continuing consumption of food provides decreasing marginal fitness benefits, while the value of food to others who have not eaten remains high. TT proposes that the decreasing fitness value of consuming more of the resource is ultimately outweighed by the realized or potential cost of continuing to defend the resource from scroungers. Once the producer is no longer willing to defend later portions of the harvest, food is transferred to avoid potential conflict. TT is also sensitive to the relative resource holding potential (the ability to defend access to the resource) of producers and scroungers predicting that some producers will "share" more than others. Conditions are favorable for TT when resources are difficult to store and come in packages greater than an individual can consume, and when resources are acquired erratically, such that on any

given day a producer can expect to encounter many scroungers for whom the producer's kill will have a high marginal fitness value. Advocates of TT as the explanation for human food sharing point out that hunters frequently kill nothing (Bliege-Bird et al., 2009; Bliege-Bird & Bird, 2008; Hawkes, 1991; Smith & Bird, 2000) and that when they are successful, hunters frequently acquire more meat than they can consume, thus creating the perfect conditions for a TT based explanation of food sharing patterns. Unfortunately (for researchers) precisely the same conditions that facilitate TT will also favor reciprocity-based food sharing.

## Ethnographic Evidence of Kin Selection, Tolerated Theft, and Reciprocal Altruism

While the evolutionary explanation of human food sharing is not the topic of this dissertation, the reasons why different foods are frequently transferred to others is a critical component of the debate about whether the purpose of men's hunting is primarily provisioning, or primarily self-advertisement. This is true because why food is re-distributed after harvest determines whether and to what degree foragers will recoup some value from food shared outside the nuclear family and kin network.

The "Show-Off" Hypothesis is based on an assumption that meat is transferred due to tolerated theft, hence the provisioning value of prey animals should be discounted by the proportion distributed to non-kin. Furthermore, TT predicts that, all else being equal, hunters should on average retain a greater proportion of the meat they acquire from hunting small game because they can consume a greater proportion before becoming satiated. This point is central to the argument of those advocating the "show-off" hypothesis, because it is the basis for suggesting that small game are superior resources

for provisioning families. If, on the other hand, meat transfers are due to RA or IR then shared portions of meat lead to potential fitness benefits that may come in the form of shares of the recipient's future kills, or some other form of care and assistance provided by recipients to the donor, his mate, and his offspring. In a social system characterized by reciprocal transfers of goods and services, large game, which generally have higher return rates from an OFT perspective, are likely to be more valuable for assisting families, since their direct provisioning value and trade value are both greater than those of small game.

## Kin Selection

No study has directly empirically assessed KS as an explanation for human food sharing patterns because doing so would require a measurement of the impact of food transfers on fitness of donors and recipients. Instead, empirical studies have focused on detecting a kin bias in food sharing. If food sharing is designed to increase inclusive fitness, data should show that food is shared more frequently or in larger portions with the nuclear and extended family based on coefficient of relatedness and reproductive value, and that foraging effort should increase when offspring or close kin are co-resident. There is abundant evidence of kin biased food sharing in humans (Allen-Arave, Gurven, & Hill, 2008; Altman, 1987; Gurven, Allen-Arave, Hill, & Hurtado, 2001; Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000; Hill & Kaplan, 1989; Hooper, 2011; Jaeggi & Gurven, 2013; Koster, 2011; Lyles, Hill, & Hurtado, 1990; Stearman, 1989; Wood & Marlowe, 2013; Ziker & Schnegg, 2005).

Because of the high degree of genetic relatedness within nuclear families, kin biased food sharing (assuming producer control of distributions) should usually result in

the household of the food producer keeping a larger than average share of the food when shares are distributed widely or to all families in a settlement. In a Yora settlement of 11 households the pattern of meat distribution favored the producer's nuclear family, with producers keeping approximately 40% of all meat produced (Hill & Kaplan, 1989). Likewise, among the Hiwi (Gurven, Hill, et al., 2000; Lyles et al., 1990), Gunwinggu (Altman, 1987), Yanomamo (Hames, 2017), and Yuqui (Stearman, 1989), nuclear families kept a disproportionately large portion of kills. Among the Hiwi, meat was transferred in greater quantities to more closely related kin even after controlling for residential proximity (Gurven, Hill, et al., 2000). Kinship and need were found to be significant predictors of food sharing among the Mayanga and Miskito (Koster, 2011), as well as the Tsimané (Hooper, 2011).

However, not all societies show kin bias in meat distributions. On forest treks, the Aché did not share more meat with kin than non-kin (Kaplan, Hill, Hawkes, & Hurtado, 1984). Likewise, the Mamainde (Aspelin, 1979) showed a fairly egalitarian food distribution pattern in which food was divided based on group and household size, and distributions did not favor kin. Bliege-Bird and Bird (1997) did not report kin bias in the sharing of turtle meat during feasts.

It is important to remember when evaluating these studies that kin-biased food transfers do not necessarily indicate that food is transferred because of inclusive fitness effects. It could also be the case that kin are preferred reciprocity partners based on proximity, trust, familiarity, or social norms. Among the Aché it was found that food transfers on reservations did favor genetically related individuals (Gurven et al., 2001),

but that kin-biased food sharing was probably better explained by reciprocity than KS (Allen-Arave et al., 2008). Specifically, the effect of contingency on amounts of food transferred between families increased with increasing relatedness, indicating that kin may be more reliable partners for reciprocal exchange. Further supporting the idea of kin as preferred trade partners, patterns of reciprocal sharing within Dolgan meal sharing networks showed strong clustering based on kinship, with more closely related households sharing meals more frequently (Ziker & Schnegg, 2005).

Finally, it is important to note that food sharing precedence was not limited to genetically related individuals in some studies, as would be expected if KS was the sole explanation for kin biased food sharing. Instead, close kin often include affinal kin who share no genes directly but do share a common genetic interest in the welfare of close kin of the food donor. For example, among the Hadza, food sharing was shown to favor both consanguineal and affinal kin despite the lack of genetic relatedness between a hunter and his affinal kin (Wood & Marlowe, 2013). Recent theoretical work has suggested that human inclusive fitness studies will often have to include cooperation with affinal kin in order to fully appreciate the importance of kin assistance (Dyble, Gardner, Vinicius, & Migliano, 2018).

### Tolerated Theft

If the TT model is the correct explanation for food transfer and it is assumed that both resource holding potential and need are constant across individuals, then foragers would be expected to "share" food with most or all members present in a group (high sharing breadth), but not to store food for those who aren't present to claim a share.

Likewise, there should be evidence that individuals attempt to hide resources from others in order to avoid the cost of sharing. Evidence for contingency in food sharing would directly contradict TT. Outside the framework of costly signaling and the show-off hypothesis, TT does not predict that individuals should want to provision public goods.

Ethnographic reports of "demand-sharing" (verbally requesting a share, with a tone of assertion) among members of small-scale societies are common, as are reports of individuals trying to hide food from others (Altman & Peterson, 1988; Gurven, 2004b; Hames, 2017; Lee, 1979; Patton, 2005; Peterson, 1993; Wiessner, 1977). These observations provide qualitative support for the notion that foragers would like to share less than they do. However, it is important to note that "demand-sharing" is almost always embedded in a context of the donor owing shares to the recipient because of past sharing to the donor. There are no ethnographic reports in any society of individuals threatening that if they aren't given a share of harvested food that they will fight to take it away (the classic scenario of tolerated theft).

Quantitative support for TT based explanations of human food sharing is limited. For example, among the Aché on forest treks (Kaplan et al., 1984), the Hadza during big game distributions (Hawkes et al., 2001a), and the Meriam Islanders during ritual feasts (Bliege-Bird & Bird, 1997), food was shared with almost all members of the band as might be expected from the TT model. Likewise, Bliege-Bird and colleagues (Bliege-Bird et al., 2001) report that in the context of Meriam Islander food sharing, there is no discrimination against free riders. Importantly, however, although high sharing breadth (the number of people receiving shares of food from a harvest) is CONSISTENT with

TT, it is not sufficient as evidence FOR TT. No evidence was found that resource holding potential affects sharing in any society, nor is there evidence of any physical cost ever paid by a producer who failed to share (except for an anecdote about an Aché man who was clubbed for not sharing with his wife (Bertoni, 1941)). Also contrary to the predictions of TT, the Aché often saved food for those who were not present to claim a share (Kaplan et al., 1984); the Meriam Islanders actively sought out opportunities to provide a public good for ritual feasts (Bliege-Bird et al., 2001; Smith & Bird, 2000); and the Hadza showed increasing producer advantage as a function of prey body size, meaning that hunters kept a larger proportion of the meat from larger game despite its diminishing marginal value to the producer (Hawkes et al., 2001a; Wood & Marlowe, 2013).

TT models also provide no reason to expect that amounts received by individuals will be correlated with amounts given by them in co-resident dyads (contingency). Nevertheless "contingent" food sharing is commonly observed. One study examined contingency in food sharing between dyads in 8 small-scale populations (Gurven, 2004c). Data were available on the correlation between amount given and amount received of all food resources for 7 of the 8 populations, and statistically significant correlations ranging from ($r = 0.18$ to $r = 0.65$) were detected in 6 of the 7 populations. Likewise, data on meat distributions were available for 5 groups, and it was shown that amount of meat given is positively correlated with amount of meat received for 4 out of 5 populations. No contingency was detected in Meriam islander turtle sharing, nor was contingency detected among the Aché on forest treks (but contingency in meat sharing was detected for the Aché while resident in the colony).

## Reciprocity

Many researchers have proposed that direct or indirect reciprocity account for much of the patterning of human food sharing (Allen-Arave et al., 2008; Altman, 1987; Gurven, 2004b, 2004a; Gurven et al., 2001; Gurven, Hill, & Kaplan, 2002; Hames & McCabe, 2007; Hill & Kaplan, 1989; Hooper, 2011; Jaeggi & Gurven, 2013; Koster, 2011; Lyles et al., 1990; Nolin, 2010; Patton, 2005; Stearman, 1989; Wood & Marlowe, 2013; Ziker & Schnegg, 2005).

Reports of contingency in food sharing between dyads vary among study populations and authors. In Aché reservation settlements, food sharing was contingent between households (Allen-Arave et al., 2008; Gurven et al., 2001, 2002), but on forest treks food was shared evenly among those present (Kaplan et al., 1984). Among the Hiwi, food sharing was contingent among households and the strength of contingency was greater when households were not related (Gurven, Hill, et al., 2000). Likewise, contingency in food sharing was detected between households in the community of Conambo (Patton, 2005), with the Mikea (Tucker, 2004), and with the Ye'kwana (Hames & McCabe, 2007). Among the Lamalera, Nolin (Nolin, 2010) reported that kinship, residential distance, and reciprocity all played a role in food sharing, but that reciprocity seemed to structure sharing while kinship and proximity seemed to be more important in partner choice.

Not all benefits received from food sharing are repaid in the same currency. Benefits provided while a cooperative partner is sick or injured provide another potentially important opportunity for repayment (Gurven, 2004c; Gurven, Allen-Arave, et

al., 2000; Kaplan et al., 1984; Sugiyama & Chacon, 2000). Among the Aché, the best hunters and most generous sharers received more food from more people during periods of illness or injury (Gurven et al., 2001).

In addition to quantitative evidence of contingent food sharing, there is substantial qualitative evidence for the exclusion or punishment of non-sharers in small-scale societies (Gurven, 2004c). Punishment may include not receiving food, being gossiped about (reputational consequences), or even severe physical punishment in extreme cases. For example, Aspelin (1979) quoted a Maimande informant saying that those who do not give were excluded from receiving food shares. Aspelin also noted multiple occasions wherein a very unproductive family was excluded from receiving shares. Altman (1987) described a similar situation among the Gunwinggu, wherein two families intentionally shared less with a third, less productive family. Wiessner (1977, 1977) has shown among the !Kung that there were strict controls over sharing and sanctioning of defectors for non-food goods. Among the Nyae Nyae !Kung, Lee (1979) reported that accusations of stinginess were among the most severe insults that could be made. Among the Yanomamo, Hames (2017) reported that having more than a one-day supply of anything could result in accusations of stinginess if the resource wasn't shared. Among the most severe punishments reported for not sharing, Bertoni (1941) spoke of an Aché man who never shared with his wife until some men grew so angry that they speared and clubbed him to death.

## Food Sharing Summary

The quantitative and qualitative evidence reviewed here suggests that observed patterns of food sharing in small-scale societies are shaped by a combination of kin biased sharing, dyadic reciprocity, and indirect reciprocity, with some debate over whether TT contributes to observed food sharing patterns (Allen-Arave et al., 2008). Jaeggi and Gurven (2013) conducted a meta-analysis of the effects of food given on food received among 32 populations of monkeys, apes, and humans. In their analyses, they examined a set of 10 populations (3 ape and 7 human) which reported effect sizes (Pearson Correlation Coefficients) for the relative influence of KS, RA, and TT on patterns of food sharing. Their measures of effect size for RA were based on the correlation between food given and food (or benefits) received, while KS and TT were based on whatever operationalization the original study authors used. They found that RA, KS, and TT each had independent and statistically significant weighted effect sizes (KS $r = 0.14$, RA $r = 0.20$, TT $r = 0.22$).

While evidence of non-contingent food sharing and attempts to hide resource in some societies is consistent with what would be expected according to a TT based sharing system, the prevalence of social norms excluding non-sharers, combined with evidence that many groups save shares of food for those who aren't present, or even specifically seek out opportunities to provision feasts (or travel to distant camps "in order to share") suggest that most cases which might be explained as tolerated theft are probably better explained by indirect reciprocity.

The presence of reciprocity-based and kin-biased sharing, as well as evidence for social norms of sharing, and for punishment of non-sharers are not consistent with the assumption of the SOH, that food is shared according to TT (Allen-Arave et al., 2008). Generalized sharing may present a collective action problem in the context of food sharing, but solutions such as sharing norms, reciprocity, and kin biased sharing allow that collective action problem to be solved without the need to appeal to signaling models (Gurven & Hill 2009). Hence, food sharing patterns do not lead to the conclusion that showing off is the only reasonable explanation why men hunt widely shared game, and the best evidence for CST linked to expected redistribution is currently limited to ritualized contexts and feast provisioning (Bliege-Bird et al., 2001; Bliege-Bird & Bird, 1997; Smith et al., 2003; Smith & Bird, 2000; Sosis, 2000, 2002) rather than daily foraging activities.

# CHAPTER 3: Aché Methods and Results

## Research Questions

In the first chapter of this dissertation, two competing explanations for the evolutionary purpose of men's hunting were examined. The provisioning hypothesis proposed that purpose of men's hunting is to attract and retain a quality mate and to provision a hunter's offspring. To accomplish this goal, the provisioning hypothesis proposes that men will seek to maximize the utility of harvested prey both directly as a source of food for wife and offspring, and indirectly as a trade good (reciprocal altruism) or insurance premium (indirect reciprocity). The family provisioning hypothesis (FPH) proposes that men's hunting represents both mating effort and parental investment. The "show-off" hypothesis (SOH), on the other hand, proposed that the purpose of men's hunting is to "show-off" and attract the attention of potential extra pair mates. To accomplish this goal, the "show-off" hypothesis proposes that men will seek to maximize the utility of prey harvested as a signal of quality to attract extra pair mates. This is accomplished when men focus their foraging effort on harvesting large package resources which are shared widely outside of the nuclear family, and thus result in positive social attention for the hunter. Drawing on CST, the SOH additionally proposes that men can better attract more or better-quality mates by specifically targeting prey which are more difficult to hunt, because the difficulty serves as a costly signal of the hunter's phenotypic quality.

Ethnographic evidence for and against these hypotheses were presented in the second chapter, alongside a review of food sharing patterns in small scale societies. In chapters 3 and 4, the results are presented of research carried out with members of two

subsistence societies in which hunting is a substantial contributor to diet. Five lines of questioning were proposed in the first chapter which will address important aspects of the ongoing debate about the role of signaling in men's foraging decisions. These are:

**1)** Prey provide nutrient biomass to consumers, and hunters who bring in more total biomass may inadvertently "signal" their ability to provide food. But some prey might also be exceptionally hard to find or kill, indicating exceptional skill and strength of hunters who kill them. **Are there clear examples of prey whose value as a signal of hunter-phenotype is associated with the costs of acquiring them (HtF, HtK), and not simply a function of how much food value they contain?** In other words, are there smaller but hard to find or kill prey that might signal to an audience greater hunter skill and strength, and are there larger prey that provide no real signal of hunter strength or skill because they are easy to find or kill? Or, do all same size prey species carry approximately the same signal value about hunter characteristics?

**2)** Harvesting specific types of prey could potentially provide signals of hunter phenotype. **Is it true that killing different prey lead informants to infer variation in hunter phenotype on dimensions of a) Expected Future Provisioning; b) Hunter Strength; c) Fighting – the likelihood to win physical contests with other men; d) Health – hunter, Disease Susceptibility?**

**3)** Some hunting strategies and prey sets may be better than others for signaling specific aspects of hunter phenotype. **Which aspect of perceived hunter phenotype have the greatest influence on whether that hunter will be preferred as a mate or ally?**

**4)** There could be a divergence between hunting strategies that provide high food biomass and hunting strategies that signal positive hunter phenotypes. **Are a hunter's**

**perceived phenotypic quality and preferred status influenced more by their ability to capture lots of prey or by their ability to capture very impressive prey species?**

**5)** Both the SOH and CS claim that there is a difference between the hunting strategies which are best for provisioning families, and the strategies which are best for signaling good phenotype. **Is there a tradeoff between hunting for maximum food value vs. hunting for maximum signal value? Which strategy would lead to better mating opportunities or more social partners as judged by informant preference?**

Field Site

To answer the research questions posed above, structured interview data were collected with two populations. This chapter describes the materials, methods, and results of interviews conducted with Aché hunter gatherers from the Atlantic forests of eastern Paraguay. The Aché were chosen as the first field site because of their relatively recent history as full-time nomadic hunter gatherers (the contact period occurred during the mid-1970s), and because of the abundance of quantitative data on their foraging behavior, food sharing practices, and reproductive strategies (Gurven et al., 2001, 2002; A. M. Hurtado & Hill, 1996; Kaplan & Hill, 1985). Aché foraging practices are heavily influenced by their pre-contact life as nomadic hunter gatherers, while the Tsimané (presented in the next chapter) are hunter-horticulturalists meaning that their economic success and ability to provision their families is tied less directly to their hunting success.

The Aché now live on reservations where they engage in subsistence agriculture, occasional wage labor, and small-scale collective agriculture; however, many Aché continue to make regular trips to the forest where they hunt and fish extensively while also collecting wild honey, fruit, palm starch, and other plant resources. The last time it was measured, forest resources only constituted 7% of the Aché diet while they were in the reservation settlements (Kaplan et al., 2000). The Mbaracayú forest preserve where they hunt contains more than 60,000 hectares of partially protected forest. Guards patrol the forest to discourage poaching and logging, however, these practices still occur, resulting in depletion of prey near the edges of the forest. The Aché are allowed to hunt and harvest resources for non-commercial use from the reserve, however, they are not permitted to use firearms. As a result, bow hunting is still a common and well-maintained skill for those who continue to forage. Foraging trips last days and sometimes weeks, and the majority of food brought into the forest from the reservation is typically consumed within the first couple of days. Hunting is carried out with bows and arrows and hunted game provided roughly 78% of calories consumed during observed hunts in the 1980s (Kaplan et al., 2000), while honey, and plants foods made up most of the rest. Gender roles are more strictly defined in the forest than in the reservation settlements, and men provide the majority of meat and honey in the forest while women focus on collecting plant foods. Food sharing is also more extensive and egalitarian in the forest than on reservation settlements, with all band members receiving equal shares of the days harvest regardless of their own personal success or failure (Gurven et al., 2002).

## Field Methods

To answer the research questions above, structured interview data were collected from May to July of 2015 with Northern Aché informants (n=52 adults ages 15-76; 46% Female) from the communities of Arroyo Bandera, Kue Tuvy, and Chupa Pou. A stratified sample of informants, balanced by marital status and sex, were selected based on availability and willingness to participate. Interviews were conducted with single informants either in a closed room or outdoors near informant's homes, within the community. Interviews were conducted in Aché language using a male translator who was bilingual in Spanish and Aché. Some Aché interviews were conducted directly by KH with the translator observing in order to learn interview protocol. Interviews consisted of 4 tasks that will be described in turn. Permission to access the site and collect data was granted by Aché community leaders. All informants provided informed consent and all protocols were approved by the Arizona State University Internal Review Board. Special permission was granted to interview informants under the age of 18 due to a scarcity of unmarried women over the age of 18.

## Task 1: Prey Rankings

### Methods

Informants were asked to rank 16 prey species based on how hard they are to find and how hard they are to kill after being found. The purpose of the prey ranking task was to ascertain informant views about the costs of pursuing different species. Rankings from these tasks were used alongside estimates of prey body weights as predictors in later analyses. Because the signal value of a killed prey species might be exceptionally high if the species is large (high food value), difficult to kill, or very hard to find, the species

selected for comparison represent a range of body sizes, and included both animals common in the local diet, as well as animals that were believed to be hard to kill, and animals known from previous hunting studies and census transects to be hard to find (Figure 3.1).



**Figure 3.1** Aché prey species. Depicted are the 16 animal species drawings used for the Aché interviews. 9 of these 16 images were also used during Tsimané interviews described in the next chapter. A single Aché hunter is depicted for scale.

Informants were first asked to rank 16 prey species by how hard they were to find (HtF), and then by how hard they were to kill (HtK) once found. HtK and HtF were elicited by first showing two randomly selected animals from the prey set and asking the informant, "which of these animals is most difficult to find (or kill once found)?" then placing the picture of the most difficult animal at one end of a line and the least difficult

on the other end. The remainder of the 16 species were then added to the ranking, one at a time, until all prey species had been placed in rank order. Informant rankings (1-16) of each species were recorded with higher rank numbers indicating that a species is harder to kill or find. All prey ranked as "tied" by informants were given the mean ranking of the set of prey species that had tied each other (i.e. two prey tied for rank 2 and 3 were given a mean rank score of 2.5). Final prey rankings were taken as the mean of the individual informant ranks for each prey species. 51 out of 52 Aché informants completed the prey ranking tasks.

In addition to the HtF and HtK rankings established by interviews, all 16 Aché prey species were assigned mean body weight (Wt) based on prior hunting observations or published information. Body weights for 11 species (tapir, red brocket deer, white lipped peccary, collared peccary, paca, tayra, 9 banded armadillo, coati, capuchin, tegu, guan) were taken from Janssen & Hill (2014). For bush dog (Speothos venaticus), weights were estimated as the average of the range reported in the oxford academic list of mammalian species (Beisiegel & Zuercher, 2005). Likewise, the weight of Jaguars (Panthera onca) was estimated based on the mean of the values (77.7 kg for females and 94.8 for males) reported in the oxford academic list of mammalian species (Schaller & Vasconcelos, 1978; Seymour, 1989). For unknown reasons, the mean was incorrectly calculated as 88kg rather than 86.25 kg, and the error was not caught until after analyses were complete. These analyses were not run again after identifying this error. Providing estimated weights for reptiles was difficult due to a scarcity of available information on the topic, and due to the fact that reptiles continue to grow after reaching sexual maturity, meaning that adult weights are subject to considerable variation. The weight for green

anaconda (Eunectes murinus) was estimated at 50 kg, however, this estimate was based on limited available information. This size estimate was taken as the mean of the range of weights (9.25 kg – 82.5 kg) reported in survey of green anacondas (Rivas, 2001), rounded to the nearest 10 kg. No source could be found to estimate the weight of a snake of the species Bothrops jararaca, therefore the weight was arbitrarily estimated as 0.7 kg. Likewise, for tortoises the weight was arbitrarily estimated as 1 kg. The fact that the estimated weights for reptiles in the sample are either heavily rounded estimates or pure guesses is a significant limitation for the methodology.

## Cultural Consensus Analysis

The results of the prey ranking task were analyzed using cultural consensus analysis (CCA) techniques. CCA is a statistical method for examining the correlation between informant responses in order to determine if there is shared cultural information about a specific domain of knowledge, and to identify the culturally correct answers to questions about that domain. CCA is also useful for identifying cultural experts because it yields competency scores which are measures of the proportion of answers that a specific informant gave the culturally correct answers to. Negative competencies indicate that the views of an individual informant are systematically different from the culturally correct answers. Consensus is said to be achieved when the ratio of the first second eigenvalues from the analysis exceeds 3 and when there are no negative competencies. CCA was carried out independently on both sets of informant rankings from task 1. Prey ranking data were analyzed using an interval model of CCA.

## Task 1: Results

### Rankings

Aché prey species included the following in rank order of size (see Table 3.1): 1) tapir; 2) jaguar; 3) anaconda; 4) red brocket deer; 5) white-lipped peccary; 6) collared peccary; 7) paca; 8) bush dog; 9) tayra; 10) nine-banded armadillo; 11) coatimundi; tied for 12$^{th}$ and 13th) tegu lizard and capuchin monkey; 14) tortoise; 15) rusty-margined guan; 16) Bothrops snake. Comparisons asking which hunter had killed more meat in task 3 (discussed later) suggest that Aché informants are well aware of the true differences in body mass of these prey.

| Prey Ranking Results | | | | | |
|---|---|---|---|---|---|
| Species | Body Weight in Kg (Wt) | Hard to Find (HtF) | | Hard to Kill (HtK) | |
| | | Mean | SD | Mean | SD |
| Tapir | 177 | 10.87 | 2.70 | 12.28 | 3.14 |
| Jaguar | 88 | 12.70 | 2.35 | 14.43 | 1.66 |
| Anaconda | 50 | 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 | 6.6 | 2.90 |
| Bush Dog | 5.5 | 14.46 | 1.12 | 11.38 | 3.14 |
| Tayra | 4 | 10.42 | 3.00 | 9.98 | 3.24 |
| 9 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 | 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 |

**Table 3.1** Aché task 1 prey traits. Wt, mean rank HtF, and mean rank HtK for each species calculated from all informant responses to the prey ranking task.

Aché mean rank order for HtK was 1) anaconda; 2) jaguar; 3) tapir; 4) bush dog; 5) deer; 6) tayra; 7) w-l peccary; 8) c peccary 9) coatimundi; 10) capuchin; 11) guan; 13) paca; 14) tortoise; 15) tegu lizard; 15) snake; 16) armadillo. Table 3.1 shows that mean

rank scores for adjacent ranked prey could either be very close (e.g. coatimundi and bush dogs ranked almost exactly the same difficulty to kill) or very different (e.g. jaguar ranked much harder to kill than tapir, which was ranked much harder to kill than deer).

Since final rankings are based on the mean rank of 51 informant opinions, there are several ways that consistency of opinion can be examined. First, the correlation between the Aché ranking and the Co-PI's (KH) ranking guess prior to analyses (based on hunting research) was r = 0.93. This suggests that focal hunting experience and listening to Aché hunting stories, had provided the Co-PI (KH) with an accurate picture about which prey were harder or easier to kill upon encounter. Next, the standard deviation of informant rankings for each species was examined. The standard deviations around the mean rank of HtK score were lowest for jaguar (s.d. = 1.7, very hard to kill) and armadillo (s.d. = 1.9, very easy to kill) indicating high informant agreement about these two species. The standard deviations of the mean score for snake (s.d. = 3.69, medium difficult to kill) and tortoise (s.d. = 4.69, easy to kill) indicate worse informant agreement about the difficulty of killing these species when encountered (some informants may have confused the land tortoise - easy to kill- with the water turtle - hard to kill). There is virtually no sex difference in mean rank HtK scores provided by the 28 men and 23 women in this sample (correlation of men's and women's mean scores: $r^2$ = 0.95).

Aché mean rank order for HtF was 1) anaconda; 2) bush dog; 3) tortoise; 4) jaguar; 5) tapir; 6) tayra; 7) snake; 8) deer; 9) c peccary; 10) w-l peccary; 11) coatimundi; 12) guan; 13) tegu lizard; 14) paca; 15) capuchin; 16) armadillo. Again, the correlation

with the rank guess made by the Co-PI (KH) prior to analyses was high (r = 0.91) as was the correlation between opinions of men and women ($r^2$ = 0.90).

Finally, the mean informant rank of HtF and HtK for the set of prey are moderately correlated with each other (r = 0.44), indicating that these two prey characteristics are not completely independent but that they have enough non-overlapping variance to be useful as predictors of informant beliefs and preferences in a multiple regression model. Each of these prey character ranks is moderately correlated with body weight for the 16 prey (r = 0.06 HtF with weight, r = 0.33 HtK with weight), but the association is low enough that multiple regression using all three variables should be able to examine the effect of each independently with the others controlled.

## Cultural Consensus Analysis Results

CCA results indicate good consensus among Aché informants about the rankings of prey in terms of HtF and HtK (Table 3.2). For both prey rankings, the ratio of the first and second eigenvalue exceeded 3, average competency was high, and there was only 1 negative competency (for HtK). In short Aché informants (and the research team) are in very high agreement about what prey species are hardest to find or kill. Because of this high agreement, Aché hunters have an excellent opportunity to signal the particular phenotypic qualities that are associated with killing such prey by targeting them to the exclusion of other prey. Likewise, Aché men and women should be able to choose such men for mates or social interactants if such qualities are desired over other hunter attributes (such as simply bringing back more meat).

| Cultural Consensus analysis Results | | |
|---|---|---|
| | HtF | HtK |
| n = | 50 | 50 |
| 1st Eigen Value | 31.41 | 28.17 |
| 2nd Eigen Value | 3.91 | 4.94 |
| Ratio (1st/2nd) | 8.04 | 5.7 |
| # Negative Competencies | 0 | 1 |
| Mean Competency | 0.77 | 0.71 |
| S.D. of Competency | 0.19 | 0.21 |

**Table 3.2** Cultural Consensus Analyses of Aché HtF and HtK rankings. This table contains the results of CCA examining agreement among informants about the ranks HtF and HtK of prey. Consensus is said to be achieved when the ratio of the first and second Eigenvalue exceeds 3 and there are few or no negative competencies. Competency is a measure of the proportion of culturally correct answers that an informant gives. Negative competencies indicate that an informant is systematically incorrect in their responses because they don't share a cultural model with the group.

Task 2: Paired Comparisons

Methods

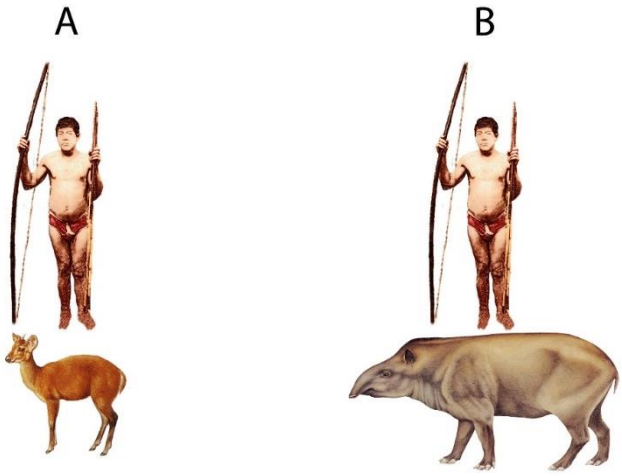



**Figure 3.2** Aché paired comparisons. Example images from Aché paired comparison task.

The purpose of task 2 is to determine how killing different species impacts perceptions of a hunter's Expected Future Provisioning ability (EFP), Strength, Fighting Ability, Disease Susceptibility, and desirability as a Mate, or as a Cooperative Partner. To accomplish this, informants were shown images depicting pairs of otherwise identical male hunters from the informant's ethnogroup standing next to various combinations of animals that they had killed on that day. Informants were asked to compare the two hunters on four aspects of phenotype and two aspects of preferred status (Figure 3.2). Informants were divided into four subgroups containing approximately 13 individuals each, and each subgroup of informants answered six questions about 30 unique prey combinations from a total of 120 possible prey combinations. The methods are described in greater detail below.

Informants were presented with an image and 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 random order comparing the depicted hunters on four aspects of their phenotype, as well as their preferred status as mates or allies. English translations of the six questions can be seen in Table 3.3. The four phenotypic traits examined are: 1) Expected Future Provisioning (EFP); 2) Strength; 3) Fighting Ability; and 4) Disease Susceptibility.

| **Preferred Status** | **Interview Question:** |
|---|---|
| **Mate** | (Unmarried Women) Who would you prefer to marry?<br>(Married Women & Men) Who would you prefer to have your daughter marry?<br>(Unmarried Men) Which animal would you have preferred to kill? |
| **Cooperative Partner** | Who would you rather go on a forest trek with? |
| **Phenotypic Quality** | **Interview Question:** |
| **EFP** | 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? |

**Table 3.3** Aché interview schedule. Aché Paired Comparison Interview Questions in English.

To produce the image of the hunters, an old photo of an Aché man was digitally altered using adobe photoshop CS3 to look like a drawing of a generic hunter. The background of the photo was erased, leaving only the man holding a bow and arrows. Contrast, saturation, and hue were altered, and the image was blurred slightly to reduce detail. The face of the man was altered by changing the size, rotation, and relative

positions of the features of the face, including the eyes, ears, mouth, and nose to remove any chance that the informants could recognize the hunter depicted on the cards, and attribute phenotypic qualities to them based on their real-world reputations. The same image was used to depict both hunters in a given comparison, with the only difference being the animals which the hunters had killed.

Task 2 used the same animal images that were used as in the previous ranking tasks and attempts were made to scale them to approximately the correct size relative to the hunters. Although the animal images were not altered to appear dead (no blood or wounds were depicted), this did not seem to confuse informants.

Interview Questions

The first paired comparison question is intended to assess how the animal that a hunter kills on one day impacts the perceptions of observers about how much meat that hunter will probably acquire on future foraging expeditions (EFP). This is interpreted as a measure of perceived future provisioning but not necessarily a measure of hunting skill, since no attempt was made to differentiate whether informants believed that a given hunter would bring back more meat due to superior abilities or superior work effort.

The second paired comparison question is designed to assess how the prey species that a hunter kills impacts perceptions of that hunter's physical strength. In the Aché language, the word "chija" (strong) implies both short burst strength as well as aerobic stamina.

The third paired comparison question asks whether killing different prey signals anything about Fighting Ability. Fighting between members of the local community is

now taboo in Aché society, however, violent conflict does sometimes occur (and did frequently in the past), and perceived or real fighting ability may have an impact on lifetime fitness. For the pre-contact Aché, most intragroup aggression took place in the context of ritualized club fights. For this reason, Aché informants were shown pictures of two hunters with their prey and simply asked: "which of these two men would win a club fight?"

The fourth paired comparison question about Disease Susceptibility is intended to assess whether successfully hunting certain prey might signal immunocompetence. Researchers studying the relationship between health and mate choice in humans have theorized and examined multiple pathways by which signals and cues of health may impact human mate choice (Tybur & Gangestad, 2011) and have further suggested that a desire to avoid exposure to parasites and pathogens may have contributed to cultural and population divergence (Fincher & Thornhill, 2008). Although none of the costly signaling in human foraging literature has directly suggested that hunters are attempting to signal disease resistance through the animals that they hunt, studies in non-human species have often hypothesized that heritable immunocompetence is a trait that might be assessed via costly phenotypic signals (Folstad & Karter, 1992a; Hamilton & Zuk, 1982).

In addition to four questions about the phenotypic traits of hunters that killed specific prey, the paired comparison task also included questions designed to determine whether the animals that a hunter kills affects his desirability as a mate. The precise wording of these questions varied slightly depending on the sex and marital status of the informant. Unmarried female informants were asked: "which of these two hunters would

you prefer to marry?" Married male and female informants were both asked, "which hunter would you prefer to marry your daughter?" Unmarried male informants were asked: "which animal would you prefer to kill?" By asking which animal an unmarried hunter would prefer to kill, it was possible to determine whether young men prefer to kill the same prey species that would make them desirable as mates according to unmarried women and married women and men, although these particular analyses were not carried out as part of this dissertation.

Finally, in order to determine whether the animals a hunter kills affects his desirability as a social partner, informants were asked to indicate which of the two hunters they would prefer to have as a social companion. In order to frame this question within ecologically relevant contexts for cooperation, Aché informants were asked: "which hunter would you prefer to go on a forest trek with?"

Prey Dyads

For the interviews, all six interview questions were asked for every possible combination of two prey species (16 species = 120 potential dyads x 6 questions = 720 unique questions in total). For each question, informants could respond by preferring hunter A, hunter B, indicating a tie, or by refusing to answer. Interviews were repetitive and tedious, so to avoid problems with informant fatigue, the 52 informants were divided randomly into 4 groups (A-D) containing approximately 13 informants per group. Each group answered questions about a unique subset of 30 prey dyads. The comparisons in each subset were drawn randomly from the original 120 possible prey dyads without replacement. Informants were interviewed about every prey dyad in their subset in

random order. The result is that all 6 questions were answered for each prey dyad by approximately 13 different informants.

Statistical Methods

Paired comparison data were analyzed using a series of multinomial logistic regressions to determine the effects of prey traits (Wt, HtK, HtF) on beliefs about hunters' phenotypes (EFP, Strength, Fighting Ability, Disease Susceptibility), and social preferences for hunters (Preferred Mate or Preferred Cooperative Partner). In each model, the dependent variable was whether or not hunter A was chosen (hunter A = 1, hunter B = 0, tie = 0.5) as having a better phenotype or as a preferred social partner. Each of 6 models differed in the outcome variable of interest, asking whether hunter A was characterized by higher: EFP, physical Strength, Fighting Ability, and Disease Susceptibility, and whether A or B was the Preferred Mate, or Preferred Cooperative Partner. The predictor variables employed in the model were the difference in Wt, difference in rank HtF, and difference in rank HtK between animals killed by hunter A and hunter B (e.g., Wt of prey killed by A – Wt of prey killed by B). The predictors were standardized [(measure prey A - measure prey B)/ std. deviation of interview sample) in order to facilitate direct comparisons of effect sizes of the three predictor variables. Hence the probability of choosing hunter A was modeled as a function of std. deviation units' difference between prey A and prey B in weight, rank HtK, rank HtF.

Harder to find and harder to kill animals were always assigned higher rank values (highest = 16, lowest = 1), such that positive values for differences between A and B (hunter A rank – hunter B rank) indicate that hunter A killed the harder to find or harder

to kill species. The statistical models therefore assess whether **larger differences between A and B in prey characteristics favoring A (std. Wt, std. HtF, std. HtK) are associated with higher probabilities of informants choosing the hunter who killed prey type A** in the dyadic comparison.

A second set of analyses were performed on Aché paired comparison data using binomial generalized linear models in order to determine how ratings of hunter phenotype (strong, good provisioner, etc.) relate to preferences for that hunter as a mate or ally. For these analyses, the dependent variable was which of the two hunters an informant chose as a preferred Mate, or a preferred Cooperative Partner (dichotomized as "chose hunter A" = 1, “did not choose” hunter A = 0). The predictors in each model are which of the two hunters were rated by that informant as having greater EFP, Strength, Fighting Ability, and Disease Susceptibility (e.g. hunter A has greater Strength = 1, hunter A doesn't have greater Strength = 0). The statistical models are logistic regression with multiple dichotomous categorical predictor variables. All predictors and outcome variables were standardized in order to facilitate comparisons between predictors (model coefficients and effect sizes are measured as change in the probability of choosing A as a function of a 1 s.d. change in the measure of the independent variable).

Task 2: Results

Multinomial Logistic Regression Results

| Task 2 Regressions: Hunter Phenotype Questions | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | EFP | | Strength | | Fighting Ability | | Disease Susceptibility | |
| Standardized predictors | Std. Beta | p < | Std. Beta | P < | Std. Beta | P < | Std. Beta | P < |
| Intercept | -0.56 | 0.001 | -0.22 | 0.001 | -0.12 | 0.04 | 0.16 | 0.006 |
| diff. Body Weight (A – B) | 0.88 | 0.001 | 0.88 | 0.001 | 0.65 | 0.001 | -0.57 | 0.001 |
| diff. HtF (A – B) | -1.49 | 0.001 | -1.19 | 0.001 | -0.92 | 0.001 | 0.84 | 0.001 |
| diff. HtK (A – B) | 1.13 | 0.001 | 1.33 | 0.001 | 1.20 | 0.001 | -1.00 | 0.001 |

**Table 3.4** Aché Task 2 predicting hunter phenotype from prey traits. This table presents the results of 4 multinomial logistic regressions predicting perceptions of hunter phenotype (EFP, Strength, Fighting Ability, Disease Susceptibility) based on differences between animals killed. For each model, the predictors are standardized differences between the prey killed by hunter A and hunter B in Wt (kg), rank HtF, or rank HtK, and the outcome is predicted preference for hunter A.

| Task 2 Regressions: Preferred Status Questions | | | | |
|---|---|---|---|---|
| | Preferred Mate | | Preferred Cooperative Partner | |
| Standardized predictors | Std. Beta | P > | Std. Beta | P > |
| Intercept | -0.61 | 0.001 | -0.66 | 0.001 |
| Difference Body Weight (A – B) | 0.91 | 0.001 | 0.83 | 0.001 |
| Difference HtF (A – B) | -1.55 | 0.001 | -1.60 | 0.001 |
| Difference HtK (A – B) | 1.14 | 0.001 | 1.21 | 0.001 |

**Table 3.5** Ache Task 2 predicting hunter preferred status from prey traits. This table presents the results of 2 multinomial logistic regressions predicting the preferred status of the hunter as a Mate or Cooperative Partner based on differences between animals killed. For each model, the predictors are standardized differences between the prey killed by hunter A and hunter B in Wt (kg), rank HtF, or rank HtK, and the outcome is predicted preference for hunter A.

A series of multinomial logistic regressions were run on Aché paired comparison interview data (Table 3.4). In each regression, three predictors based on differences in ranked prey characteristics (standardized difference in Wt, standardized difference in rank HtF, standardized difference in rank HtK) were entered together in the model and regressed against the probability that hunter A was selected as "better" on one of four phenotypic ratings (EFP, Strength, Fighting Ability, disease resistance).

All three prey traits were significant predictors of choosing a specific hunter as possessing one of the hunter characteristics examined (EFP, Strength, Fighting Ability, Disease Susceptibility). In the multi-variate models, killing a larger animal (with the effect of the other two prey characteristics controlled) was associated with being perceived as having greater EFP, Strength, Fighting Ability, and decreased Disease Susceptibility. Killing a HtK animal (with other variable effects controlled) was also associated with being perceived as having a greater EFP, Strength, Fighting Ability, and lesser Disease Susceptibility. In contrast, killing a HtF animal (with Wt differences and HtK effects controlled) was associated with being perceived as having lesser EFP, lesser Strength, lesser Fighting Ability, and greater Disease Susceptibility.

Likewise, standardized difference in Wt, HtF, and HtK were significant predictors of whether a hunter was preferred as a Mate or Cooperative Partner. Killing a larger or HtK animal was associated with an increased probability of being preferred as a Mate or Cooperative Partner, while killing a HtF animal was associated with a decreased preference for that hunter (Table 3.5). Notable in the results is that all p values for the

effects reported are much less than 0.001 demonstrating that effects are not simple due to random sample error.

## Multinomial Logistic Regression Plots

To visualize these associations reported, 18 regression plots were created based on the multiple regression results, with each plot representing the regression coefficient of one of the three predictor variables (with other effects controlled) on one of the six outcome variables (Figures 3.3-3.8). In each plot, the vertical axis represents the probability that hunter A will be chosen, and the horizontal axis represents the differences between standardized predictors, with the value for hunter A being subtracted from the value for hunter B.

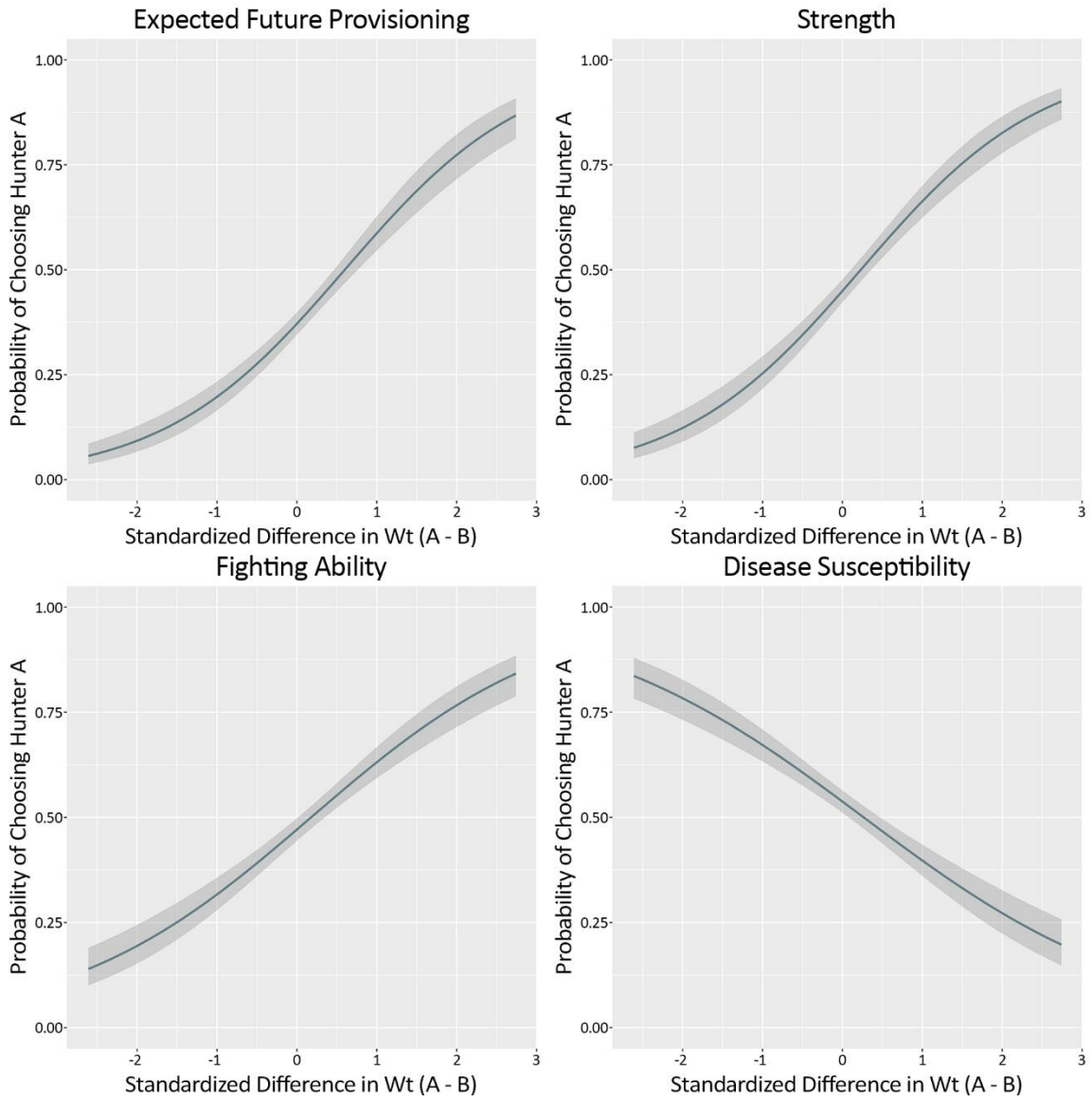



**Figure 3.3** Ache Task 2 predicting perceptions of hunter phenotype from differences in prey weight. These figures depict the results of multinomial logistic regressions examining the effects of standardized differences between prey species traits (in this case, difference in Wt between animal A and animal B) on the probability that a hunter is rated as having a better phenotype (EFP, Strength, Fighting Ability, Disease Susceptibility). Shaded areas represent 95% confidence intervals.

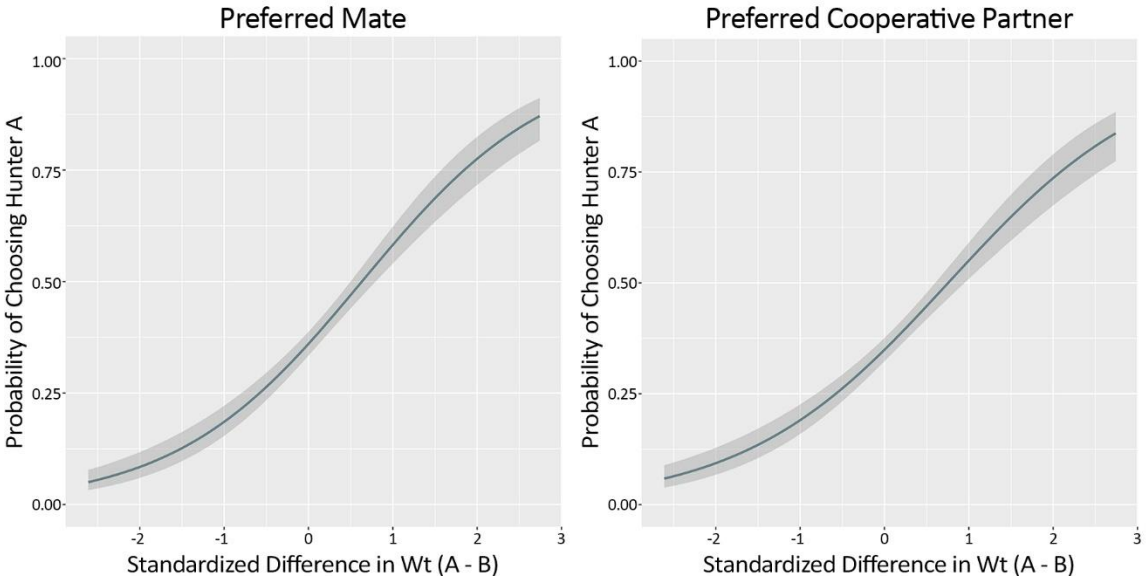



**Figure 3.4** Ache Task 2 predicting preferred status from differences in prey weight. These figures depict the results of multinomial logistic regressions examining the effects of standardized differences between prey species traits (in this case, difference in Wt between animal A and animal B) on the probability that a hunter is preferred as a Mate or Cooperative Partner. Shaded areas represent 95% confidence intervals.

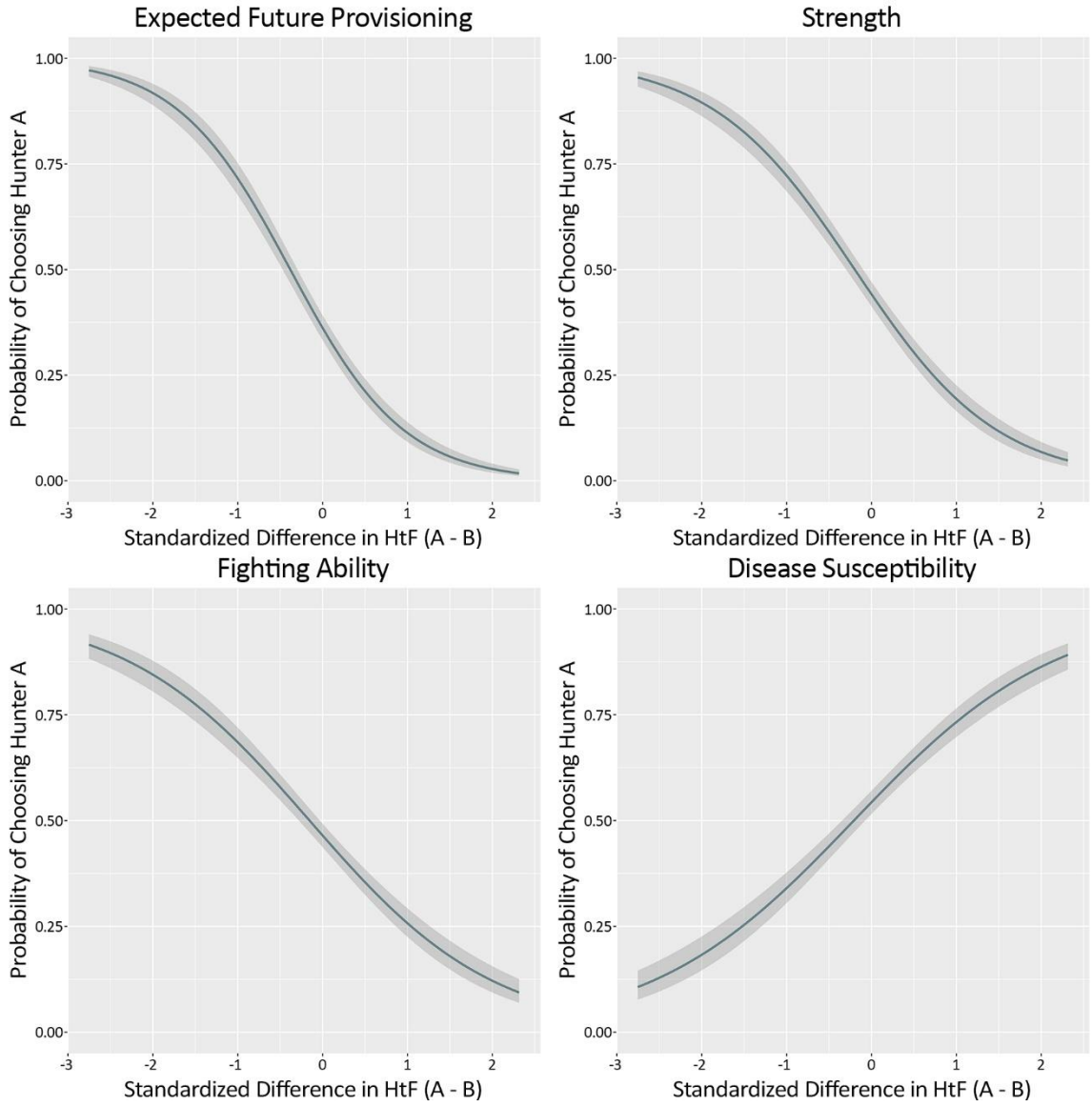



**Figure 3.5** Ache Task 2 predicting perceptions of hunter phenotype from differences in HtF. These figures depict the results of multinomial logistic regressions examining the effects of standardized differences between prey species traits (in this case, difference in rank HtF between animal A and animal B) on the probability that a hunter is rated as having a better phenotype (EFP, Strength, Fighting Ability, Disease Susceptibility). Shaded areas represent 95% confidence intervals.

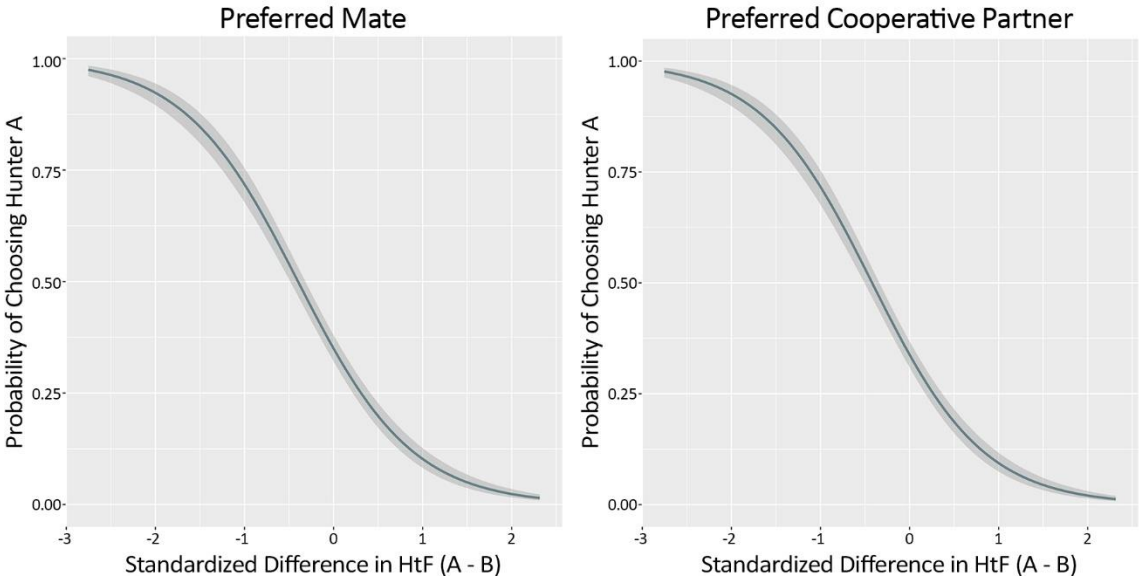



**Figure 3.6** Ache Task 2 predicting preferred status from differences in HtF. These figures depict the results of multinomial logistic regressions examining the effects of standardized differences between prey species traits (in this case, difference in rank HtF between animal A and animal B) on the probability that a hunter is preferred as a Mate or Cooperative Partner. Shaded areas represent 95% confidence intervals.

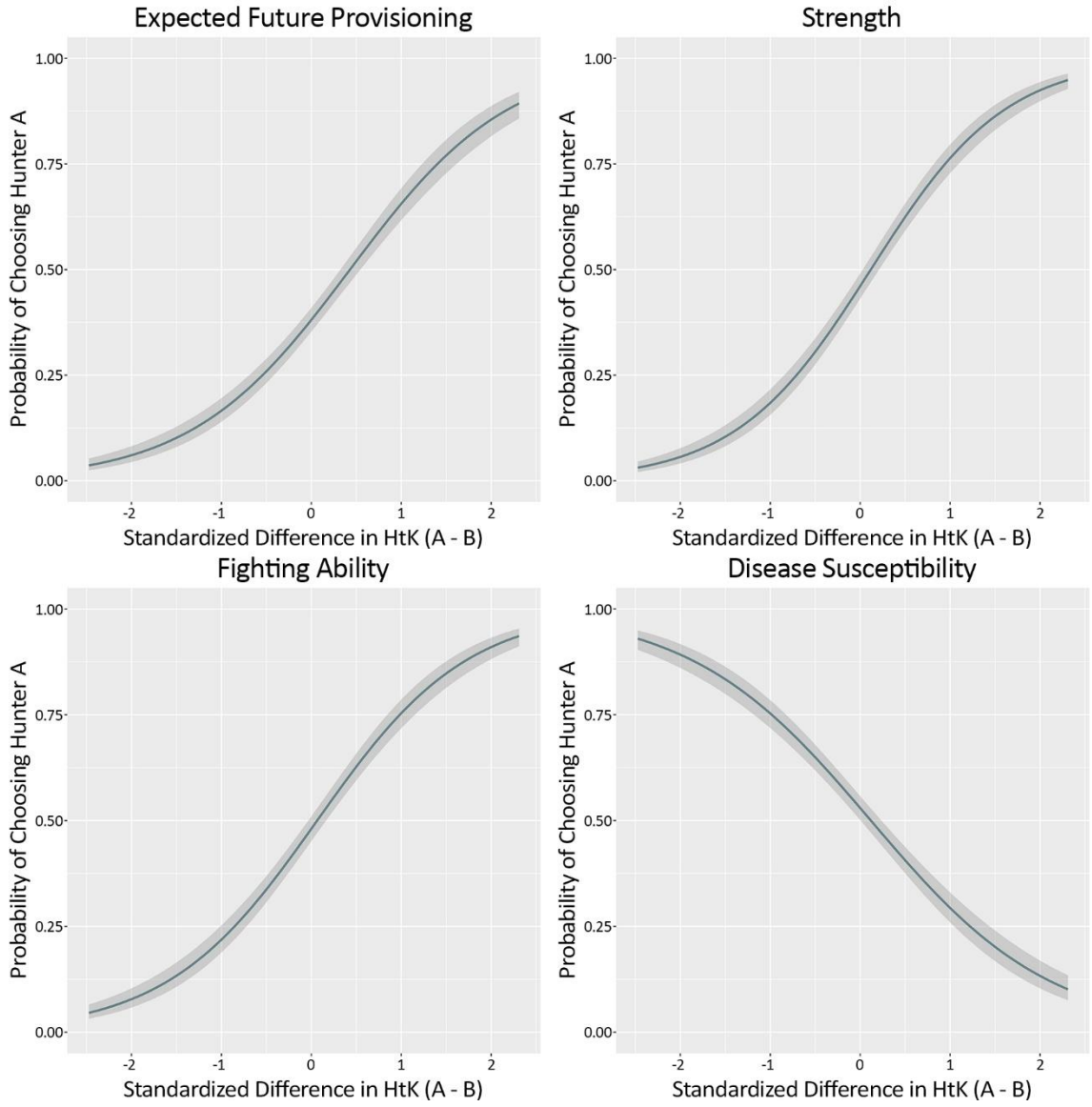



**Figure 3.7** Ache Task 2 predicting perceptions of hunter phenotype from differences in HtK. These figures depict the results of multinomial logistic regressions examining the effects of standardized differences between prey species traits (in this case, difference in rank HtK between animal A and animal B) on the probability that a hunter is rated as having a better phenotype (EFP, Strength, Fighting Ability, Disease Susceptibility). Shaded areas represent 95% confidence intervals.

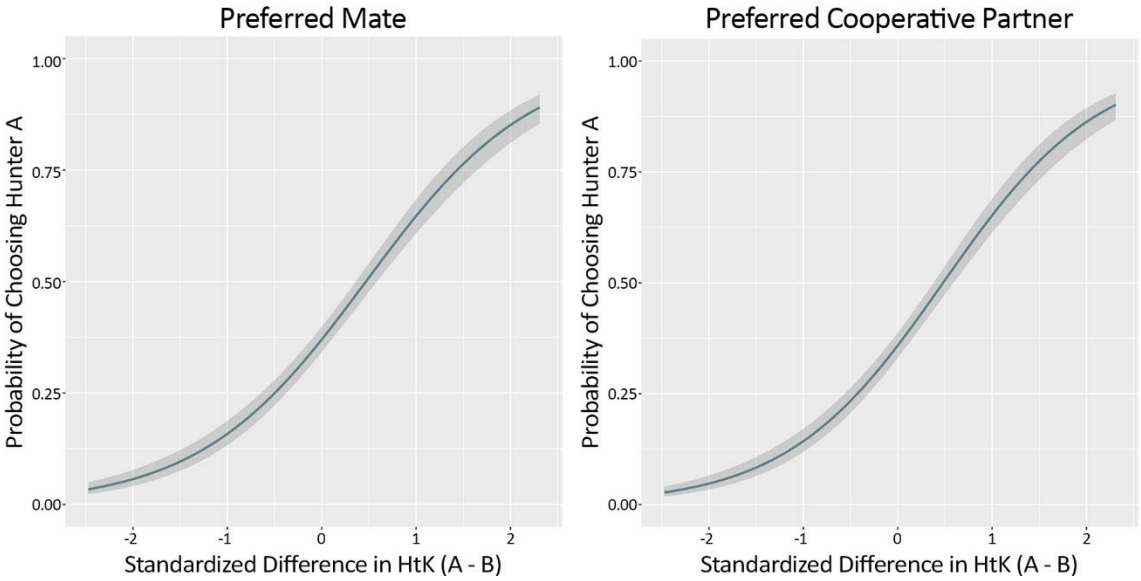



**Figure 3.8** Ache Task 2 predicting preferred status from differences in HtK. These figures depict the results of multinomial logistic regressions examining the effects of standardized differences between prey species traits (in this case, difference in rank HtF between animal A and animal B) on the probability that a hunter is preferred as a Mate or Cooperative Partner. Shaded areas represent 95% confidence intervals.

## Agreement by Sex

The Aché paired comparison multi-variate analyses were repeated examining the responses of 28 male and 24 female informants separately. For both sexes, hunters who killed larger, or, harder to kill animals were perceived as having significantly ($p < 0.001$ for all) greater EFP, Strength, Fighting Ability, and decreased Disease Susceptibility, and hunters who killed larger or harder to kill animals were preferred as Mates and Cooperative Partners by both sexes when analyzed independently (Appendix A Tables 1 - 4). Hunters who killed harder to find animals were also perceived by both men and women as having significantly lower ($p < 0.001$ for all) EFP, physical Strength, Fighting Ability, and increased Disease Susceptibility, and were less preferred as Mates or Cooperative Partners.

In sum, there is no detectable difference in the way that male and female informants associate prey characteristics with hunter characteristics or preferences for mating and social partners. Since analyses on each sex alone replicates the overall analyses, it can be concluded that the associations reported are very robust in the Aché population.

Prey Dyads of Interest

Additional insight into the impacts of killing an animal on perceived phenotypic quality and preferred status can be gained by examining cases in which informants were unanimous in their preference of one species over another. For a given dependent variable (Preferred Mate, Preferred Cooperative Partner, EFP, Strength, Fighting Ability, Disease Susceptibility) there were a number of prey dyads (ranging from 26 to 37 out of a total of 120 dyads) where informants were unanimous in their selection one species over another. Table 3.6 shows the categorization of prey based on combinations of HtF and HtK ranks, and with staple prey species (those that comprise >1% of total prey biomass harvested: (Hill & Padwe, 2000; table 5.2)) in the Aché diet highlighted in red.

| Categorizing Prey on HtF & HtK | | |
|---|---|---|
| | Hard to Find<br>Ranks: 9 - 16 | Easy to Find<br>Ranks: 1 - 8 |
| Hard to Kill Ranks: 9 - 16 | Anaconda, Bush dog, Jaguar, Tapir, Tayra | Red Brocket Deer, White Lipped Peccary |
| Easy to Kill Ranks: 1 - 8 | Tortoise, snake | Collared Peccary, Coati, Guan, Capuchin, Paca, Tegu lizard, 9 banded armadillo |

**Table 3.6** Categorization of Prey on HtF and HtK. This table categorizes all 16 species based on their mean ranks of HtF and HtK. Animals highlighted in red are species that are major contributors to the Aché diet. Values in parentheses show the range of ranks included in a cell.

On the question of which hunter was preferred as a Cooperative Partner, 37 out of 120 prey dyads had unanimous responses from informants. Of these, the prey species that were unanimously NOT preferred against any other species were bush dog (7 dyads), snake (12 dyads), tayra (3 dyads), and turtle (8 dyads). This dispreference was particularly striking when those rare species were compared against dietary staple species. In the 7 unanimous cases comparing 2 staple species, the larger species was always preferred. Finally, of the 24 unanimous cases comparing a staple species to a non-staple species, the staple species was always preferred. In short, Aché informants are more impressed by hunters who kill commonly eaten species rather than harder to kill rare species.

On the question of which hunter was preferred as a Mate, 32 out of 120 prey dyads received unanimous responses from informants. Of these, the majority of species

that were unanimously NOT preferred were again bush dog (5 dyads), snake (10 dyads), tayra (3 dyads), and turtle (8 dyads), all very rarely eaten species. In the 7 unanimous cases comparing 2 staple species, the larger species was always preferred. Again, for the 22 unanimous opinions comparing a staple species to a non-staple species, the staple species was always preferred.

Examination of which hunter was perceived as having higher EFP showed a similar pattern. Unanimous preferences were found for 36 out of 120 prey dyads, and of these, the majority of species that were unanimously NOT considered signals of high EFP were bush dog (5 dyads), snake (12 dyads), tayra (3 dyads), turtle (7 dyads), and guan (4 dyads), all rare species. For the 7 unanimous cases comparing 2 staple species, the larger species was always preferred, and for the 23 unanimous cases comparing a staple species to a non-staple species, the staple species was always preferred.

On the question of which hunter was perceived as having greater Strength, 26 out of 120 prey dyads had unanimous responses from informants. Of these, the majority of species that were unanimously NOT considered signals of high Strength were snake (5 dyads), tayra (3 dyads), and turtle (8 dyads), all rare species. In the 7 unanimous cases comparing 2 staple species, the larger species was always preferred, and in the 19 unanimous cases comparing a staple species to a non-staple species, the staple species was preferred (17/19) times.

On the question of which hunter was perceived as having greater Fighting Ability, 36 out of 120 prey dyads had unanimous responses from informants. Of these, the majority of species that were unanimously NOT considered signals of high Fighting

Ability were bush dog (3 dyads), snake (7 dyads), tayra (3 dyads), and turtle (8 dyads), all rare species. In the 9 unanimous cases comparing 2 staple species, the larger species was always preferred, and for the 17 unanimous cases comparing a staple species to a rare species, the staple species was preferred (14/17) times.

On the question of which hunter was perceived as having greater Disease Susceptibility, 26 out of 120 prey dyads had unanimous responses from informants. Of these, the majority of species that were unanimously NOT considered signals of Disease Susceptibility were Tapir (7 dyads), white lipped peccary (6 dyads), collared peccary (3 dyads) all large staple species, and the majority of species that were unanimously considered signals of higher Disease Susceptibility were snake (6 dyads), and turtle (8 dyads). For the 9 unanimous cases comparing 2 staple species, the smaller species was always considered a signal of higher Disease Susceptibility. In the 14 unanimous cases comparing a staple species to a non-staple species, the staple species was always considered a signal of better disease resistance (17/17) times.

The qualitative trend that is clear in all these data indicates that informants believe that, all else being equal, killing larger animals is better than killing smaller animals, and that killing animals that are common to the diet is better than killing rarely hunted species on all dimensions.

Predicting Social Preferences from Perceived Hunter Phenotype

Two generalized linear models examined relationships between individual assessment of hunter A's phenotype (e.g. stronger, greater EFP, etc.) and preferences for hunter A, by the same informant, as a Mate or Cooperative Partner (Table 3.7). Informant

preferences for a hunter as a Mate were significantly positively associated with their choice of that hunter as having greater EFP ($p < 0.001$) or Strength ($p < 0.05$), but not by their choice of that hunter as possessing greater Fighting Ability or Disease Susceptibility. Informant preferences for hunter A as an ally were also significantly ($p < 0.001$) positively associated with their choice of that hunter as having greater EFP or Strength, but not by Disease Susceptibility or Fighting Ability.

| **Social Preferences by Hunter Traits** | | | | | | |
|---|---|---|---|---|---|---|
| | Preferred Mate | | | Preferred Social Partner | | |
| Standardized predictors | Beta | std. Error | p < | Beta | std. Error | p < |
| Intercept | -3.74 | 0.54 | 0.001 | -3.88 | 0.54 | 0.001 |
| EFP Response | 4.66 | 0.29 | 0.001 | 4.58 | 0.29 | 0.001 |
| Strength Response | 1.50 | 0.57 | 0.008 | 2.21 | 0.53 | 0.001 |
| Fighting Ability Response | 0.63 | 0.58 | 0.282 | -0.09 | 0.56 | 0.869 |
| Disease Susceptibility | -0.29 | 0.48 | 0.544 | -0.12 | 0.47 | 0.793 |

**Table 3.7** Ache Task 2 predicting social preferences from hunter phenotypic rankings. This table reports the results of two GLM analyses examining the association between being preferred as a Mate or Cooperative Partner and having been ranked as having greater EFP, Strength, Fighting Ability, or Disease Susceptibility based on hunter-harvested prey species. Estimates and standard errors have been rounded to two decimal place, and P values have been rounded to three decimal places.

Cultural Consensus Analysis Results

CCA was carried out on responses from each subgroup of informants (A-D) to the questions in the paired comparison task (table 3.8). Paired comparison data were analyzed using a categorical model. CCA results indicate consensus within all subsets of informants who completed task. This suggests that there is agreement among informants

about prey qualities, about the relative values of prey as indicators of hunter phenotype, and about the relative value of prey for attracting mates and allies.

| Cultural Consensus Analysis Results: Ache Task 2 | | | | |
|---|---|---|---|---|
| | Group A | Group B | Group C | Group D |
| n = | 13 | 14 | 13 | 12 |
| 1st Eigen Value | 6.23 | 8.38 | 6.68 | 6.16 |
| 2nd Eigen Value | 0.92 | 2.04 | 1.36 | 0.92 |
| Ratio (1st/2nd) | 6.75 | 4.12 | 4.91 | 6.7 |
| # Negative Competencies | 0 | 0 | 0 | 0 |
| Mean Competency | 0.66 | 0.77 | 0.68 | 0.67 |
| S.D. of Competency | 0.23 | 0.11 | 0.23 | 0.27 |

**Table 3.8** Cultural Consensus Analyses of Aché informant responses to Task 2. This table depicts the Results of CCAs examining agreement among informants about which hunter should be selected in the paired comparison task. Consensus is said to be achieved when the ratio of the first and second Eigenvalue exceeds 3 and there are few or no negative competencies. Competency is a measure of the proportion of culturally correct answers that an informant gives. Negative competencies indicate that an informant is systematically incorrect in their responses because they don't share a cultural model with the group. Each group (A-D) completed the ranking task on a unique set of 30 prey dyads.

### Task 3: Multi-Prey Comparisons Controlling for Total Prey Weight Harvested

#### Methods

Informants were shown images of two hunters, one standing next to a single large animal and the other standing next to a number of smaller animals of a single species with a total estimated weight similar to that of the single large animal (Figure 3.9). Informants were asked to imagine that they have encountered these two hunters and observed a week's worth of kills by each. Informants compared hunters on EFP, Strength, Fighting Ability, and Disease Susceptibility, as well as their desirability as a Preferred Mate or Cooperative Partner. The same interview questions were used as in task 2. In

addition, informants were asked, “which of these men has killed more meat?”, making it possible to validate whether they viewed the two sets of animals as representing similar amounts of food.

Due to time constraints, not every combination of prey was tested. Nine different species were divided into 3 groups based on body size: large animals (tapir, anaconda, jaguar), medium sized animals, (deer, white lipped peccary, collared peccary), and small animals (armadillo, coati, paca). 24 unique prey combinations were created, each comparing a single animal from a larger prey class to several small animals (of a single species) from a smaller prey class. Tapir was never compared to animals from the smallest weight class because it wasn’t possible to fit enough small animals on a single card to equal the weight of a tapir. Each comparison was set up such that hunter A had killed the single large animal, while hunter B had killed the smaller animals.

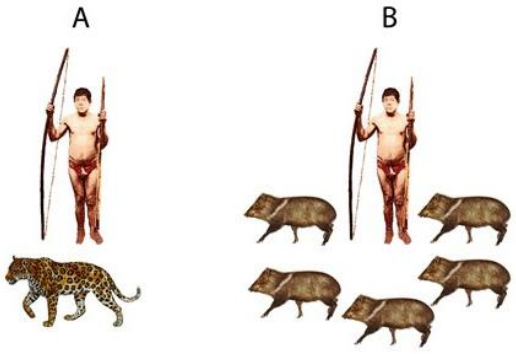



**Figure 3.9** Aché Task 3 multi-prey comparisons. This figure depicts an example of the types of comparisons being made in the multi-prey comparison task.

## Statistical Methods

Two methods were used in order to validate that informants did indeed perceive both sets of prey as containing approximately the same total amount of meat. First, the

mean and standard error of the proportion of informants selecting the single large animal as having more total meat across all dyads was examined (this should generally be 50% since both sets are approximately equivalent). Next a univariate regression was run predicting the proportion of informants choosing hunter A as having killed more meat, by the estimated difference in weight between the single large and multiple small animals.

Multi-prey comparison data were then analyzed using a series of multinomial logistic regression models predicting the probability that hunter A was chosen as having a better phenotype or as a preferred Mate or Cooperative Partner based on differences between the prey killed by hunter A and hunter B. Differences between species (animal killed by hunter A – animal killed by hunter B) on Wt, HtF, HtK, and differences between prey sets on total weight and number of prey killed were used as predictors in these models. All predictors were standardized by dividing the mean difference between traits by the standard deviation of differences between traits.

Since attempts were made to control for biomass of each set, the number of animals in set B should be proportional to the difference in Wt between animal A and a single animal from set B. If informant responses are driven only by total food provided, then their responses should show equal preference for A and B. If the number of animals killed is a preferred criterion, hunter B should always be chosen, and if killing large, rare, or hard to kill species is the driver of informant responses then preferences should be seen for set A.

## Task 3: Results

### Validating Controls for Weight

Among Aché informants, the mean proportion of informants that selected the single large animal as representing greater total biomass across all 24 comparison dyads was: $\mu = 0.51$, SEM = 0.001. A linear regression shows that informants perceive the single large animal as having a greater total biomass 51% of the time, with the estimated true difference in biomass between sets A and B having no impact on their perceptions, despite a range from the large animal weighing 14 kg more than the small animals, to the small animals weighing almost 4 kg more than the large animal (Figure 3.10). Informants selected the hunter who killed many small animals (Hunter B) as having killed more meat in 33% of comparisons, and they said both hunters had killed the same amount in 16% of comparisons. These results suggest that informants perceived both sets of prey as equivalent in weight across all the dyads that were compared.

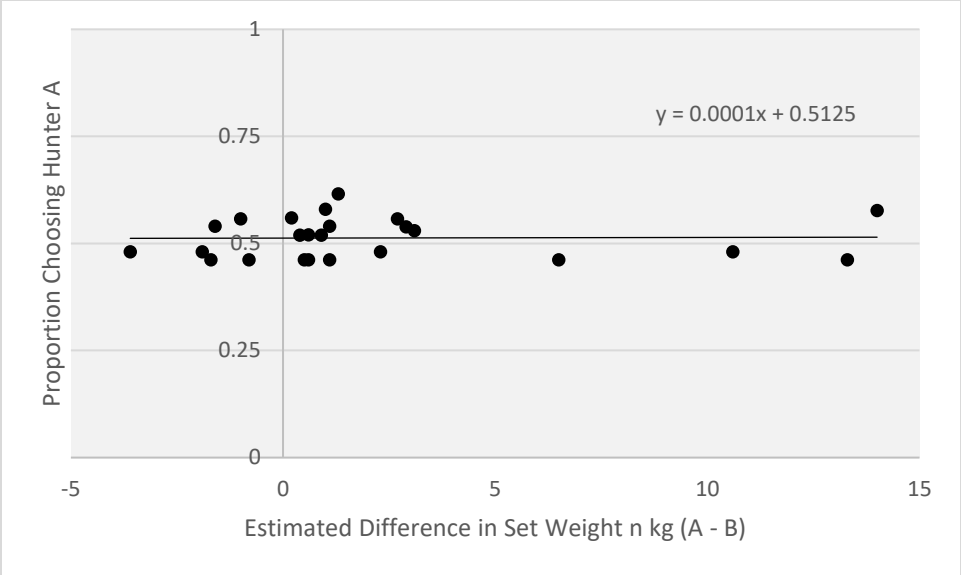



**Figure 3.10** Probability that hunter A is chosen as having killed more meat. Univariate regression showing the proportion of informants choosing hunter A (single large animal) as having killed more meat plotted against the calculated difference in weight (Kg) between the two sets (A – B) as determined from the data sources used in this study. Each dot represents a single prey dyad. In all cases informants were more likely to choose hunter B as having killed more meat.

## Multinomial Logistic Regression Results

| Aché Multi-prey Comparison Multinomial Logistic Regression: Hunter Phenotype Questions | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | EFP | | Strength | | Fighting Ability | | Disease Susceptibility | |
| Standardized predictors | Std. Beta | P < | Std. Beta | P < | Std. Beta | P < | Std. Beta | P < |
| Intercept | -0.41 | 0.021 | -0.56 | 0.001 | -0.32 | 0.027 | -0.27 | 0.069 |
| diff. Set Weight (A – B) | -0.19 | 0.033 | -0.33 | 0.000 | 0.02 | 0.779 | -0.03 | 0.643 |
| diff. Body Weight (A – B) | 0.00 | 0.849 | 0.00 | 0.522 | 0.00 | 0.967 | 0.00 | 0.696 |
| diff. HtF (A – B) | -0.70 | 0.009 | -0.76 | 0.003 | -0.09 | 0.613 | -0.12 | 0.545 |
| diff. HtK (A – B) | -0.16 | 0.552 | 0.06 | 0.828 | 0.10 | 0.605 | 0.13 | 0.508 |

**Table 3.9** Aché Task 3 predicting hunter phenotypic ratings from prey set traits. This table contains the results of two multinomial logistic regressions examining the effects standardized differences between prey set traits on the probability that a hunter is chosen as have greater phenotypic quality (EFP, Strength, Fighting Ability, Disease Susceptibility).

| Aché Multi-Prey Comparison Multinomial Logistic Regression: Preferred Status Questions | | | | |
|---|---|---|---|---|
| | Preferred Mate | | Preferred Cooperative Partner | |
| Standardized predictors | Std. Beta | P > | Std. Beta | P > |
| Intercept | -0.717 | 0.000 | -0.352 | 0.021 |
| Difference Set Weight (A – B) | -0.241 | 0.010 | -0.186 | 0.015 |
| Difference Body Weight (A – B) | 0.002 | 0.242 | -0.002 | 0.317 |
| Difference HtF (A – B) | -0.749 | 0.007 | -0.374 | 0.072 |
| Difference HtK (A – B) | -0.030 | 0.913 | 0.014 | 0.945 |

**Table 3.10** Aché Task 3 predicting preferred status from prey set traits. This table contains the results of two multinomial logistic regressions examining the effects standardized differences between prey set traits on the probability that a hunter is preferred as a Mate or Cooperative Partner.

EFP

Informant preferences for hunter A as having greater EFP were modelled using all four predictors (Table 3.9). Across all prey dyads, hunter A was perceived as having greater EFP 16% of the time (mean proportion choosing A = 0.16, S.E. = 0.011). Differences in set weight and HtF were both significant predictors of informant preferences for hunter A. The likelihood that an informant preferred hunter A decreased when the single large animal was relatively harder to find, and when hunter A was calculated to have killed relatively greater set weight.

Strength

Informant preferences for hunter A as having greater Strength were modelled using all four predictors (Table 3.9). Across all prey dyads, hunter A was perceived as having greater Strength 17% of the time (mean proportion choosing A = 0.17, S.E. =

0.011). Differences in set weight and HtF were both significant predictors of informant preferences for hunter A. The likelihood that an informant preferred hunter A decreased when the single large animal was relatively harder to find, and when hunter A was calculated to have killed a relatively greater set weight.

Fighting Ability

Informant preferences for hunter A as having greater Fighting Ability were modelled using all four predictors (Table 3.9). Across all prey dyads, hunter A was perceived to have greater Fighting Ability 40% of the time (mean proportion choosing A = 0.40, S.E. = 0.014). Differences in Fighting Ability were not predicted by any of the four predictors.

Disease Susceptibility

Informant preferences for hunter A as being a more desirable Mate were modelled using all four predictors (Table 3.9). Across all prey dyads, hunter A was perceived to have greater Disease Susceptibility 39% of the time (mean proportion choosing A = 0.39, S.E. = 0.014). Differences in Fighting Ability were not predicted by any of the four predictors.

Preferred Mate

Informant preferences for hunter A as a Mate were modelled using all four predictors (Table 3.10). Across all prey dyads, hunter A was preferred as a Mate 15% of the time (mean proportion choosing A = 0.15, S.E. = 0.010). Differences in set weight and HtF were both significant predictors of informant preferences for hunter A. The likelihood that an informant preferred hunter A decreased when the single large animal

was relatively harder to find, and when hunter A was calculated to have killed a relatively greater set weight.

Preferred Cooperative Partner

Informant preferences for hunter A as a Cooperative Partner were modelled using all four predictors (Table 3.10). Across all prey dyads, hunter A was preferred as a Cooperative Partner 26% of the time (mean proportion choosing A = 0.26, S.E. = 0.012). Differences in set weight were significant predictors of informant preferences for hunter A, and differences in HtF approached significance as predictors. The likelihood that an informant preferred hunter A decreased when the single large animal was calculated to contain a relatively greater set weight.

Overall

Of the four predictors used in the model, only differences in HtF and set weight were significant predictors of informant preference on EFP, Strength, and desirability as a Mate or Cooperative Partner. None of the predictors used in the model successful predicted informant preferences for hunter A on Fighting Ability or Disease Susceptibility. The findings that hunters who killed harder to find animals were perceived as having lower EFP, Strength and were less desired as Mates is not surprising given the results of the paired comparison task. It was unexpected that killing a greater total set weight would result in being perceived as having lower EFP, Strength, and in being less preferred as a mate or ally, especially given that attempts were made to control for differences in set weight.

One possible explanation is that there is systematic, unintended bias in which prey sets were had a greater set weight difference A-B. The mean difference in set weight for all 24 prey combinations in the multi-prey Comparison task was 2.19 kg (s.d. = 4.54) indicating a bias toward hunter A (single large animal) having killed more meat. Thus, it may be that difference in set weight (A – B) is a significant negative predictor of informant preference simply because the single large animal tended to have a greater total set weight while the hunter who killed many small animals tended to be preferred.

Another possible explanation is that the single large animal most commonly associated with having a large positive difference in set weight may be systematically less preferred for some other reason. On closer inspection it was noticed that the mean and standard deviation of differences in set weight was higher in the 6 cases where jaguar was the single large animal (mean = 5.40, s.d. = 5.62) versus the 18 cases not involving jaguar (mean = 1.12, s.d. = 3.71). It may be that informants are simply not impressed by hunters who kill jaguars relative to other potential prey types.

Although in a few cases difference in HtF or difference in total prey set weight were statistically associated with informant assessment of and preference for hunter A, the overall trend in the data was for most informants to prefer the hunter who killed many small animals, with HtF and total set weight differences only modifying but not changing that trend. On Disease Susceptibility and Fighting Ability, informant preferences for hunter A were somewhat below 50% (40% and 39% respectively). On EFP, Strength, and preferred status as a Mate or Cooperative Partner, strong preferences for the hunter who killed many small animals were observed (percent choosing hunter A were: 16%, 17%,

15%, and 26% respectively). This is true in spite of the fact that informants were slightly more likely to choose Hunter A as having killed more meat than Hunter B (51% of informants chose hunter A as having killed more meat vs 33% who chose hunter B and 16% who rated both hunters as having killed the same amount).

Task 4: "Show-off" vs Provider Comparison

Methods

Informants completed an interview task in which they were asked to compare two hunters who follow either a "show-off" or provider strategy by killing different quantities and types of prey over a 15-week period. Two sets of 15 note cards representing 15 weeks of hunting returns were created. Informants were shown note cards one at a time in random order from each set, and told that each note card represented 1 week of hunting returns for hunter A or B. Informants were asked to compare hunter A and B three times, after seeing 5, 10, and 15 cards from each set (representing increments of 5 weeks). Female informants were asked to indicate which hunter was more desirable as a mate for themselves or for their daughters, while male informants were asked which set of animals they would prefer to kill.

The "show-off hunter" (hunter A) set of 15 cards contained 10 weeks where the hunter killed one large and HtF or HtK species (as indicators of high phenotypic quality and preferred status) and 5 weeks where the hunter killed nothing at all. The "provisioner hunter" (hunter B) set contained 15 weeks of successful harvest, with each week's harvest consisting of a variety of small and low ranked (HtF, or HtK) animals (see Figure 3.11 for samples of showoff and provider cards). In total, the showoff set depicted 3

brocket deer, 4 collared peccaries, and 3 white lipped peccaries, while the provisioner set depicted 15 coati, 30 capuchin, 15 armadillo, and 15 paca.

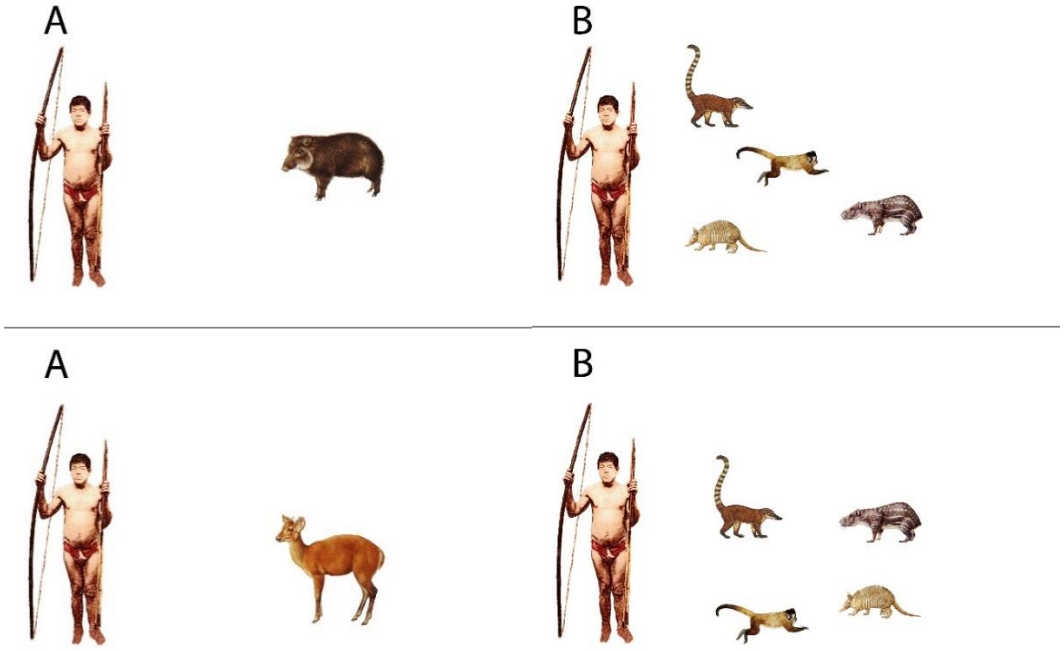



**Figure 3.11** Sample of Aché "show-off" and "provider" cards. These figures are examples of cards depicting the show-off hunter (hunter A) and the provisioning hunter (hunter B) from task 3. The top four hunters represent four weeks of hunting returns for the "show-off". The bottom four hunters represent four weeks of hunting returns for the "provider".

The total biomass of all animals in the "provisioning" set was 1/3 greater than that of the "show-off" set, however, the ranks of individual prey species as signals of phenotype and preferred status were greater for the "show-off" set. This was meant to test the hypothesis that informants would prefer "show-off" hunters even if their total food contribution over time were less than the "provisioner hunters".

To calculate the mean rankings for prey sets containing a variety of species, the individual rankings for each prey species (Table 3.11) were first multiplied the number of animals of that species in the set and these values were then summed across all species in the set and divided by the total number of animals in the set. The resulting mean ranks are

thus weighted by the number of animals of a given species included in the set. Mean ranks were calculated for EFP, Strength, Fighting Ability, Disease Susceptibility, and desirability as a Mate or Cooperative partner. Differences between card sets can be seen in Figure 3.12 and Table 3.12.

For each aspect of phenotype or preferred status, the individual rankings of each species were calculated as the proportion of all paired comparisons in Task 2 involving that species in which the animal was preferred as a signal, multiplied by 16 (see Table 3.11 for a list of individual prey ranks by species for each signal type).

| Prey Rankings for Hunter Phenotype and Preferred Status | | | | | | |
|---|---|---|---|---|---|---|
| Species | Mate | Ally | EFP | Strength | Fighting | Disease Susceptibility |
| Tapir | 14.09 | 14.39 | 14.22 | 13.88 | 13.09 | 12.88 |
| White Lipped Peccary | 14.21 | 13.96 | 13.38 | 13.08 | 12.22 | 11.82 |
| collard peccary | 11.86 | 12.15 | 11.96 | 11.41 | 11.07 | 11.07 |
| deer | 12.19 | 12.24 | 12.18 | 11.07 | 10.86 | 10.52 |
| jaguar | 8.19 | 8.49 | 9.00 | 12.45 | 12.48 | 11.16 |
| paca | 11.41 | 11.44 | 10.61 | 9.65 | 8.40 | 9.14 |
| armadillo | 9.83 | 9.12 | 9.75 | 7.82 | 7.84 | 8.01 |
| coati | 8.96 | 9.03 | 9.02 | 8.32 | 8.09 | 8.41 |
| capuchin | 9.00 | 8.67 | 8.38 | 7.20 | 7.11 | 6.92 |
| anaconda | 5.03 | 4.88 | 5.42 | 8.50 | 9.42 | 8.85 |
| bush dog | 5.82 | 5.59 | 6.10 | 7.34 | 7.86 | 7.45 |
| tayra | 5.51 | 5.43 | 5.51 | 5.66 | 6.13 | 6.45 |
| lizard | 4.47 | 4.86 | 4.89 | 3.63 | 3.87 | 4.55 |
| guan | 4.07 | 4.08 | 4.02 | 3.62 | 4.09 | 4.73 |
| tortoise | 2.11 | 2.31 | 2.47 | 2.01 | 2.72 | 3.27 |
| Snake | 1.25 | 1.38 | 1.08 | 2.35 | 2.75 | 2.78 |

**Table 3.11** Ranks of prey as signals of hunter phenotype. A list of prey ranks for each species on 2 aspects of preferred status and 4 aspects of hunter phenotype. Ranks were calculated as the proportion of all comparisons involving a given prey species in which that prey species was preferred, multiplied by 16.

| Prey Set Characteristics | Showoff Set | Provisioning Set |
|---|---|---|
| # Prey in Set | 10.00 | 75.00 |
| Total Weight (Kg) of Set | 217.30 | 279.00 |
| Mean HtF | 8.22 | 4.98 |
| Mean HtK | 9.57 | 6.42 |
| Mean Mate Rank | 12.70 | 9.72 |
| Mean Cooperative Partner Rank | 12.77 | 9.53 |
| Mean EFP | 12.56 | 9.52 |
| Mean Strength | 11.91 | 8.34 |
| Mean Fighting Ability | 11.41 | 7.90 |
| Mean Disease Susceptibility | 11.17 | 8.20 |
| Informant Preference | 5.00 | 148.00 |

**Table 3.12** Characteristics of the "show-off" and "provider" prey sets (numerical). The animals in the showoff set are larger, more difficult to kill, harder to find, and were rated more highly as signals of EFP, Strength, Fighting Ability, and Disease Susceptibility than those in the provisioning set. Furthermore, hunters who killed the animals in the showoff set were more likely to be rated as desirable mates and social partners. On the other hand, there is more total meat depicted and hunters bring back meat every week with the provisioning set (lower acquisition variance).

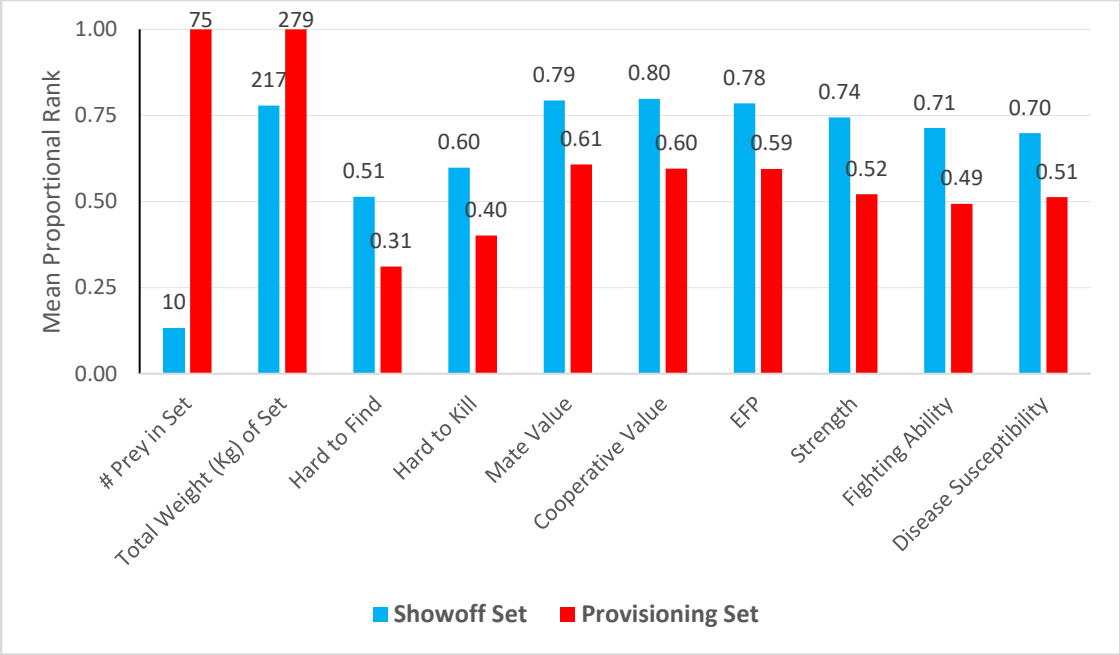



**Figure 3.12** Characteristics of the "show-off" and "provider" prey sets (graphical). This figure shows the differences in characteristics attributed to prey in the "showoff" and "provider" prey harvest sets. Number of prey in set and total weight of set are depicted. Mean ranks attributed to hunters who kill the prey types in each set (from the prey ranking task) have been converted into proportions, where 1 represents the maximum value possible for the set (the highest possible attribute ranks).

## Results

When 52 informants were given 3 opportunities to choose between a "showoff" prey set of 5 cards and a "provisioner" prey set of 5 cards, 94% of informants (49/52 informants) unanimously choose the "provisioner" set for all 3 comparisons, 4% (2/52 informants) choose the "provisioner" set 2 out of 3 times, and 2% (1/52 informants) preferred the "showoff" set of prey for all 3 comparisons. In short, Aché men and women overwhelmingly prefer hunters who bring in a slightly larger amount of meat in the form of small prey animals, rather than "showoff" hunters who bring in large, hard to find and hard to kill prey, but slightly less total meat.

Task 1 – 4 Summary

Ache informants completed four tasks designed to test various aspects of the CSH and the SOH. 51 Aché informants ranked 16 species of prey on how hard they were to find (HtF) and how hard they were to kill once found (HtK). Informants achieved consensus in their rankings on both prey traits. In task 2, informants compared pairs of hunters standing next to various combinations of prey species. Hunters were compared on four aspects of phenotype (EFP, Strength, Fighting Ability, Disease Susceptibility) and preferred status as a Mate or Cooperative partner. Hunters who killed large and hard to kill prey were viewed as having better phenotypes on all measures and were more preferred as Mates and Cooperative partners. Hunters who killed hard to find prey were viewed as worse on all four aspects of hunter phenotype and both aspects of preferred status. In task 3, informants were asked to compare pairs of hunters on four aspects of phenotype and two aspects of preferred status. In this task, informants compared hunters who killed a single large and impressive animal to ones who killed several smaller animals of an approximately equivalent weight. Informants preferred hunters who killed several smaller animals on all measures. In task 4 female informants were asked to select which hunter would be a more desirable mate, while males were asked which set of prey they would rather kill themselves. They were asked to choose between a "show-off" hunter who killed large and impressive animals and a "provisioner" hunter who killed small game consistently and brought in more kilos of meat. Informants showed strong preferences for the provisioner hunter.

# CHAPTER 4: Tsimané Methods and Results

## Research Questions

In the first chapter of this dissertation three competing explanations for the purpose of men's hunting in small scale societies were presented. The family provisioning hypothesis (FPH) proposed that purpose of men's hunting is to attract and retain a quality mate and to provision a hunter's offspring. The "show-off" hypothesis (SOH) proposed that the purpose of men's hunting is to show-off and attract the attention of potential extra pair mates by pursuing large and widely shared prey species. The costly signaling hypothesis (CSH) proposed that men intentionally target hard to acquire prey in order to signal their hidden phenotypic quality to potential mates and allies. In the second chapter the ethnographic evidence pertaining to these competing explanations was reviewed. In the third chapter results of research carried out with the Aché hunter-gatherers of Paraguay were presented. In this chapter the results of a comparable case study carried out with the Tsimané hunter-horticulturalists of Bolivia are presented. As in the previous chapter, this research is guided by five lines of questioning which address important aspects of the ongoing debate about the role of signaling in men's foraging decisions. These are:

**6)** Prey provide nutrient biomass to consumers, and hunters who bring in more total biomass may inadvertently "signal" their ability to provide food. But some prey might also be exceptionally hard to find or kill, indicating exceptional skill and strength of hunters who kill them. **Are there clear examples of prey whose value as a signal of hunter-phenotype is associated with the costs of acquiring them (HtF, HtK), and not simply a**

**function of how much food value they contain?** In other words, are there smaller but hard to find or kill prey that might signal to an audience greater hunter skill and strength, and are there larger prey that provide no real signal of hunter strength or skill because they are easy to find or kill? Or, do all same size prey species carry approximately the same signal value about hunter characteristics?

**7)** Harvesting specific types of prey could potentially provide signals of hunter phenotype. **Is it true that killing different prey lead informants to infer variation in hunter phenotype on dimensions of a) Expected Future Provisioning; b) Hunter Strength; c) Fighting – the likelihood to win physical contests with other men; d) Health – hunter, Disease Susceptibility?**

**8)** Some hunting strategies and prey sets may be better than others for signaling specific aspects of hunter phenotype. **Which aspect of perceived hunter phenotype have the greatest influence on whether that hunter will be preferred as a mate or ally?**

**9)** There could be a divergence between hunting strategies that provide high food biomass and hunting strategies that signal positive hunter phenotypes. **Are a hunter's perceived phenotypic quality and preferred status influenced more by their ability to capture lots of prey or by their ability to capture very impressive prey species?**

**10)** Both the SOH and CS claim that there is a difference between the hunting strategies which are best for provisioning families, and the strategies which

are best for signaling good phenotype. **Is there a tradeoff between hunting for maximum food value vs. hunting for maximum signal value? Which strategy would lead to better mating opportunities or more social partners as judged by informant preference?**

Field Site

This chapter describes the materials, methods, and results of interviews conducted with Tsimané forager-horticulturalists of the Bolivian Amazon. The Tsimané were chosen as a second field site in order to avoid drawing broad conclusions based on studies of a single population or economic system. The Tsimané hunt many of the same species as the Aché making comparisons between the two populations easier, however, they are likely to differ in their foraging practices due to differences in their historical economic systems. Aché practices while on foraging trips are heavily influenced by their pre-contact life as nomadic hunter gatherers, while the Tsimané are forager-horticulturalists whose economic success and ability to provision their families would have historically been less directly tied to their hunting success.

There are approximately 16,000 Tsimané spread out among about 90 villages (typically containing from 50 to 500 individuals) in their lowland forests and savannas territories in the Beni department of northern Bolivia (Gurven et al., 2017). Because of a lack of access to communities via roads and navigable rivers, the Tsimané maintained traditional lifeways throughout the first half of the 20$^{th}$ century. Since then, levels of market integration have been increasing with the creation of logging roads and the expanded use of small outboard motors for boats (Gurven et al., 2017). Tsimané villages located close to major roads or towns have better access to education, health services, and

have more market integration and access to wage labor. More remote communities have little access to wage labor, and correspondingly low levels of market integration (Gurven, 2004a).

Tsimané families provide most of their calories through slash and burn horticulture. Important agricultural crops include rice, plantains, and sweet manioc which is fermented into chichi. Local cotton is cultivated, spun, and woven by hand. In addition to gardening, the Tsimané fish in rivers, streams, and lagoons; hunt neotropical animals of varying body sizes; and collect fruit, honey, nuts, and other forest products. Fishing is an important economic activity, which is done via bow and arrow, poison, or using purchased nets or hooks and fishing line (Gurven et al., 2017). Although cultivated crops (and to a lesser extent, domesticated animals) provide a steady source of calories, hunted game is still important as a source of protein and lipids, and hunting is common in many communities even today, making up 17% of all calories consumed (Martin et al., 2012). In the communities where hunting has been studied quantitatively, men averaged approximately 1-2 hunting trips per week (Gurven, Kaplan, & Gutierrez, 2006; Trumble et al., 2014). It is unclear whether a (historically) decreased dependence on hunted game as a major source of calories should predict an increase in "show-off" hunting among men (who would have less to fear from an unsuccessful hunt) or a decrease in "show-off" hunting (if men can gain greater mating benefits from maintaining a larger or better garden than they can get from showoff hunting).

Hunters employ shotguns, .22 rimfire rifles, and hunt with bows and arrows. Gurven and colleagues (Gurven et al., 2006) report that shotguns were used in 56% of hunts they observed, while bows were used on 47% of hunts (indicating overlap).

However, ammunition is costly and access to buy new cartridges or shells is limited, whereas bows and arrows can be made using local materials and are of high quality. Most of the adult men spoken to claimed to be proficient with a bow and arrow. The most important species by biomass harvested are (in descending order): collared peccary, Brazilian tapir, grey-brocket deer, howler monkey, agouti paca, white faced capuchin monkey, and coati. While cultivated food is typically shared within the household meat, fish, and chicha are shared more widely.

Data collection for the present study Tsimané was conducted in three communities ranging from remote to very accessible. Because the two main communities in which data was collected were small, community names are not listed to preserve the anonymity of informants. Much of the data collection (n=17) occurred in a community that is located along a logging road, and members of this community have access to a one room school, hand pumped well water, and can reach town by walking for a full day. A similarly sized group of interviewees (n=18) came from a more remote community that is located one day's walk down a foot path past the end of the logging road. This community had an open-air school, and no wells, and was located approximately two days journey from town. In order to incorporate enough young men for a sufficiently balanced sample, additional interviews (n=5) were conducted in a more acculturated community located on the main road a few kilometers from the town of San Borja. Data collection in an acculturated community was necessary to achieve target number of unmarried male informants because many young men in their teens and early 20s leave the remote villages to seek wage labor, and there were correspondingly few young unmarried men in the first two communities. The young men interviewed in the

acculturated community gave the impression of having less hunting knowledge and experience than the older men living in more rural locations.

## Field Methods

Structured interview data were collected from June to August of 2016 with Tsimané forager-horticulturalists (n=40 adults ages 14-65; 45% Female). A stratified sample of informants, balanced by marital status and sex, were selected based on availability and willingness to participate. Interviews were conducted with single informants outdoors near informant's homes, within the community. Interviews were conducted in the Tsimané language using a male translator who was bilingual in Spanish and Tsimané. Practice interviews were conducted with the translator before data was collected. Interviews consisted of 4 tasks (similar to tasks completed by Aché informants) that will be described in turn. Permission to access the site and collect data was granted by the Tsimané Gran Consejo and the leader of each community. All informants provided informed consent and all protocols were approved by the Arizona State University Internal Review Board. Special permission was granted to interview informants under the age of 18 due to a scarcity of unmarried women over the age of 18.

## Task 1: Prey Ranking

### Methods

The purpose of the prey ranking task was to ascertain prey characteristics that might potentially influence opinions about hunters that successfully acquire those prey types in tasks 2-4. Because the signal value of a killed prey species might be exceptionally high if the species is large (high food value), hard to kill (HtK), or hard to find (HtF), the species selected for comparison represent a range of weights and included

both animals common in the local diet, as well as animals that were suspected to be hard to kill, and animals that were suspected to be hard to find based on previous hunting studies and published information about animal densities (Figure 4.1). Rankings from these tasks were used alongside estimates of prey body weights as predictors in later analyses.

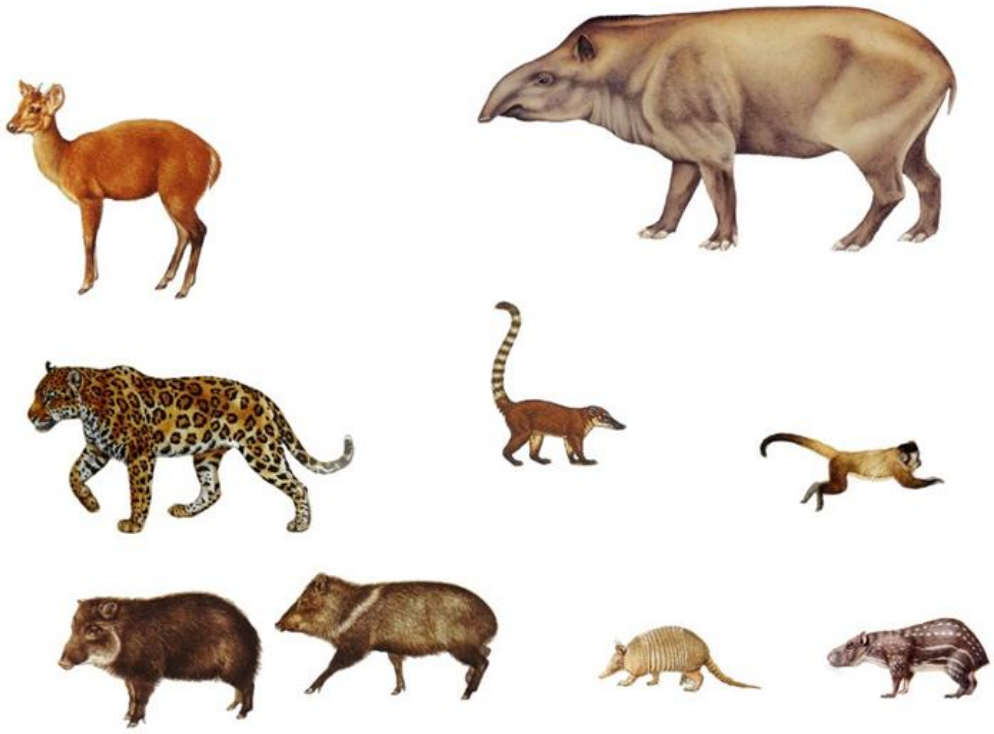


**Figure 4.1** Tsimané prey species. Depicted are the animal images used in Tsimané interviews. 9 animal species drawings were used for the Tsimané interviews.

Informants were asked to rank ten prey species by how hard they were to find (HtF), and how hard they were to kill (HtK) once found. HtK and HtF were elicited by first showing two randomly selected animals from the prey set and asking the informant, "which of these animals is most difficult to find (or kill once found)?" then placing the picture of the most difficult on one end of a line and the least difficult on the other end.

Additional images of animals were held up one at a time next to the already ranked species and the question was repeated until all prey had been placed in their rank order. Informant rankings (1-10) of each species were recorded such that higher rank numbers indicate that a species is harder to kill or find. All prey ranked as "tied" by informants were given the mean ranking of the set of prey species that were with tied each other (i.e. two prey tied for rank 2 and 3 were given a mean rank score of 2.5). Final prey rankings were taken as the mean of the individual informant ranks for each prey species.

Among the Tsimané, women and young male informants expressed a lack of knowledge and unwillingness to rank prey in terms of how difficult they were to find or kill, so informant rankings were based on subset of 16 interviews conducted with older adult men and a single interview conducted with an adult woman. For consistency, only the ranks assigned by the 16 men were used in subsequent analyses. It was discovered after data collection was complete that some Tsimané informants had inconsistently interpreted anaconda as a common small snake. Because there are large differences in size, difficulty to find, and difficulty to kill between anacondas and smaller snakes, anacondas were removed from the Tsimané data set. This left a final list of nine species whose ranks were adjusted after the removal of anaconda from the study set.

In addition to ranks HtF and HtK, Tsimané prey species were assigned mean body weight (Wt) based on data shared by members of the Tsimané Life History Project (Trumble, personal communication). These weights differ from those used for the Aché and are largely based on observed foraging data (apart from Jaguar and Tapir, which are rarely killed).

## Cultural Consensus Analysis

The results of the prey ranking task were also analyzed using cultural consensus analysis (CCA) techniques. CCA is a statistical method for examining the correlation between informant responses in order to determine if there is shared cultural information about a specific domain of knowledge, and to identify the culturally correct answers to questions about that domain. CCA is also useful for identifying cultural experts because it yields competency scores which are measures of the proportion of questions to which a specific informant gave the culturally correct answers. Negative competencies indicate that the views of an individual informant are systematically different from the culturally correct answers. Consensus is said to be achieved when the ratio of the first second eigenvalues from the analysis exceeds 3 and when there are no negative competencies. CCA was carried out independently on both sets of informant rankings from the prey ranking task. The prey ranking task data were analyzed using an interval model of CCA.

Task 1: Prey Ranking Results

Ranking Results

| Prey Ranking Results | | | | | |
|---|---|---|---|---|---|
| Species | Weight in Kg (Wt) | Hard to Find (HtF) | | Hard to Kill (HtK) | |
| | | Mean | SD | Mean | SD |
| Tapir | 141 | 7.56 | 1.79 | 6.97 | 2.45 |
| Brocket Deer | 28.5 | 5.19 | 1.83 | 5.44 | 1.66 |
| Jaguar | 79.5 | 6.37 | 3.2 | 6.62 | 3.06 |
| Collared Peccary | 18.8 | 4.44 | 2.1 | 5.15 | 2.55 |
| White Lipped Peccary | 30 | 3.87 | 2.19 | 5.09 | 1.52 |
| Paca | 6.5 | 5 | 2.22 | 4.21 | 2.53 |
| Capuchin | 3 | 2.69 | 2.18 | 2.94 | 2.46 |
| Coatimundi | 4.5 | 4.19 | 2.29 | 3.24 | 1.75 |
| Armadillo | 4.1 | 5.87 | 2.19 | 5.26 | 2.21 |

**Table 4.1** Tsimané Task 1 prey traits. Mean Wt and ranks HtF, HtK for Tsimané prey. Ranks here are inverted, so higher numbers in this table mean higher ranks.

Tsimané prey species included the following in rank order of Wt (Table 4.1): 1) tapir; 2) jaguar 3) white lipped peccary; 4) Brocket deer; 5) collared peccary; 6) paca; 7) coati; 8) capuchin monkey; 9) nine-banded armadillo.

Tsimané mean rank order for HtK was: 1) tapir; 2) jaguar; 3) brocket deer; 4) armadillo; 5) collared peccary; 6) white lipped peccary; 7) paca; 8) coatimundi; 9) capuchin. There is variation in the spacing between adjacently ranked prey, with slight clumping of ranks at both extremes of the spectrum (e.g. tapir with jaguar, and coatimundi with capuchin), clumping among middle ranked prey (brocket deer, armadillo, collared peccary, w-l peccary), and some spacing between the clumps. Because only a subset of adult male informants (n=16) and 1 adult female completed the

ranking tasks, it was not possible to compare informant responses based on sex or marital status of informants. The standard deviations around the mean rank score were lowest for White lipped peccary (SD = 1.52, medium difficulty to kill), brocket deer (SD = 1.66, medium difficulty to kill), and coatimundi (SD = 1.75, easy to kill) indicating a higher degree of agreement among informants about the ranking of these three species. The standard deviation around the mean rank score was highest for jaguar (SD = 3.06, very hard to kill), collared peccary (SD = 2.55, medium difficulty to kill), and Paca (SD = 2.53, easy to kill) indicating a lower level of agreement among informants about this species. Overall there was limited variation in the mean rankings assigned to prey by the Tsimané, which, combined with the high standard deviations of informant responses, suggests that informants don't have a strong and agreed upon cultural model for the ordering of prey by difficulty to kill.

Tsimané mean rank order for HtF was: 1) tapir; 2) jaguar; 3) armadillo; 4) deer; 5) paca; 6) collared peccary; 7) coatimundi; 8) white lipped peccary; 9) capuchin. As with HtK there is some clumping in the rankings of middle ranked prey, with the greater spacing at both the hardest to find (tapir) and easiest to find (capuchin) ends of the spectrum. The standard deviations around the mean rank score were lowest for tapir (SD = 1.79, hardest to find) and brocket deer (SD = 1.83, medium difficulty to find), indicating a higher degree of agreement among informants about the ranking of these two species. The standard deviation around the mean rank score was highest for jaguar (SD = 3.20, very hard to find), indicating a lower level of agreement among informants about this species.

Cultural Consensus Analysis Results

CCA results do not indicate good consensus among Tsimané informants about the rankings of HtF or HtK for specific prey (Table 4.2). A lack of consensus among informants about the ranks of each prey suggests that there is not a single shared model of which animals are the hardest to find or hardest to kill. If individual informants do not share beliefs about the HtF and HtK rankings of animals, it would make signaling to an audience by killing HtF and HtK prey animals difficult. Despite this lack of consensus on rank HtF and HtK, the mean of the HtF and HtK ranks assigned by each informant to each species are used as the rank for that species in all further analyses.

| **Tsimané Consensus Analysis Results** | | |
|---|---|---|
| | HtF<br>n = 16 | HtK<br>n = 16 |
| 1st Eigen Value | 5.35 | 7.19 |
| 2nd Eigen Value | 3.26 | 3.33 |
| Ratio (1st/2nd) | 1.64 | 2.15 |
| No. Negative Competencies | 2 | 3 |
| Mean Competency | 0.39 | 0.44 |
| SD of competency | 0.44 | 0.49 |

**Table 4.2** Cultural Consensus Analyses of HtF and HtK rankings. This table contains the results of CCA examining agreement among informants about the ranks HtF and HtK of prey. Consensus is said to be achieved when the ratio of the first and second Eigenvalue exceeds 3 and there are few or no negative competencies. Competency is a measure of the proportion of culturally correct answers that an informant gives. Negative competencies indicate that an informant is systematically incorrect in their responses, possibly because they don't share a cultural model with the group.

The correlation between the mean rank HtF and mean rank HtK for each species was calculated. The correlation between these means is quite high ($r = 0.85$) indicating collinearity of these variables for the Tsimané. Likewise, both variables were moderately correlated with Wt (correlation HtK with Wt $r = 0.83$, HtF with Wt $r = 0.77$). This complicates the use of mean rank HtF and mean rank HtK as independent predictors in a multiple regression model because the high correlation between these predictors limits

their independent predictive power. It appears that Tsimané generally view species as large, hard to find and hard to kill, or small and easy to find or kill.

Task 2: Paired Comparisons

Methods

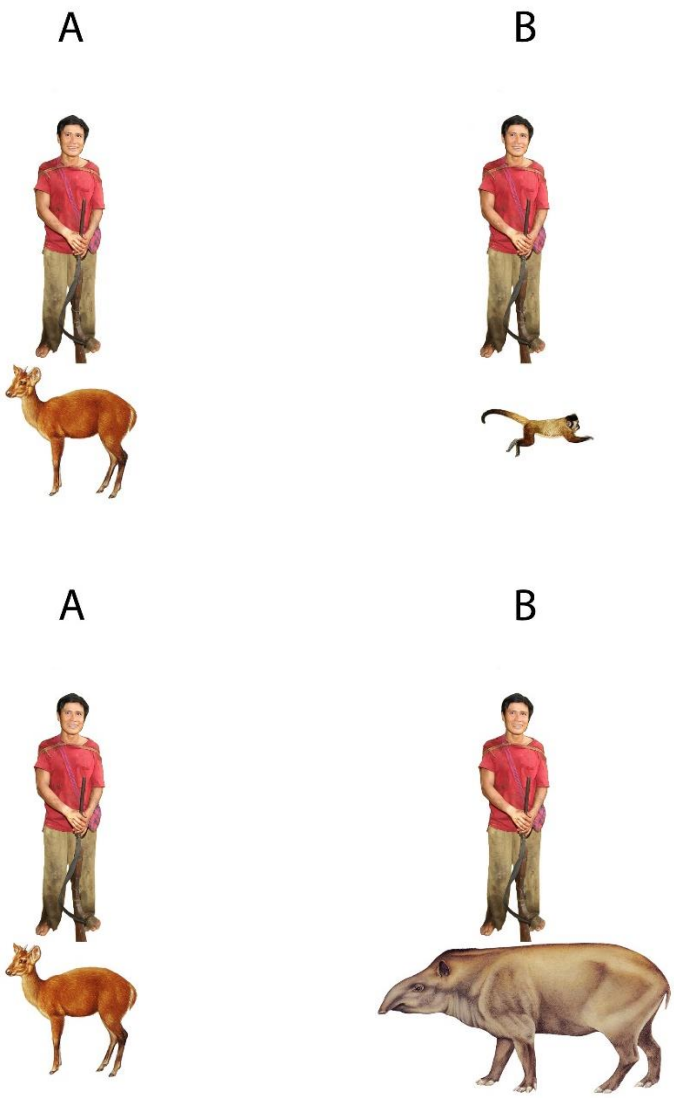



**Figure 4.2** Tsimané paired comparison images. Example of the types of comparisons presented in the paired comparison task.

In order to determine hunter characteristics ascribed to hunters who kill specific prey types, and the social preferences for such characteristics by potential mates or social

partners, informants were shown images depicting pairs of otherwise identical male hunters from the informant's ethnogroup as well as images depicting all 10 animal species (Figure 4.2).

Informants were told: "Here are pictures of two hunters. One day, one went to the forest and killed this animal, while the other went to forest and killed this animal." Informants were then asked six interview questions in random order comparing the depicted hunters on four aspects of their phenotype, as well as their preferred status as mates or allies (Table 4.3). The four phenotypic traits examined are: 1) Expected Future Provisioning (EFP); 2) physical Strength; 3) Fighting Ability; and 4) Disease Susceptibility.

Tsimané interview methods were modified slightly from those used with the Aché, since there were fewer Tsimané informants and fewer prey species to compare. Rather than the dyadic comparison method used with the Aché, Tsimané informants completed a ranking task. Cutout images of animals were presented representing the animals killed by the two hunters, and the vignette was described. Individual informants were asked a given interview question, comparing the hunters based on the two species killed, and then the species were placed in rank order based on the informant response. Next, a new species was selected and compared to a few of the previously ranked species, in order to place them in the proper rank order. This process was completed until all species had been compared and placed in rank order with respect to the four phenotypic traits and the two social preference questions.

All ranks were initially recorded using normal ranking conventions (such that low ranks were better) and were later inverted (new rank = 10 – old rank) such that higher rank numbers indicate that a hunter who killed that species was considered to have greater EFP, Strength, Fighting Ability, and lesser Disease Susceptibility. Likewise, high rank numbers indicate that a hunter was a more Preferred Mate or Cooperative Partner. One drawback of the method used for the Tsimané is that it assumes rankings are transitive (if A > B, and B > C, then A > C) despite the fact that not all possible dyadic comparisons were explored in the ranking process. However, the ranking process was much faster than the method used for the Aché and this helped prevent informant fatigue, which threatened the ability of the field team to recruit willing informants. It was eventually realized that some Tsimané informants were misinterpreting anaconda for a common snake. Due to the huge differences in weight, difficulty to find, and difficulty to kill between anacondas and common vipers, anacondas were removed from the rankings, and all ranks were adjusted accordingly.

| Preferred Status | Interview Question: |
|---|---|
| **Mate** | (Unmarried Women) Who would you prefer to marry?<br>(Married Women & Men) Who would you prefer to have your daughter marry?<br>(Unmarried Men) Which animal would you have preferred to kill? |
| **Cooperative Partner** | (Married Men) Who would you rather have as a neighbor and friend?<br>(Married Women) Who would you rather have as a neighbor or friend of your husband?<br>(Unmarried Men and Women) Who would you rather have as a neighbor or friend of your father? |
| **Phenotypic Quality** | **Interview Question:** |
| **EFP** | Who will bring more meat in the future? |
| **Physical Strength** | Who is stronger? |
| **Fighting Ability** | Who would win in a fight? |
| **Disease Susceptibility** | If a common sickness comes to the community, not a punishment from the forest spirits, who will get sick first? |

**Table 4.3** Tsimané Interview Schedule. Tsimané Paired Comparison Interview Questions in English.

To produce the hunters, old photos of Tsimané men were digitally altered using adobe photoshop CS3 to look like generic hunter drawings. The backgrounds of the photos were erased, leaving only the men holding a rifle. Contrast, saturation, and hue were altered, and the image was blurred slightly to reduce detail. The faces of the men were altered by changing the sizes, rotations, and relative positions of the features of the face, including the eyes, ears, mouths, and noses in order to remove any chance that the informants could recognize the actual hunters depicted on the cards, and attribute phenotypic qualities to those hunters based on real-world reputations.

Animals were depicted next to the hunter to represent their kills for the day. The same animal images were used as in the previous ranking tasks and attempts were made to scale them to approximately the correct size relative to the hunters. Although the animal images were not altered to appear dead (no blood or wounds were depicted), this did not seem to confuse informants.

Interview Questions

The first paired comparison task question is intended to assess how the animal that a hunter kills on one day impacts the perceptions of observers about how much meat that hunter will probably acquire on future foraging expeditions (EFP). To elicit this, informants were asked: "which of these hunters will bring back more meat in the future?" The responses make it possible to determine whether hunters would be able to adjust their hunting choices in order to intentionally signal their long-term provisioning ability to potential mates or allies. This is interpreted as a measure of perceived future provisioning ability, but is not necessarily a measure of hunting skill, since no attempt was made to differentiate whether informants believed that a specified hunter would bring back more meat due to superior abilities or superior work effort.

The second question of the paired comparison task is designed to assess how the prey species that a hunter kills impacts perceptions of that hunter's physical strength. Informants were asked: "which hunter is stronger?" and in Tsimané language the word "Ferki" (strong) implies both short burst strength as well as aerobic stamina.

The third question asks whether killing different prey provides information about Fighting Ability. Fighting between members of the local community is taboo in Tsimané societies, however, violent conflict does sometimes occur, and perceived or real fighting

ability may have an impact on lifetime fitness. Tsimané informants were asked: "which of these two men would win in a fight?" In response to the question, Tsimané informants typically insisted that there were no fights in the community, and only a subset of informants were willing to respond to this question directly. Attempts were made to modify how the question was asked in order to get more informants to respond, including suggesting that the two men were from rival communities, that the two men were fighting over a Tsimané woman, or that the two men had gotten drunk and got into fight. None of these attempts were successful and all responses analyzed here are from the 18 informants who did respond to the original question.

The fourth question about Disease Susceptibility was intended to assess whether successfully hunting certain prey might signal immunocompetence. Although none of the costly signaling human foraging literature has directly suggested that hunters are attempting to signal disease resistance through the animals that they hunt, studies in non-human species have often hypothesized that heritable immunocompetence is a trait that can be assessed via costly phenotypic signals (Folstad & Karter, 1992b; Hamilton & Zuk, 1982). Tsimané culture includes the belief that the animals of the forest have spirits which own them, and that these spirits sometimes become angry with men who kill too many animals or fail to bury the fetus of a pregnant animal that they kill, and punish those men with illness. Therefore, Tsimané informants had an automatic cultural bias to believe that the hunter who killed more animals, or the hunter who killed a bigger animal was more likely to get sick. To counter this problem, Tsimané informants were asked: "Imagine that a common illness comes to the community, one that is not a punishment from the forest spirits. Which of these two men will get sick first?" Instead of simply

asking which man would get sick, they were asked which man would get sick FIRST because informants insisted that if a common illness came, both men would end up getting sick eventually.

In addition to four questions about the phenotypic traits of hunters that killed specific prey, the paired comparison task also included questions designed to determine whether the animals that a hunter kills affects his desirability as a Mate (Table 4.3). The precise wording of these questions varied slightly depending on the sex and marital status of the informant. Unmarried female informants were asked: "which of these two hunters would you prefer to marry?" Married male and female informants were both asked, "which hunter would you prefer to marry your daughter?" Unmarried male informants were asked: "which animal would you prefer to kill?"

Finally, in order to determine whether the animals a hunter kills affects his desirability as a cooperative social partner, informants were asked to indicate which of the two hunters they would prefer to have as a social companion. In order to frame this question within ecologically relevant contexts for cooperation, Tsimané informants were asked: "which hunter would you prefer to have as your neighbor, and friend (OR "friend of your father" for unmarried informants, OR "friend of your husband" for married female informants)?"

Statistical Methods

Tsimané task 2 rank data were analyzed using a series of 6 ordinal logistic regressions models to determine the effects of standardized prey traits (Wt, HtK, HtF) on the ranks of prey as signals of hunters' phenotypes (EFP, Strength, Fighting Ability, Disease Susceptibility), and social preferences for hunters (Preferred Mate or Preferred

Cooperative Partner). Ordinal logistic regression is a form of logistic regression which is capable of handling categorical predictor variables which are both non-dichotomous and rank ordered. The estimates produced by this kind of regression are ordered log odds. In each model, the dependent variable was the ranking of a species as a signal of a hunter's phenotypic quality, or desirability as a Mate or Cooperative Partner. The phenotypic rankings used for the dependent variables were individual informant rankings rather than the mean of rankings across informants. Ordinal logistic regression was used because the dependent variables were rank ordered categorical variables. Dependent variables were not treated as continuous because no information was collected about the magnitude of difference between prey with adjacent rankings. All ties were rounded up to the nearest whole rank. The independent variables were the mean values of Wt, rank HtF, and rank HtK. To facilitate direct comparisons of effect sizes of the three independent variables (Wt, rank HtK, rank HtF) on the dependent variable for the model, all variables were standardized.

After examining the association between prey characteristics and hunter characteristics a set of ordinal generalized linear models were run in order to determine how hunter characteristics (measured as the hunter phenotypic rank for each prey species) related to social preferences for a mate or ally. For these analyses, the dependent variables were the mean ranks of each species as predictors of a being a Preferred Mate or a Preferred Cooperative Partner. The independent variables were the mean ranks of species as signals of EFP, Strength, Fighting Ability, and Disease Susceptibility. Each dependent variable was run as a separate model, with all four independent variables

included simultaneously as predictors. Independent and dependent variables were standardized to compare effect size.

Finally, it should be noted that sample size for some regression models was smaller than for other models because (22/38) Tsimané informants would not respond to questions about Disease Susceptibility, saying it was unrelated to hunting, and (21/38) did not respond to questions about Fighting Ability, saying that there are no fights in the community.

## Task 2: Results

### Ordinal Logistic Regression Model

In the ordinal logistic regression including all three predictors simultaneously, prey Wt was a significant predictor in all 6 models (Tables 4.4 and 4.5). Hunters who killed larger animals were perceived as having greater EFP, Strength, Fighting Ability, Disease Susceptibility, and as being more desirable mates and allies. HtK was an independently significant predictor of Fighting Ability, with hunters who killed hard to kill animals being perceived as having greater Fighting Ability even when prey body Wt effects were controlled. Interestingly, with the effects of prey Wt and difficulty to kill controlled, HtF was a significant negative predictor of both perceived physical Strength and of preferred status as a Cooperative Partner. This may indicate a slight disfavoring of men who harvest hard to find animals (when all else is equal) out of the prey species that were examined. This negative relationship between HtF and perceived hunter phenotype is consistent with findings from analysis of Aché paired comparison data.

| Task 2 Regressions: Hunter Phenotype Questions | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | EFP | | | Strength | | | Fighting Ability | | | Disease Susceptibility | | |
| predictor | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < |
| Wt (std) | 1.10 | 0.20 | 0.001 | 0.92 | 0.20 | 0.001 | 0.63 | 0.28 | 0.024 | 0.62 | 0.28 | 0.026 |
| HtF (std) | -0.27 | 0.23 | 0.246 | -0.54 | 0.25 | 0.028 | -0.45 | 0.34 | 0.188 | -0.37 | 0.34 | 0.270 |
| HtK (std) | 0.03 | 0.23 | 0.886 | 0.44 | 0.24 | 0.066 | 0.84 | 0.34 | 0.012 | 0.25 | 0.32 | 0.432 |

**Table 4.4** Tsimané Task 2 predicting hunter phenotypic rankings from prey traits. This table contains the estimates, standard errors, and p values for each of the independent variables (Wt, HtF, HtK) on each of the dependent variables (EFP, Strength, Fighting Ability, Disease Susceptibility) from the multiple ordinal logistic regressions. Independent variables were standardized. Dependent variables were the ranks assigned by individual informants to prey species.

| Task 2 Regressions: Preferred Status Questions | | | | | | |
|---|---|---|---|---|---|---|
| | Preferred Mate | | | Preferred Cooperative Partner | | |
| predictor | Beta | std. Error | p < | Beta | std. Error | p < |
| Wt (std) | 0.75 | 0.19 | 0.001 | 1.48 | 0.20 | 0.001 |
| HtF (std) | -0.13 | 0.22 | 0.570 | -0.73 | 0.23 | 0.002 |
| HtK (std) | -0.06 | 0.22 | 0.792 | -0.08 | 0.22 | 0.709 |

**Table 4.5** Tsimané Task 2 predicting preferred status rankings from prey traits. This table contains the estimates, standard errors, and p values for each of the independent variables (Wt, HtF, HtK) on each of the dependent variables (Preferred Mate, Preferred Cooperative Partner) from the multiple ordinal logistic regressions. Independent variables were standardized. Dependent variables were the ranks assigned by individual informants to prey species.

Agreement by Sex

When the same multiple regression models were run on male and female responses separately (APPENDIX A tables 5 – 8), some minor differences emerged. Hunters who killed larger animals were perceived by female informants as having significantly greater EFP and Strength, and as being more desirable Mates or Cooperative Partners. Neither HtF nor HtK were significant predictors of any of the dependent variables.

On the other hand, while male informants also rated hunters who killed larger animals as having significantly greater EFP, Strength, higher Disease Susceptibility, and as being significantly preferred as Mates and Cooperative Partners, male informants also showed some preferences for hunters who killed HtK prey and a negative rating of

hunters who harvested HtF prey. Specifically, hunters who killed hard to kill prey were perceived as significantly stronger, and better fighters, while hunters who killed hard to find animals were perceived as significantly weaker, less disease susceptible, and were less preferred as cooperative partners.

Predicting Social Preference by Perceived Hunter Phenotype

In a GLM of preference as a mate by hunter phenotype, EFP was the only significant predictor of being a Preferred Mate. Likewise, in a separate model, EFP was also the only significant predictor of preferred status as a Cooperative Partner (Table 4.6).

| **Social Preferences by Hunter Traits** | | | | | | |
|---|---|---|---|---|---|---|
| | Preferred Mate | | | Preferred Cooperative Partner | | |
| Predictor | Estimate | Std. Error | P < | Estimate | Std. Error | P < |
| Intercept | 2.19 | 0.65 | 0.001 | 2.39 | 0.64 | 0.001 |
| EFP | 0.35 | 0.13 | 0.008 | 0.53 | 0.13 | 0.001 |
| Strength | 0.22 | 0.13 | 0.093 | -0.06 | 0.13 | 0.614 |
| Fighting Ability | -0.02 | 0.12 | 0.843 | 0.09 | 0.12 | 0.430 |
| Disease Susceptibility | 0.03 | 0.11 | 0.801 | -0.03 | 0.11 | 0.763 |

**Table 4.6** Tsimané Task 2 predicting social preferences from hunter phenotypic rankings. This table reports the results of two GLM analyses examining the association between being preferred as a Mate or Cooperative Partner and having been ranked as having greater EFP, Strength, Fighting Ability, or Disease Susceptibility based on hunter-harvested prey species. Estimates and standard errors have been rounded to two decimal place, and P values have been rounded to three decimal places.

Cultural Consensus Analysis Results

Informant responses to were analyzed using cultural consensus analyses. Tsimané informants achieved consensus in their responses to the paired comparison task (table 4.7), indicating that they agree about which prey species harvested make a hunter more desirable as a mate or ally and about which prey species indicate that a hunter has a superior phenotype. Informant consensus on the paired comparison task supports the

possibility that hunters could influence their desirability or perceptions of their phenotype by targeting specific prey species, however, the lack of consensus on rank HtF and HtK indicate that the signal value of prey is not likely to be based on factors such as how hard an animal is to find or kill.

| **Tsimané Consensus Analysis Results: Paired Comparisons** | |
|---|---|
| | n = 38 |
| 1st Eigen Value | 20.699 |
| 2nd Eigen Value | 2.178 |
| Ratio (1st/2nd) | 9.505 |
| No. Negative Competencies | 0 |
| Mean Competency | 0.719 |
| SD of competency | 0.170 |

**Table 4.7** Cultural Consensus Analyses of Tsimané informant responses to Task 2. Results of CCA examining agreement among informants about which hunter should be preferred in the paired comparison task. Consensus is said to be achieved when the ratio of the first and second Eigenvalue exceeds 3 and there are few or no negative competencies. Competency is a measure of the proportion of culturally correct answers that an informant gives. Negative competencies indicate that an informant is systematically incorrect in their responses, possibly because they don't share a cultural model with the group.

Task 3: Multi-prey Comparisons Controlling for Weight

Methods

Informants were shown images of two hunters, one standing next to a single large species and the other standing next to an approximately equivalent weight of smaller animals of a single species (Figure 4.9). Informants were asked to imagine that they had just encountered two hunters standing next to all of the animals they killed in a week. They were then asked to compare hunters based on the standard four hunter phenotypic traits as well as preference for the hunter as a Mate or Cooperative Partner. The question's asked were identical to those asked in the paired comparison task. Finally,

they were also asked, “which of these men has killed more meat?”, making it possible to validate that they viewed the two sets of animals as having similar food value.

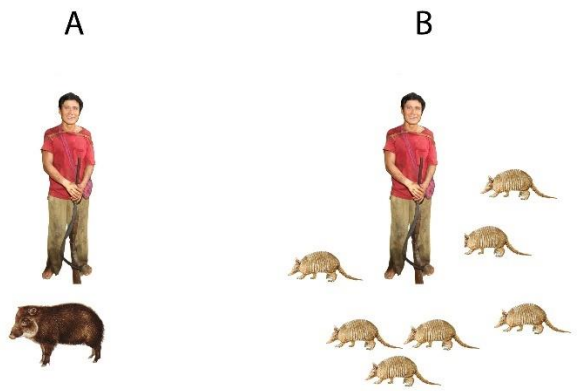



**Figure 4.9** Tsimané Task 3 multi-prey comparison. Example of the types of comparisons being made in the Tsimané multi-prey comparison task.

Unlike the paired comparison task, not every combination of prey species was tested. 24 Animal dyads were selected a priori by the researchers to represent a mix of Wt and HtK or HtF and to include both economically important and unimportant species. The 9 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, coati, paca). Dyads were compared across, but not within groups. Tapir was not compared to the animals in the smallest class because the huge size difference made it impractical to fit an equivalent weight of the smaller animals on a single interview card. Also, the 6 prey dyads involving anaconda were later removed from the final data set once it was realized that some informants were confusing anacondas with common snakes. The final comparison set comes from 18 pairs of well recognized prey species.

Body weight estimates are identical to those used elsewhere in this chapter and were based on published foraging data or Aché weight estimates when other data were not available. The species and number of prey in set A and B were identical to those used for the Aché multi-prey comparison task in the previous chapter, however, estimates of body weights differed between the two populations, and as a result the average difference in weight between hunter A and hunter B was lower for the Aché (mean = 3.07 kg, std. deviation = 3.97) than it was for the Tsimané (mean = 15.54 kg, std. deviation = 21.43). The imbalance in prey set weight for the Tsimané comparison were mainly due to three specific comparisons: 1 tapir vs 7 deer gave a weight difference of 58.5 kg; 1 tapir vs 10 collared peccaries represented a weight difference of 47 kg; and, 1 tapir vs 7 white lipped peccaries was estimated as a 69 kg weight difference.

Statistical Methods

Two methods were used to assess whether informants were perceiving both sets of meat as containing approximately the same total biomass. First, the mean and standard error of the proportion of informants selecting the single large animal as having more total meat was examined across all dyads. Second, a simple linear regression was done of the proportion of informants choosing the single large animal (as representing more meat) as a function of the calculated difference in weight between the single large and multiple small animals.

Multi-prey comparison data were then analyzed using a series of multinomial logistic regression models predicting the probability that hunter A was chosen as having a better phenotype or as a preferred Mate or Cooperative Partner based on differences

between the prey killed by hunter A and hunter B. Differences between species (animal killed by hunter A – animal killed by hunter B) on Wt, HtF, HtK, and differences between prey sets on total weight and number of prey killed were used as predictors in these models. All predictors were standardized by dividing the mean difference between traits by the standard deviation of differences between traits.

Since attempts were made to control for biomass of each set, the number of animals in set B should be proportional to the difference in Wt between animal A and a single animal from set B. If informant responses only influenced by total food provided then their responses should show equal preference for A and B. If the number of animals killed is the primary factor influencing informant responses, then then there should be a preference for set B, and if killing large, rare, or hard to kill species is the driver of informant responses then there should be a preference for set A.

Task 3: Results

Validating Controls for Weight

Among Tsimané informants, the mean and standard deviation of the proportion of informants choosing the single large animal as having greater total biomass across all 18 prey dyads was: $\mu = 0.16$, SEM = 0.006. These results indicate that informants perceive that the hunter who killed a single large animal (Hunter A) had killed more total biomass in only 16% of comparisons, while the hunter who killed many small animals (Hunter B) was chosen as having killed a greater total biomass in 84% of comparisons. No ties were recorded. A simple linear regression shows that the calculated difference in biomass has little relation to the perception that the large animal usually represents less meat (Figure

4.10). Relative to the prey weights used in the Aché analysis, the weight estimates for large game were slightly lower, and the weight estimates for small to mid-sized game were slightly higher, resulting in a few cases where the estimated weight of small game greatly exceeded (> 30 kg difference) the estimated weight of the single large animal.

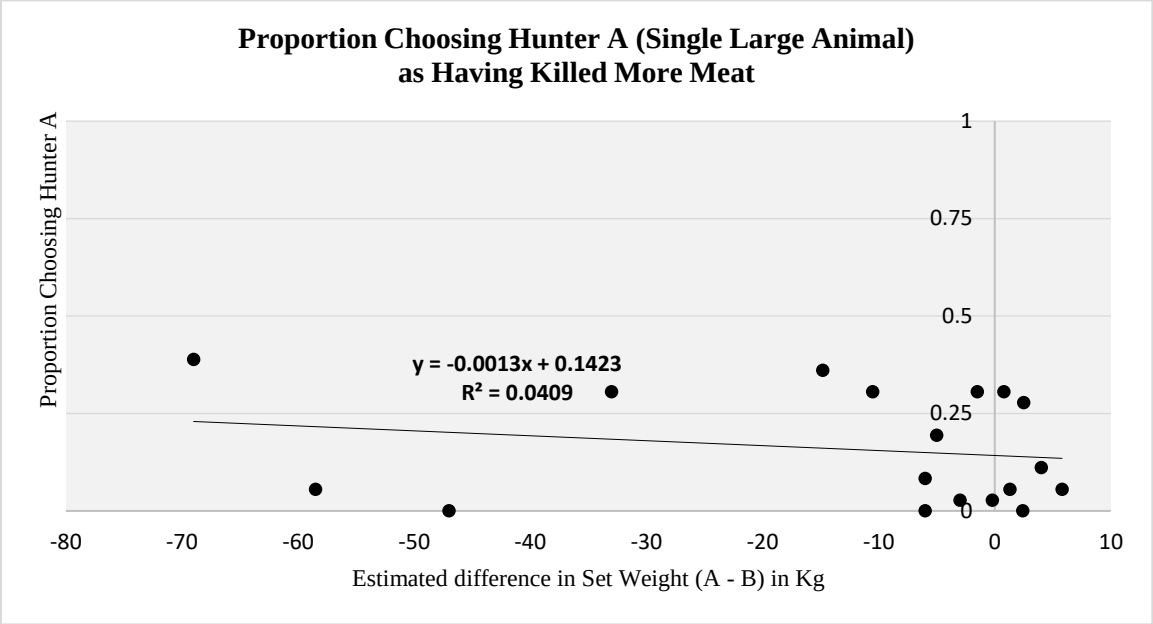



**Figure 4.10** Probability that hunter A is chosen as having killed more meat. Univariate regression showing the proportion of informants choosing hunter A (single large animal) as having killed more meat plotted against the calculated difference in weight (Kg) between the two sets (A – B) as determined from the data sources used in this study. Each dot represents a single prey dyad. In all cases informants were more likely to choose hunter B as having killed more meat.

Multinomial Logistic Regression Models

| Tsimané Multi-prey Comparison Multinomial Logistic Regression Results: Hunter Phenotype Questions | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | EFP | | | Strength | | | Fighting Ability | | | Disease Susceptibility | | |
| Predictor | Estimate | Std. Error | P < | Estimate | Std. Error | P < | Estimate | Std. Error | P < | Estimate | Std. Error | P < |
| Intercept | -1.38 | 0.10 | 0.001 | -1.21 | 0.09 | 0.001 | -0.52 | 0.13 | 0.001 | -0.63 | 0.14 | 0.001 |
| Diff. Wt (A - B) | -1.30 | 0.32 | 0.001 | -0.91 | 0.31 | 0.004 | 0.32 | 0.43 | 0.459 | -0.82 | 0.46 | 0.073 |
| Diff. Set Weight (A - B) | -0.63 | 0.25 | 0.013 | -0.39 | 0.25 | 0.117 | -0.01 | 0.36 | 0.984 | -0.22 | 0.37 | 0.557 |
| Diff. HtK Rank (A - B) | 0.58 | 0.11 | 0.001 | 0.44 | 0.11 | 0.001 | -0.16 | 0.15 | 0.298 | 0.36 | 0.16 | 0.022 |
| Diff. HtF Rank (A - B) | 0.92 | 0.23 | 0.001 | 0.68 | 0.22 | 0.002 | -0.32 | 0.29 | 0.270 | 0.86 | 0.32 | 0.008 |

**Table 4.8** Tsimané Task 3 predicting hunter phenotypic ratings from prey set traits. This table contains the results of two multinomial logistic regressions examining the effects standardized differences between prey set traits on the probability that a hunter is chosen as have greater phenotypic quality (EFP, Strength, Fighting Ability, Disease Susceptibility).

| Tsimané Multi-prey Comparison Multinomial Logistic Regression Results: Preferred Status Questions | | | | | | |
|---|---|---|---|---|---|---|
| | Mate | | | Cooperative Partner | | |
| Predictor | Estimate | Std. Error | P < | Estimate | Std. Error | P < |
| Intercept | -1.35 | 0.10 | 0.001 | -1.18 | 0.09 | 0.001 |
| Diff. Wt (A - B) | -1.29 | 0.33 | 0.001 | -0.97 | 0.31 | 0.002 |
| Diff. Set Weight (A - B) | -0.47 | 0.25 | 0.064 | -0.24 | 0.24 | 0.334 |
| Diff. HtK Rank (A - B) | 0.41 | 0.11 | 0.001 | 0.53 | 0.10 | 0.001 |
| Diff. HtF Rank (A - B) | 0.93 | 0.23 | 0.001 | 0.86 | 0.22 | 0.001 |

**Table 4.9** Tsimané Task 3 predicting preferred status from prey set traits. This table contains the results of two multinomial logistic regressions examining the effects standardized differences between prey set traits on the probability that a hunter is preferred as a Mate or Cooperative Partner.

EFP

Perception of hunter phenotype based on whether they killed a single large prey (hunter A) or many small animals (hunter B) was modelled (Table 4.8). The first multiple logistic regression model examined informant responses to the question of which hunter will have greater EFP. Across all prey dyads, hunters who killed a single large animal (hunter A) were perceived as having greater EFP only 22% of the time (mean proportion

choosing A = 0.22, S.E. = 0.015). Using all 4 predictors simultaneously, differences in HtF, HtK, prey body size, and total set biomass were all significant predictors of informant preference for hunter A. The likelihood that an informant preferred hunter A increased when the single large animal was relatively harder to find or harder to kill than the small animals, but informants were increasingly less likely to prefer hunter A as the difference in prey Wt or difference in total set biomass between the large and small animals increased.

It should be noted that difference in Wt (A – B) and difference in set weight (A – B) are strongly negatively correlated (r = -0.90, df = 17) which may account for the confusing results of the multivariate analyses. Informants were less likely to pick hunter A with increases in the relative size of the larger animal, a finding which only makes sense in light of the overall informant bias toward hunters who kill many small animals.

Informants were also less likely to pick hunter A when the set weight of the single large animal was greater relative to the set weight of the many small animals. This finding is somewhat counter intuitive. As with the Aché, the possibility of systematic bias in the direction of differences in set weight was examined. The mean difference in set weight for all 18 prey combinations in the multi-prey comparison task was -13.21 kg (s.d. = 22.81) indicating a bias toward hunter A (single large animal) having killed less meat on average than hunter B. This negative bias is partially due to 4 outlier cases (3 involving tapir and 1 involving jaguar) in which the set weight of the single large animal was substantially (> 30 kg) lower than the set weight of the many small animals. If informants are preferring the single large animal in those cases (where difference in set

weight is both large and negative), it may explain which difference in set weight (A – B) is negatively associated with informant preference for hunter A.

These findings are hard to reconcile because a negative association between difference in body Wt and informant preference for hunter A would suggest an informant preference for the hunter who kills many small animals, while a negative association between difference in set weight and informant preference for hunter A would suggest an informant preference for the hunter who kills a single large animal.

Strength

Next, informant preferences for hunter A as having greater Strength using were modelled using all four predictors (Table 4.8). Across all prey dyads, hunter A was perceived as having greater physical Strength 24% of the time (mean proportion choosing A = 0.24, S.E. = 0.016). Differences in prey Wt, HtF and HtK were all significant predictors of assessing that hunter A was physically stronger. The likelihood that an informant preferred hunter A increased when the single large animal was relatively harder to find or harder to kill than the small animals, but informants were increasingly less likely to prefer hunter A as the difference in body weight between the large and small animals increased. Difference in set weight was not a significant predictor in this model.

Fighting Ability

Next, informant preferences for hunter A as having greater Fighting Ability were modelled using all four predictors (Table 4.8). Across all prey dyads, hunter A was perceived as having greater Fighting Ability 37% of the time (mean preference for hunter

A = 0.37, S.E. = 0.030). None of the four predictors had a statistically significant impact on preference for hunter A.

### Disease Susceptibility

Finally, informant opinions about whether hunter A was more susceptible to disease were modelled using all four predictors (Table 4.8). Across all prey dyads, hunter A was perceived as being more susceptible to disease 35% of the time (mean preference for hunter A = 0.35, S.E. = 0.030). Only difference in HtF and HtK were statistically significant predictors of preference for hunter A. The likelihood that an informant preferred hunter A increased when the single large animal was relatively harder to find or harder to kill than the small animals.

### Preferred Mate

In addition to hunter phenotype, preferred status was also modeled using all four predictors (Table 4.9). It was asked whether a hunter who killed a single large animal was preferred as a Mate or Cooperative partner over the hunter who killed many small animals. Hunter A was preferred as a Mate in just 22% percent of cases (mean preference for hunter A = 0.22, S.E. = 0.015). Differences in HtF, HtK, and Wt were all statistically significant predictors of preference for hunter A as a mate. The likelihood that an informant preferred hunter A increased when the single large animal was relatively harder to find or harder to kill than the small animals, but informants were less likely to prefer hunter A as the difference in body weight between the large and small animals increased. Difference in set weight approached significance as a predictor in this model.

### Preferred Cooperative Partner

In looking at preferences for hunter A as a Cooperative Partner (Table 4.9), hunter A was preferred as a Cooperative partner in just 25% of cases (mean preference for hunter A = 0.25, S.E. = 0.016). Differences in HtF, HtK, and animal Wt were all statistically significant predictors of preference for hunter A as a Cooperative Partner. The likelihood that an informant preferred hunter A increased when the single large animal was relatively harder to find or harder to kill than the small animals, but informants were increasingly less likely to prefer hunter A as the difference in Wt between the large and small animals increased.

Overall

In most cases total difference in HtF, difference in HtK, and difference in body Wt between the large and small prey species were statistically significant predictors of preference for hunter A, however, the overall trend in the data was for informants to prefer the hunter who killed many small animals. On Fighting Ability and Disease Susceptibility, informant preferences for hunter A were close to 40% (37% and 35% respectively), while on EFP, Strength, and preferred status as a Mate or Cooperative Partner, stronger preferences for the hunter who killed many small animals were observed (percent choosing hunter A (single large animal) were: 22%, 24%, 22%, and 25% respectively).

Difference in set weight was a significant predictor of preference for hunter A on EFP and approached significance as a predictor on preferred status as a Mate. In both cases the results are counterintuitive, with informants being more likely to pick the hunter A when hunter A killed less meat. This unusual pattern could be a byproduct of a failure

to properly control differences in set weight (for a few outliers involving tapir and jaguar the difference in set weight (A – B) was large and negative) or it might be a fluke resulting from the high negative correlation between difference in Wt of prey and difference in set weight of prey.

Task 4: "Show-off" vs Provider Comparison

Methods

Informants completed an interview task in which they were asked to compare two hunters who follow either a "show-off" or provider strategy by killing different quantities and types of prey over a 15-week period. Two sets of 15 note cards representing 15 weeks of hunting returns were created. Informants were shown note cards one at a time in random order from each set, and told that each note card represented 1 week of hunting returns for hunter A or B. Informants were asked to compare hunter A and B three times, after seeing 5, 10, and 15 cards from each set (representing increments of 5 weeks). Female informants were asked to indicate which hunter was more desirable as a mate for themselves or for their daughters, while male informants were asked which set of animals they would prefer to kill.

The "show-off hunter" (hunter A) set of 15 cards contained 10 weeks where the hunter killed one large and HtF or HtK species (as indicators of high phenotypic quality and preferred status) and 5 weeks where the hunter killed nothing at all. The "provisioner hunter" (hunter B) set contained 15 weeks of successful harvest, with each week's harvest consisting of a variety of small and low ranked (HtF, or HtK) animals (see Figure 4.11 for samples of showoff and provider cards). In total, the showoff set depicted 3

brocket deer, 4 collared peccaries, and 3 white lipped peccaries, while the provisioner set depicted 15 coati, 30 capuchin, 15 armadillo, and 15 paca.

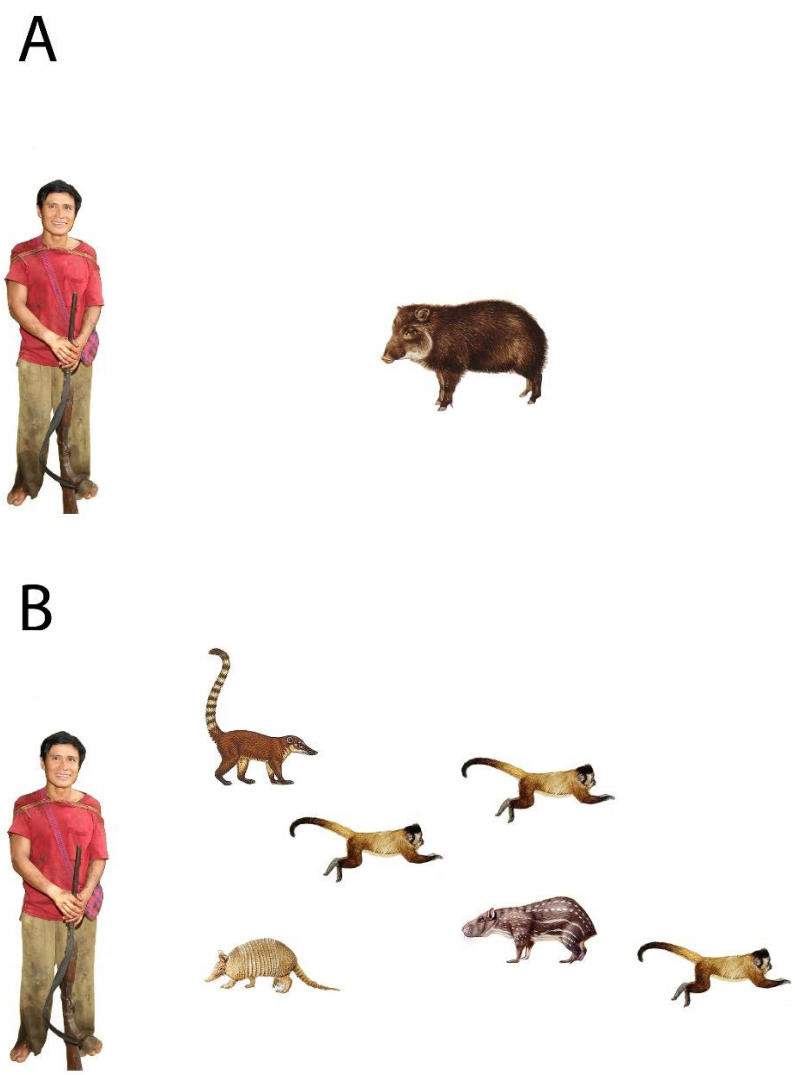



**Figure 4.11** Sample of Tsimané "show-off" and "provider" cards. The images above are examples of the types of images used in the Tsimané "show-off" vs "provider" comparison task. Hunter A is representative of the showoff set, and hunter B is representative of the provider set. Informants were shown 15 images of hunter A and hunter B depicting 15 weeks of hunting outcomes. Images varied in the number and species of animals depicted and the hunter A (showoff set) always contained 5 cards with no prey for that week.

The total mass of all animals in the "provisioning" set is 26.5% greater than that of the "show-off" set. This was meant to represent the hypothesis that informants would prefer "showoff hunters" even if their total food contribution over time were less than the

"provisioner hunters". Likewise, the prey species in the showoff set had higher individual ranks as signals of hunter phenotype and preferred status. For each species, individual rankings as a signal of hunter phenotype or preferred status were calculated as the mean of all informant rankings of that species for that question (Table 4.10).

| Prey Rankings for Hunter Phenotype and Preferred Status | | | | | | |
|---|---|---|---|---|---|---|
| Species | Mate | Ally | EFP | Strength | Fighting Ability | Disease Susceptibility |
| Coati | 4.18 | 4.39 | 4.07 | 3.72 | 3 | 3.94 |
| Capuchin | 3.38 | 4.11 | 3.07 | 3.4 | 2.62 | 3.83 |
| Armadillo | 3.97 | 2.36 | 3.17 | 3.37 | 3.65 | 3.56 |
| Paca | 4.87 | 4.42 | 4.6 | 4.16 | 4.18 | 3.94 |
| Brocket deer | 6.46 | 6.49 | 6.84 | 6.84 | 6.59 | 5.75 |
| Collared Peccary | 5.64 | 5.69 | 5.58 | 5.5 | 4.89 | 4.86 |
| White Lipped Peccary | 6.41 | 6.84 | 6.51 | 5.75 | 5.82 | 5.7 |

**Table 4.10** Ranks of prey as signals of hunter phenotype. A list of prey ranks for each species on 2 aspects of preferred status and 4 aspects of hunter phenotype.

To calculate the mean rankings for prey sets containing a variety of species, the individual rankings for each prey species were first multiplied the number of animals of that species in the set and these values were then summed across all species in the set and divided by the total number of animals in the set. The resulting mean ranks are thus weighted by the number of animals of a given species included in the set. Differences between card sets can be seen in Figure 4.12 and Table 4.11.

| Prey Set Characteristics | Showoff Set | Provisioning Set |
|---|---|---|
| # Prey in Set | 10.00 | 75.00 |
| Total Weight (Kg) of Set | 250.70 | 316.50 |
| Hard to Find | 4.06 | 3.53 |
| Hard to Kill | 4.83 | 3.24 |
| Mate Value | 6.12 | 3.96 |
| Cooperative Value | 6.28 | 3.88 |
| EFP | 6.24 | 3.60 |
| Strength | 5.98 | 3.61 |
| Fighting Ability | 5.68 | 3.21 |
| Disease Susceptibility | 5.38 | 3.82 |
| Informant Preference | 10.00 | 97.00 |

**Table 4.11** Characteristics of the "show-off" and "provider" prey sets (numerical). The animals in the showoff set are larger, more difficult to kill, harder to find, and were rated more highly as signals of EFP, Strength, Fighting Ability, and Disease Susceptibility than those in the provisioning set. Furthermore, hunters who killed the animals in the showoff set were more likely to be rated as desirable mates and Cooperative Partners. On the other hand, there is more total meat depicted and hunters bring back meat every week with the provisioning set (lower acquisition variance).

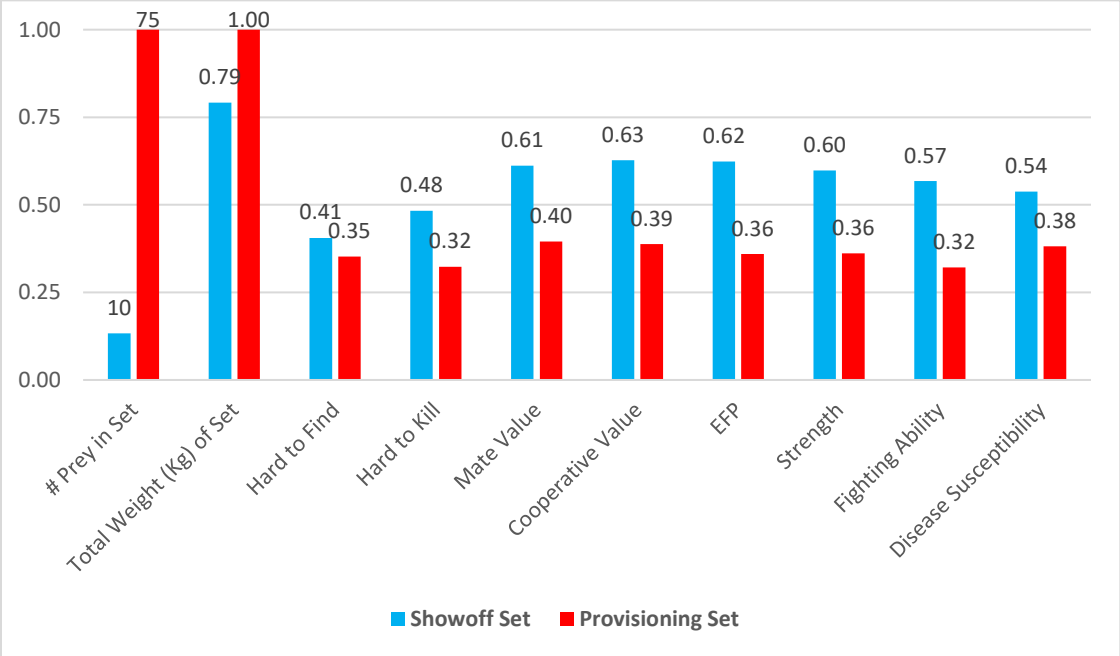



**Figure 4.12** Characteristics of the "show-off" and "provider" prey sets (graphical). This figure shows the differences in characteristics between the "show-off" and "provider" prey sets for the Tsimané Task 4. Number of prey in set and total weight of set are depicted. Mean ranks attributed to hunters who kill the prey types in each set (from the prey ranking task) have been converted into proportions, where 1 represents the maximum value possible for the set (the highest possible attribute ranks).

## Results

36 informants were given 3 opportunities (once after viewing the first 5 weeks of harvest, then again after viewing the second and third 5 weeks' harvest) to choose between a provisioning prey set and a signaling prey set. Of them, 80.5% (29/36 informants) of informants unanimously choose the provisioning set in all 3 responses, 11% choose the provisioning set 2 out of 3 times (5/36 informants), and 5.5% preferred the showoff set in all 3 responses (2/36 informants). One of the informants reported being undecided on their third choice after selected the provisioning set for their first two choices (they were counted among the 5 informants who choose the provisioning set twice). Hence, there is little support for the hypothesis that observers prefer hunters who bring in large and hard to kill prey (but with some failed hunts) over hunters who consistently bring in smaller, easier to find and kill prey.

### Task 1 – 4 Results Summary

Tsimané informants completed 4 tasks designed to test various aspects of the CSH and SOH. In task 1, informants ranked prey based on how hard they word to find (HtF) and kill (HtK). These ranks were later used as predictors in task 2 and 3. Only 16 adult men and 1 woman were willing to rank prey on these measures, with the majority of women and young men claiming not to know which animals were hardest to find and kill. Tsimané informants did not achieve consensus in their rankings of prey on HtF or HtK. In task 2, informants ranked prey as signals of four aspects of hunter phenotype and 2 aspects of preferred status. It was found that hunters who killed heavier animals were viewed as having greater EFP, Strength, Fighting Ability, Disease Susceptibility, and

were preferred as Mates and Cooperative partners. Hunters who killed hard to find animals were viewed as weaker and were less preferred as Cooperative partners. Hunters who killed hard to kill animals were viewed as having greater fighting ability. In task 3, informants compared hunters who killed a single large and impressive animal and hunters who killed several smaller animals of an approximately equivalent weight. Informants compared hunters on four aspects of hunter phenotype and two aspects of preferred status. Informants were more likely to prefer the hunter who killed several small animals on all measures. In task 4 female informants were asked to select which hunter would be a more desirable mate, while males were asked which set of prey they would rather kill themselves. They were asked to choose between a "show-off" hunter who killed large and impressive animals and a "provisioner" hunter who killed small game consistently and brought in more kilos of meat. Informants showed strong preferences for the provisioner hunter.

# CHAPTER 5: Discussion

In the first chapter of this dissertation three competing explanations for men's foraging goals were introduced. Literature and debates pertaining to the "show-off" hypothesis (SOH), and the costly signaling hypothesis (CSH) of human hunting as well as the family provisioning hypothesis (FPH) of human hunting were reviewed in the second chapter. In reviewing these debates, it became apparent that the process of hunting and sharing meat involves multiple behaviors and choices on the part of the hunter, each of which could potentially serve as a signal or cue of the hunter's traits.

The first opportunity to signal is through prey choice. Hunters can influence which animals they encounter through their choice of foraging habitat, and once the encounter has occurred, they can choose whether to pursue the animal or ignore it and continue searching (Hawkes et al., 1991). The second opportunity to signal is through foraging effort. A hunter must decide how long they will hunt and whether or not they will continue to hunt after making a kill (Hawkes & Bird, 2002). A third opportunity to signal is through meat sharing, in contexts where hunters exert some control over how meat is shared. A hunter might potentially signal generosity or cooperative intent by sharing hunted game widely with kin and non-kin alike (Bliege-Bird & Power, 2015; Gurven, Allen-Arave, et al., 2000).

Although each of these signaling contexts have been explored to some degree, many of the debates reviewed in the first and second chapter have centered around foraging effort and food sharing patterns as evidence for or against the CSH. Where prey choice has been examined, attention has been focused primarily on the body size of the prey or its post encounter return rate (the average Kcals/hr that a hunter gets from hunting

and killing a given prey type after factoring in failed pursuits), since those features directly impact how widely a prey species can be shared. In contrast, relatively little empirical research has examined the signal value of prey traits such as how difficult an animal is to find or kill.

The aims of this dissertation are to address the provisioning vs signaling debate and contribute to scientific evaluation of the "prey choice as costly signaling" hypothesis by: 1) mapping out the relationships between prey traits, prey choice, and audience perceptions of hunter phenotype; and 2) comparing the impacts of a show-off strategy vs a provisioning strategy on preferences for a hunter as a mate or social partner. To accomplish these goals, five specific research questions were proposed in the first chapter of this dissertation. These are:

1) **Are there clear examples of prey whose value as a signal of hunter-phenotype is associated with the costs of acquiring them (HtF, HtK), and not simply a function of how much food value they contain?**
2) **Is it true that killing different prey lead interview informants to infer variation in hunter phenotype on dimensions of a) Expected Future Provisioning; b) Hunter Strength; c) Fighting – the likelihood to win physical contests with other men; d) Health – hunter Disease Susceptibility?**
3) **Which aspect of perceived hunter phenotype have the greatest influence on whether that hunter will be preferred as a mate or ally?**

4) **Are a hunter's perceived phenotypic quality and preferred status influenced more by their ability to capture lots of prey or by their ability to capture very impressive species?**
5) **Is there a tradeoff between hunting for maximum food value vs. hunting for maximum preferred signal value? Which strategy would lead to better mating opportunities or more social partners as judged by informant preference?**

In the third and fourth chapters of this dissertation the methods and results of studies carried out with two different populations for the purpose of answering these questions are presented. The third chapter describes the methods and results of a study carried out with the Aché hunter gatherers of eastern Paraguay, while the fourth chapter describes the closely related methods and results from a study carried out with the Tsimané horticulturalists of low-land Bolivia. In this chapter, the results of interviews conducted with members of both groups are reviewed in light of the research questions above.

Discussion of Research Questions

The interview questions provided results that, for the most part, answer all the five research questions of the dissertation. Here each question is examined and discussed in light of the answers provided by the results that were presented in chapters 3 and 4.

**1)** Prey provide nutrient biomass to consumers, and hunters who bring in more total biomass may inadvertently "signal" their ability to provide food. But some prey might also be exceptionally hard to find or kill, indicating exceptional skill and

strength of hunters who kill them. **Are there clear examples of prey whose value as a signal of hunter-phenotype is associated with the costs of acquiring them (HtF, HtK), and not simply a function of how much food value they contain?** In other words, are there smaller but hard to find or kill prey that might signal to an audience greater hunter skill and strength, and are there larger prey that provide no real signal of hunter strength or skill because they are easy to find or kill? Or, do all same size prey species carry approximately the same signal value about hunter characteristics?

Results show that both Aché and Tsimané can rank prey species by differences in HtF and HtK (Table 3.1 and 4.1) although a large fraction of Tsimané informants could not complete this task. Cultural consensus was high among the Aché for rankings of both HtF and HtK, indicating a high degree of agreement about which prey were hard to find and hard to kill (Table 3.2). Unlike the Aché however, Tsimané informants failed to achieve consensus in their ranking of prey as HtF or HtK (Table 4.2). There was not agreement among Tsimané informants about which prey is hardest to find or kill, hence it should be difficult to signal hunting skill (and associated phenotypic traits) to a co-resident audience using those traits.

Using informant rakings, the pairwise correlations between each of the three predictors in our model (HtF, HtK, Wt) were calculated. Among the Aché, rank HtF and HtK are moderately strongly correlated with each other, Wt and HtK are also somewhat correlated, and Wt is weakly correlated with HtF rank. Among the Tsimané HtF and HtK are strongly correlated with each other, and both HtF and HtK are strongly correlated with estimated Wt. Hence, the informant views on properties of prey species suggest that

some properties are not independent, especially for Tsimané. This implies that there cannot be a tradeoff between signaling certain types of hunting skill and simply harvesting more food (a basic assumption of the showoff hypothesis).

Nevertheless, the correlations between prey traits are not perfect, especially among the Aché, and there are examples in each data set of prey species which are hard to find or kill but are also relatively small. For example, among the Aché, bush dogs, and tayra are considered about as hard to find and kill as are tapir, which contains 30 times as much meat biomass. And according to the Aché, tortoises are small and easy to kill, but are extremely hard to find. For the Tsimané, armadillos are considered almost as hard to find and kill as brocket deer that weigh 6 times as much, and white lipped peccaries are considered to be the second easiest prey to find despite being about as large and hard to kill as brocket deer.

In order to disentangle acquisition costs (HtF, HtK) from food value (Wt), all three prey traits were used in a series of multivariate analyses of informant choices in dyadic prey species comparisons (Aché) or prey ranking tasks (Tsimané). For the Aché, standardized differences in Wt, rank HtF, and rank HtK were each significant predictors of informant ratings of hunter EFP, Strength, Fighting Ability, and Disease Susceptibility even with the other two prey variables controlled (Table 3.4; Figures 3.3, 3.5, 3.7). Among the Tsimané however, only prey body weight (Wt) was a significant predictor for all four aspects of hunter phenotype (Table 4.4). With effects of body size controlled, HtF was a significant negative predictor of Strength, but not of other aspects of phenotype. Likewise, HtK was a significant positive predictor of perceived Fighting Ability (with Wt controlled), but not of any other aspect of hunter phenotype.

The results show that, for the Aché, the signal value of prey IS influenced by the costs of pursuing the species (HtF, HtK) even with total food value (Wt) controlled for statistically. However, for the Tsimané, the value of a prey species as a signal of EFP, Strength, Fighting Ability, and Disease Susceptibility is influenced primarily by its value as food (Wt) and not by the costs of pursuing it, with two exceptions. The costs of pursuing a species predicted its value as a negative signal of Strength (predicted by HtF) and positive indicator of Fighting Ability (predicted by HtK). Alternatively, it could be the case that hunting costs fail predict the signal value among the Tsimané because many informants had no opinion on which prey were hardest to find or kill and because the subset of informants who ranked prey on HtF and HtK failed to achieve consensus in their rankings.

We conclude that costly prey could, in theory, be targeted by Aché (but probably not Tsimané) hunters in order to signal superior phenotypic characteristics. However, body size is a strong independent predictor of the signal value of prey for both Aché and Tsimané. Furthermore, there is generally considerable overlap between the prey that provide the most meat and those that are considered more difficult to hunt. For this reason, hunters may face very little real tradeoff between providing food effectively and signaling phenotypic qualities that are desired.

**2)** Harvesting specific types of prey could potentially provide signals of hunter phenotype. **Is it true that killing different prey lead informants to infer variation in hunter phenotype on dimensions of a) Expected Future Provisioning; b) Hunter Strength; c) Fighting – the likelihood to win**

**physical contests with other men; d) Health – hunter, Disease Susceptibility?**

Hunting could potentially signal a wide range of information about a hunter. For this study, attention was given to four aspects of hunter phenotype which a hunter might by attempting to signal. If the purpose of hunting is to signal any or all of these characteristics then informants should rate hunter quality based on the animals they have killed, and informants should generally be in agreement about those ratings.

Aché informant comments during the interview period suggest that hunting may not signal Fighting Ability or Disease Susceptibility. Several informants expressed the opinion that "hunting returns don't tell you about who will get sick", and (6/52) refused to compare hunters on Disease Susceptibility. Likewise, some Aché informants claimed that "hunting ability isn't tied to fighting ability", and (4/52) refused to compare hunters on Fighting Ability. Nevertheless, most informants were willing to make a distinction between the two hunters on these traits and Aché informants did not indicate reservations about judging a hunter's strength or provisioning ability based on the animals they killed.

Data analyses show that Aché informants believe that larger and harder to kill prey signal positive phenotypic traits (Table 3.4; Figures 3.3, 3.5, 3.7). On the other hand, harvesting hard to find prey species signals negative phenotypic characteristics. Most importantly, cultural consensus analyses show that Aché informants were generally in good agreement about which animal species a hunter should kill in order to be perceived as having a better phenotype (Table 3.8). Furthermore, there was high agreement across the sexes about which prey types signaled better phenotypic characteristics (Appendix A Tables 1-4).

Tsimané informants were willing to rank animals as signals of EFP and Strength but were generally unwilling (25/40) to rank prey as signals of Fighting Ability. In addition, most informants (26/40) were unwilling to rank prey as signals of Disease Susceptibility, stating that both good and bad hunters get sick and that it is unrelated to hunting. The few informants that did answer, typically ranked hunters who killed larger game as being more susceptible to illness. This is likely related to a Tsimané cultural belief that forest animals have spirits who own them, and these spirits punish hunters who kill too many animals, very large animals, or animals that look special, or who fail to bury the fetus of any pregnant animal that is killed.

Tsimané informants believed that prey body weight signaled better EFP, Strength, and (for those that would answer this question) Fighting Ability but also greater Disease Susceptibility (Table 4.4). They also indicated that hard to kill animals signaled better Strength and Fighting Ability, but that hard to find animals signal lower hunter Strength. Cultural consensus analyses did show that Tsimané informants were generally in agreement about the characteristics of prey as signals of some hunter phenotypes (Table 4.7). Likewise, male and female informants were generally in agreement (with only minor differences) about which prey signaled better phenotypic traits (Appendix A Tables 5 - 8).

These results suggest that prey characteristics do have the potential to signal phenotypic qualities among the Aché but not among the Tsimané. Specifically, informants from both populations were willing to make judgements about the EFP and Strength of a hunter based on the animals they killed, and their judgements were largely consistent within each population. Results also indicate that most Aché informants

believe prey characteristics are associated with hunter Fighting Ability and Disease Susceptibility. Hence, Aché hunters could advertise their Fighting Ability and Disease Susceptibility through the prey they kill. Unlike the Aché however, the majority of Tsimané informants were unwilling to draw any association between prey characteristics and Fighting Ability or Disease Susceptibility. This suggests that hunting different prey species is probably not a good strategy for advertising Fighting Ability or Disease Susceptibility among the Tsimané.

**3)** Some hunting strategies and prey sets may be better than others for signaling specific aspects of hunter phenotype. **Which aspect of perceived hunter phenotype have the greatest influence on whether that hunter will be preferred as a mate or ally?**

Hunting returns can signal several aspects of phenotypic quality among the Aché and Tsimané, however, these signals might not all result in social preferences for a hunter. If purpose of hunting is to attract mates or allies, then hunters should prioritize signaling aspects of their phenotype which result in them being preferred in those realms.

Among the Aché, informant preference for a hunter as a mate was positively associated with the assessment that the preferred hunter was also characterized by greater EFP or greater Strength. Aché social preferences were not influenced by the belief that a hunter as possessed greater Fighting Ability or greater Disease Susceptibility (Table 3.7). Informant preferences for a hunter as an ally/companion were also significantly positively associated with their choice of that hunter as having greater EFP or Strength, but not Fighting Ability or Disease Susceptibility.

Among the Tsimané, results from task 2 suggest that EFP was the only phenotype associated with preference as a Mate or a Cooperative Partner (Table 4.6). Although informant ratings of Strength failed to predict social preferences, the fact that informants were willing to rate hunters on Strength suggests that they do consider hunting returns to be a valid source of information about that aspect of phenotype. Since EFP is the only significant predictor of being a preferred as a Mate or Cooperative Partner for the Tsimané, and since body size was the only prey trait which predicted the value of a prey species as a signal of EFP, these results suggest that Tsimané hunters who kill larger prey than others on any given day will simply be preferred because they have provided more food on that day.

**4)** There could be a divergence between hunting strategies that provide high food biomass and hunting strategies that signal positive hunter phenotypes. **Are a hunter's perceived phenotypic quality and preferred status influenced more by their ability to capture lots of prey or by their ability to capture very impressive prey species?**

The findings presented up to this point have been based single day, forced choice scenarios in which each hunter of the comparison dyad kills only a single animal. In those scenarios, larger animals have more signal value (but also represent more food acquired) in both populations, while harder to kill animals have more values as signals among the Aché. In practice, however, a hunter's reputation will be based on the outcomes of many hunts, and a mix of species harvested. This means that informants aren't limited to judging hunters based solely on which species of animals they kill, but also on the

frequency of their success and the number of animals they bring home. For this reason, it is important to determine whether a hunter that is very successful at killing smaller animals will be judged more favorably than one who kills only a few larger and more impressive animals. The results of Task 3, in which hunters who kill a single large animal (Hunter A) are compared to hunters who killed an approximately equivalent weight of smaller and less impressive animals of a single species (Hunter B), addresses this question.

In this task, Aché informants overwhelmingly assigned the more positive phenotype to the hunter who killed many small animals (hunter B) rather than the hunter who killed a single large animal (hunter A) for greater EFP and Strength (Appendix A Figures 1 – 6). They were also more likely to prefer hunter B as better in Fighting Ability or Disease Susceptibility, although this preference was weaker than for EFP and Strength. Finally, hunter B was strongly preferred as a Mate and as Cooperative Partner (Chapter 3 results). In short, the Aché prefer hunters who kill small game over those who kill large game, even when the total amount of meat acquired is approximately the same.

Tsimané informants uniformly preferred the hunter who killed many small animals (hunter B) as having greater EFP, Strength, Fighting Ability, and Disease Susceptibility, and these preferences were significantly different from the null hypothesis of choosing hunter A 50% of the time (Appendix A Figures 7 - 12). Likewise, hunter B was strongly preferred as a Mate and as a Cooperative Partner. In short, Tsimané informants show an even stronger preference than Aché informants for hunters who kill small rather than large game, although both study populations show a slight bias in assigning greater Disease Susceptibility to the small game hunter.

Despite the general preference for the small game hunter (B) in task 3, our data also allowed us to determine whether larger differences between the two prey sets in overall weight, or mean HtK and HtF measures for the prey illustrated, might affect the strength of the preference for Hunter B. For the Aché, differences (Hunter A value – Hunter B value) in HtF and total prey set weight were significantly negatively associated with informant choice of hunter A on EFP, Strength, and preferred status as a Mate and Cooperative Partner (Difference in HtF approached significance as a predicter of preferred status as a Cooperative Partner), but not with their choice of hunter A on Fighting Ability or Disease Susceptibility (Table 3.9 and 3.10). Differences in HtK and in single prey body Wt were not significant predictors of Aché choice of hunter A.

Surprisingly, Aché informants were less likely to prefer hunter A in cases where the figures showed that hunter A had killed slightly more meat overall. This finding might be explained by the fact that the single large animal tended to be have a greater estimated set weight on average, while informants tended to prefer the hunter who killed many small animals.

For the Tsimané, larger differences between set A and set B in HtK and HtF were associated with an increased preference for hunter A as having greater EFP, Strength, Disease Susceptibility, and as being a more desirable Mate and Cooperative Partner (Table 4.8, 4.9, Appendix A Figures 7 - 12). However, greater differences in body weight for the two sets were negatively associated with a perception of hunter A as having greater EFP, Strength, and desirability as a Mate or Cooperative Partner. Finally, differences in set weight were negatively associated with perceptions of hunter A as having greater EFP.

While the phenotypic predictors in the models above were significantly associated with slight changes in informant preferences, none of those differences change the overall trend. Informants in both study populations showed uniform preferences for the hunter (B) who killed many small animals over the hunter (A) who killed a single large animal regardless of slight changes in the properties of the large and small prey sets.

Results suggest that a hunter's reputation is determined not only by the impressiveness of the animals they kill, but, more importantly, by the frequency of their successes. After controlling for the food value of prey being hunted, informants assigned positive phenotypes to hunters who kill a large number of less impressive animals rather than hunters who killed a single large and difficult animal. One possible explanation for this result is that hunters who killed many small animals may be viewed as reliably skilled hunters, while those who killed a single large animal may be viewed as lucky. Another possibility is that informants viewed capturing many small animals as requiring more total effort than capturing a single large one, making the former a better indicator of phenotype quality if hunter effort is important.

**5)** Both the SOH and CS claim that there is a difference between the hunting strategies which are best for provisioning families, and the strategies which are best for signaling good phenotype. **Is there a tradeoff between hunting for maximum food value vs. hunting for maximum signal value? Which strategy would lead to better mating opportunities or more social partners as judged by informant preference?**

The findings presented did not support the conclusion that there is a tradeoff between hunting for maximum food acquired versus hunting for maximum signal value in either dyadic comparisons (Task 2) or comparisons controlling for weight (Task 3). In single-day, single-prey capture scenarios examining prey dyads (task 2), the body size of a hunted animal was a good predictor of its value as a both a signal and a food source for both populations, although Aché informants also considered prey differences in HtK when making their phenotypic judgements of hunters. Task 3 showed that when the value of food value of hunted game was controlled, hunting a greater number of less impressive animals was considered a better signal of hunter phenotype than hunting a single large and HtK/HtF animal. This implies that hunters might achieve the goal of advertising their phenotypic quality either by targeting large and hard to kill animals or by successfully targeting small game, as long as they adopt the strategy that results in greater total biomass being harvested.

These findings could be criticized on the grounds that Task 2 and Task 3 look at only very short-term choices and comparisons. What happens when hunters consistently use different strategies and prey choice patterns over long periods of time? To address this potential criticism, Task 4 was designed to more closely approximate the natural patterns of hunting success and failure that would occur over a 15-week period of foraging. When Aché men were asked to choose which suite of prey they would rather kill over a 15 week period (and women were asked to choose which hunter they would prefer to marry), 94% of informants were unanimous in their preference for a "provider" strategy that consistently harvests small game and results in about 1/3 more meat being obtained, rather than a "show-off" strategy in which hunters killed large game but also

failed to kill anything in some weeks, and brought home less total meat over the 15 week period. When Tsimané informants were presented with the same choice, 80.5% of them unanimously preferred the "provider" hunter over the "show-off" hunter. These data, combined with the findings from task 2 and 3, clearly indicate that hunters who acquired more meat (or more total animals holding the food value constant) were consistently rated as having superior phenotypes and were preferred as Mates and Cooperative Partners.

## Implications of These Findings for the CSH

According to the CSH, a behavior can serve as a costly signal when several conditions are met. 1. Individuals produce a signal of varying strength which is broadcast and received by an audience. 2. The strength of the signal is determined by the costs to produce it, or by the potential costs of over-signaling. 3. The costs are honestly linked to the phenotypic quality being signaled such that higher quality individuals pay a lower marginal cost or receive a higher marginal benefit from signaling at a given level. 4. The audience responds to the strength of the signal in a way that benefits the fitness of the signaler.

The evidence presented here suggests that Aché hunting meets several of these conditions. Hunting is a costly activity, and the outcomes of hunting are frequently observed by an audience. Harder to kill prey species are considered to be better signals, suggesting that the strength of the signal is determined at least in part by the costs of producing it. The ability to kill harder to kill prey is very likely to be honestly linked to the skill and strength of the hunter, and some of the skills associated with hunting may also be associated with Fighting Ability. Killing harder to kill prey results in positive

audience assessment of EFP, Strength, and Fighting Ability, and an increased likelihood that the hunter producing the signal will be favored as a Mate or Cooperative Partner. However, the fact that Aché hunters can gain an even greater signaling benefit from killing many small animals suggests that foraging effort and consistent provisioning are more important ways to advertise quality and attract mates and cooperative partners among the Aché than prioritizing the pursuit of hard to kill prey species.

Unlike the Aché, however, little evidence is found supporting the notion that hunting can function as a costly signal among the Tsimané. While hunting is observed by an audience, and hunting outcomes do predict audience assessment of a hunter's phenotype, the strength of the signal is mainly a function of the food value of the prey being killed, and not of how hard an animal is to find or kill. Furthermore, only informant ratings of a hunter's expected future provisioning (EFP) predict their preferences for that hunter as a Mate and Cooperative Partner. Since the ability to successfully hunt and kill a greater total biomass is a direct signal of provisioning ability, it doesn't make sense to hypothesize that hunting evolved as a costly signal among the Tsimané.

Implications of these findings for the SOH

The original show-off hypothesis proposed that hunters target prey species which are suboptimal for provisioning because doing so resulted in greater levels of positive social attention for the signaler. However, this argument is built on the premises that hunters prefer to target large game, that targeting large game is suboptimal for provisioning, and that the audience prefers hunters who target large game, even if it results in less successful foraging overall. This is contradicted by the research presented above which suggests that audiences are primarily attentive to the total biomass

harvested, rather than to the unique difficulties of acquiring a large and hard to kill prey item. Men who completed our interview tasks did not show a preference for harvesting large game when doing so came at the expense of overall foraging success. Since foraging success was the primary driver of audience perceptions of a hunter's phenotype, there is little conflict between the goal of showing off, and the goal of provisioning mates, offspring, kin, and allies.

## Conclusions

The purpose of this dissertation is to advance the debates about the role of costly signaling in human foraging by: 1) assessing the relationships between prey traits, prey choice, audience perceptions of hunter phenotype, and social preferences for those phenotypes; and 2) comparing the impacts of a consistent show-off strategy vs provisioning strategy on phenotypic attribution and preferences for a hunter as a mate or social partner.

In order to map relationships between prey traits, prey choice, and audience perceptions of hunter phenotype, informants were asked about the phenotypic quality and desirability of hunters who had killed various combinations of prey. Using these methods, it was possible to differentiate between the impacts of difficulty of acquisition vs. food value on the signal value of prey species harvested. Four aspects of hunter phenotype which might plausibly be signaled via hunting were tested.

Aché informants easily ranked hunters on all four aspects of phenotype based on the animals they killed. While a few Aché specifically rejected the idea that hunting returns are informative about Fighting Ability or Disease Susceptibility, the majority

were willing to rank hunters on both of those aspects of phenotype and achieved consensus in their rankings across all four aspects of phenotype. It was discovered that the signal value of a species was predicted by both the costs of pursuing it (HtF and HtK) and its value as food (Wt). Hunting large and hard to kill animals generally had a positive impact on perceptions of phenotype, while hunting hard to find animals was negatively associated with good phenotypes. Although informants were willing to judge prey as signals of all four aspects of phenotype, not every aspect of phenotype predicted being a preferred Mate or Cooperative Partner. Only EFP and Strength predicted being preferred Mate, and a preferred Cooperative Partner.

These findings suggest that many of the necessary features are present for hunting to serve as a costly signal among the Aché, but that only signals of EFP, Strength, and Fighting Ability were likely to be associated with positive fitness consequences.

Most Tsimané informants were willing to rank prey species as signals of EFP and Strength, but a large fraction of informants were unwilling to rank prey as signals of Fighting Ability or Disease Susceptibility, suggesting that hunting choices are not functioning to signal either of those aspects of phenotype. Tsimané adults who were willing to rank prey, however, did achieve consensus in their rankings. Unlike the Aché, the difficulty of finding and killing a species was not a good predictor of signal value among the Tsimané, with only two exceptions. Pursuing hard to find species led hunters to be viewed as weaker, while harvesting hard to kill species led hunters to be viewed as better fighters. Nevertheless, EFP was the only aspect of hunter phenotype which predicted being preferred as a Mate or Cooperative Partner.

These findings suggest that Tsimané hunting may lack the necessary features to function as costly signaling. Among the Tsimané, harvesting more meat in dyadic prey choice tasks was the best strategy for advertising EFP, which in turn was the best predictor of being a preferred Mate or Cooperative Partner. However, because the subset of Tsimané informants who ranked prey on HtF and HtK were unable to achieve consensus, it is also possible that some other measure of prey characteristics would predict signal value better.

Once Aché and Tsimané informants were presented with a multi-day hunting scenario in which hunters killed either a single large animal or an equivalent weight of smaller animals, their perceptions of the signal value of harvesting different prey species changed. While larger prey were better signals than smaller animals in a one versus one comparison, multi-day and multi-prey comparisons showed that informants expressed more positive phenotypic assessment of hunters who killed many smaller animals than hunters who killed few large ones (when the food value of each prey set was approximately controlled). When choosing potential mates and allies, informants also preferred hunters who killed many small animals rather than a few large ones.

The experiments presented are not perfect tests of the CSH of human hunting or of the SOH, however they do provide some insights. The data and analyses presented imply that if a hunter wishes to advertise good phenotype and attract mates and allies, he should focus on maximizing foraging return rates and overall hunting success rather than prioritizing the harvest of difficult to hunt game species. The data suggest that there is actually very little conflict between "showing-off" and provisioning in the populations analyzed. Furthermore, these findings suggest that hunting is more likely to be used to

advertise a hunter's strength and provisioning ability than their Fighting Ability or Disease Susceptibility. Finally, the results suggest that overall foraging effort and consistent hunting success over time are treated as a more important source of information about a hunter's phenotype than is the occasional harvest of the most impressive animals in the environment.

# BIBLIOGRAPHY


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*(5), 305–318. https://doi.org/10.1016/j.evolhumbehav.2008.03.002

Altman, J. (1987). *Hunter-gatherers today: An aboriginal economy of North Australia*. Canberra: Australian Institute of Aboriginal Studies.

Altman, J., & Peterson, N. (1988). Rights to game and rights to cash among contemporary Australian hunter gatherers. In *Hunters and Gatherers: History, Evolution and Social Change* (1st ed., Vol. 1, pp. 75–94). Oxford: berg.

Alvard, M. S., & Gillespie, A. (2004, December 30). GOOD LAMALERA WHALE HUNTERS ACCRUE REPRODUCTIVE BENEFITS [Book-part]. https://doi.org/10.1016/S0190-1281(04)23009-8

Aspelin, P. L. (1979). Food Distribution and Social Bonding among the Mamaindê of Mato Grosso, Brazil. *Journal of Anthropological Research*, *35*(3), 309–327. https://doi.org/10.1086/jar.35.3.3629905

Barbosa, A., & Møller, A. P. (1999). Sexual selection and tail streamers in the barn swallow: Appropriate tests of the function of size-dimorphic long tails. *Behavioral Ecology*, *10*(1), 112–114. https://doi.org/10.1093/beheco/10.1.112

Beisiegel, B. de M., & Zuercher, G. L. (2005). Speothos venaticus. *Mammalian Species*, *2005*(783), 1–6. https://doi.org/10.1644/783.1

Bergstrom, C. T., & Lachmann, M. (1997). Signalling among relatives. I. Is costly signalling too costly? *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *352*(1353), 609–617. https://doi.org/10.1098/rstb.1997.0041

Bergstrom, C. T., & Lachmann, M. (2001). Alarm calls as costly signals of antipredator vigilance: The watchful babbler game. *Animal Behaviour*, *61*(3), 535–543. https://doi.org/10.1006/anbe.2000.1636

Bergstrom, C. T., Számadó, S., & Lachmann, M. (2002). Separating equilibria in continuous signalling games. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1427), 1595–1606. https://doi.org/10.1098/rstb.2002.1068

Bertoni, M. (1941). *Los Guayakis*. Revista de la Socieded Scientifica De Paraguay.

Bird, D. W., Codding, B. F., Bliege Bird, R., Zeanah, D. W., & Taylor, C. J. (2013). Megafauna in a continent of small game: Archaeological implications of Martu

Camel hunting in Australia's Western Desert. *Quaternary International*, *297*, 155–166. https://doi.org/10.1016/j.quaint.2013.01.011

Bliege Bird, R., Codding, B. F., & Bird, D. W. (2009). What Explains Differences in Men's and Women's Production? *Human Nature*, *20*(2), 105–129. https://doi.org/10.1007/s12110-009-9061-9

Bliege Bird, R., & Power, E. A. (2015). Prosocial signaling and cooperation among Martu hunters. *Evolution and Human Behavior*, *36*(5), 389–397. https://doi.org/10.1016/j.evolhumbehav.2015.02.003

Bliege Bird, R., Smith, E., & Bird, D. W. (2001). The hunting handicap: Costly signaling in human foraging strategies. *Behavioral Ecology and Sociobiology*, *50*(1), 9–19. https://doi.org/10.1007/s002650100338

Bliege-Bird, R., & Bird, D. W. (1997). Delayed Reciprocity and Tolerated Theft: The Behavioral Ecology of Food-Sharing Strategies. *Current Anthropology*, *38*(1), 49–78. https://doi.org/10.1086/204581

Bliege Bird, R., & Bird, D. W. (2008). Why Women Hunt: Risk and Contemporary Foraging in a Western Desert Aboriginal Community. *Current Anthropology*, *49*(4), 655–693. https://doi.org/10.1086/587700

Blurton Jones, N. G. (1984). A selfish origin for human food sharing: Tolerated theft. *Ethology and Sociobiology*, *5*(1), 1–3. https://doi.org/10.1016/0162-3095(84)90030-X

Boone, J. L. (1998). The evolution of magnanimity. *Human Nature*, *9*(1), 1–21. https://doi.org/10.1007/s12110-998-1009-y

Boyd, R., & Richerson, P. J. (1989). The evolution of indirect reciprocity. *Social Networks*, *11*(3), 213–236. https://doi.org/10.1016/0378-8733(89)90003-8

Boyd, R., & Richerson, P. J. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology*, *13*(3), 171–195. https://doi.org/10.1016/0162-3095(92)90032-Y

Brown, J. K. (1970). A Note on the Division of Labor by Sex1. *American Anthropologist*, *72*(5), 1073–1078. https://doi.org/10.1525/aa.1970.72.5.02a00070

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*(1717), 2502–2509. https://doi.org/10.1098/rspb.2010.2403

Cotton, S., Fowler, K., & Pomiankowski, A. (2004). Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap

hypothesis? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1541), 771–783. https://doi.org/10.1098/rspb.2004.2688

Dawkins, M. S., & Guilford, T. (1991). The corruption of honest signalling. *Animal Behaviour*, *41*(5), 865–873. https://doi.org/10.1016/S0003-3472(05)80353-7

Dwyer, P. D., & Minnegal, M. (1993). Are kubo hunters 'show offs'? *Ethology and Sociobiology*, *14*(1), 53–70. https://doi.org/10.1016/0162-3095(93)90018-D

Dyble, M., Gardner, A., Vinicius, L., & Migliano, A. B. (2018). Inclusive fitness for in-laws. *Biology Letters*, *14*(10), 20180515. https://doi.org/10.1098/rsbl.2018.0515

Endler, J. A. (1980). NATURAL SELECTION ON COLOR PATTERNS IN POECILIA RETICULATA. *Evolution*, *34*(1), 76–91. https://doi.org/10.1111/j.1558-5646.1980.tb04790.x

Engelmann, D., & Fischbacher, U. (2003). *Indirect Reciprocity and Strategic Reputation Building in an Experimental Helping Game*.

Fincher, C. L., & Thornhill, R. (2008). A parasite-driven wedge: Infectious diseases may explain language and other biodiversity. *Oikos*, *117*(9), 1289–1297. https://doi.org/10.1111/j.0030-1299.2008.16684.x

Fisher, R. A. (1930). *The genetical theory of natural selection*. Clarendon Press.

FitzGibbon, C. D., & Fanshawe, J. H. (1988). Stotting in Thomson's gazelles: An honest signal of condition. *Behavioral Ecology and Sociobiology*, *23*(2), 69–74. https://doi.org/10.1007/BF00299889

Folstad, I., & Karter, A. J. (1992a). Parasites, Bright Males, and the Immunocompetence Handicap. *The American Naturalist*, *139*(3), 603–622. https://doi.org/10.1086/285346

Folstad, I., & Karter, A. J. (1992b). Parasites, Bright Males, and the Immunocompetence Handicap. *The American Naturalist*, *139*(3), 603–622. https://doi.org/10.1086/285346

Getty, T. (1998). Handicap signalling: When fecundity and viability do not add up. *Animal Behaviour*, *56*(1), 127–130. https://doi.org/10.1006/anbe.1998.0744

Getty, T. (2002). Signaling Health versus Parasites. *The American Naturalist*, *159*(4), 363–371. https://doi.org/10.1086/338992

Getty, T. (2006). Sexually selected signals are not similar to sports handicaps. *Trends in Ecology & Evolution*, *21*(2), 83–88. https://doi.org/10.1016/j.tree.2005.10.016

Godfray, H. C. J. (1991). Signalling of need by offspring to their parents. *Nature*, *352*(6333), 328–330. https://doi.org/10.1038/352328a0

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*(4), 517–546. https://doi.org/10.1016/S0022-5193(05)80088-8

Gurven, M. (2004a). Economic Games Among the Amazonian Tsimane: Exploring the Roles of Market Access, Costs of Giving, and Cooperation on Pro-Social Game Behavior. *Experimental Economics*, *7*(1), 5–24. https://doi.org/10.1023/A:1026256404208

Gurven, M. (2004b). Reciprocal altruism and food sharing decisions among Hiwi and Ache hunter–gatherers. *Behavioral Ecology and Sociobiology*, *56*(4), 366–380. https://doi.org/10.1007/s00265-004-0793-6

Gurven, M. (2004c). To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences*, *27*(4), 543–559. https://doi.org/10.1017/S0140525X04000123

Gurven, M., Allen-Arave, W., Hill, K., & Hurtado, A. M. (2001). Reservation food sharing among the Ache of Paraguay. *Human Nature*, *12*(4), 273–297. https://doi.org/10.1007/s12110-001-1000-3

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*(4), 263–282. https://doi.org/10.1016/S1090-5138(00)00032-5

Gurven, M., & Hill, K. (2009). Why Do Men Hunt? A Reevaluation of "Man the Hunter" and the Sexual Division of Labor. *Current Anthropology*, *50*(1), 51–74. https://doi.org/10.1086/595620

Gurven, M., Hill, K., & Kaplan, H. (2002). From Forest to Reservation: Transitions in Food-Sharing Behavior among the Ache of Paraguay. *Journal of Anthropological Research*, *58*(1), 93–120. https://doi.org/10.1086/jar.58.1.3631070

Gurven, M., Hill, K., Kaplan, H., Hurtado, A., & Lyles, R. (2000). Food Transfers Among Hiwi Foragers of Venezuela: Tests of Reciprocity. *Human Ecology*, *28*(2), 171–218. https://doi.org/10.1023/A:1007067919982

Gurven, M., Kaplan, H., & Gutierrez, M. (2006). How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *Journal of Human Evolution*, *51*(5), 454–470. https://doi.org/10.1016/j.jhevol.2006.05.003

Gurven, M., & Rueden, C. von. (2006). Hunting, social status and biological fitness. *Social Biology*, *53*(1–2), 81–99. https://doi.org/10.1080/19485565.2006.9989118

Gurven, M., Stieglitz, J., Trumble, B., Blackwell, A. D., Beheim, B., Davis, H., … Kaplan, H. (2017). The Tsimane Health and Life History Project: Integrating anthropology and biomedicine. *Evolutionary Anthropology: Issues, News, and Reviews*, *26*(2), 54–73. https://doi.org/10.1002/evan.21515

Gurven, M., & Walker, R. (2006). Energetic demand of multiple dependents and the evolution of slow human growth. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1588), 835–841. https://doi.org/10.1098/rspb.2005.3380

Hames, R. (2017, September 8). Reciprocal Altruism in Yanomamö Food Exchange. https://doi.org/10.4324/9781351329200-23

Hames, R., & McCabe, C. (2007). Meal sharing among the Ye'kwana. *Human Nature*, *18*(1), 1–21. https://doi.org/10.1007/BF02820843

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, *7*(1), 17–52. https://doi.org/10.1016/0022-5193(64)90039-6

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, *218*(4570), 384–387. https://doi.org/10.1126/science.7123238

Hart, J. A. (1978). From subsistence to market: A case study of the mbuti net hunters. *Human Ecology*, *6*(3), 325–353. https://doi.org/10.1007/BF00889029

Hawkes, K., O´Connell, J. F., Blurton Jones, N. G., Oftedal, O. T., Blumenschine, R. J., Widdowson, E. M., … Bone, Q. (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 of London. Series B: Biological Sciences*, *334*(1270), 243–251. https://doi.org/10.1098/rstb.1991.0113

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (2001a). Hadza meat sharing. *Evolution and Human Behavior*, *22*(2), 113–142. https://doi.org/10.1016/S1090-5138(00)00066-0

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (2001b). Hunting and Nuclear Families: Some Lessons from the Hadza about Men's Work. *Current Anthropology*, *42*(5), 681–709. https://doi.org/10.1086/322559

Hawkes, Kristen. (1991). Showing off: Tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology*, *12*(1), 29–54. https://doi.org/10.1016/0162-3095(91)90011-E

Hawkes, Kristen, & Bird, R. B. (2002). Showing off, handicap signaling, and the evolution of men's work. *Evolutionary Anthropology: Issues, News, and Reviews*, *11*(2), 58–67. https://doi.org/10.1002/evan.20005

Hawkes, Kristen, O'Connell, J. F., & Blurton Jones, N. G. (2014). More Lessons from the Hadza about Men's Work. *Human Nature*, *25*(4), 596–619. https://doi.org/10.1007/s12110-014-9212-5

Hawkes, Kristen, O'Connell, J. F., & Coxworth, J. E. (2010). Family Provisioning Is Not the Only Reason Men Hunt: A Comment on Gurven and Hill. *Current Anthropology*, *51*(2), 259–264. https://doi.org/10.1086/651074

Henrich, J., & Boyd, R. (2001). Why People Punish Defectors: Weak Conformist Transmission can Stabilize Costly Enforcement of Norms in Cooperative Dilemmas. *Journal of Theoretical Biology*, *208*(1), 79–89. https://doi.org/10.1006/jtbi.2000.2202

Henrich, N., & Henrich, J. P. (2007). *Why Humans Cooperate: A Cultural and Evolutionary Explanation*. Oxford University Press.

Hill, K, & Kaplan, H. (1989). Population description and dry season subsistence patterns among the newly contacted Yora (Yaminahua) of Manu National Park, Peru. *National Geographic Research*, *3*, 317–324.

Hill, K, & Padwe, J. (2000). Sustainability of Aché hunting in the Mbaracayu reserve, Paraguay. *Hunting for Sustainability in Tropical Forests*, 79–105.

Hill Kim, & Hurtado A. Magdalena. (2009). Cooperative breeding in South American hunter–gatherers. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1674), 3863–3870. https://doi.org/10.1098/rspb.2009.1061

Hill, Kim, Kaplan, H., & Hawkes, K. (1993). On Why Male Foragers Hunt and Share Food. *Current Anthropology*, *34*(5), 701–710. https://doi.org/10.1086/204213

Hooper, P. (2011). The structure of energy production and redistribution among Tsimane' forager-horticulturalists. *Anthropology ETDs*. Retrieved from https://digitalrepository.unm.edu/anth_etds/33

Hurd, P. L. (1995). Communication in discrete action-response games. *Journal of Theoretical Biology*, *174*(2), 217–222. https://doi.org/10.1006/jtbi.1995.0093

Hurd, P. L. (1997). Is Signalling of Fighting Ability Costlier for Weaker Individuals? *Journal of Theoretical Biology*, *184*(1), 83–88. https://doi.org/10.1006/jtbi.1996.0246

Hurd, P. L., & Enquist, M. (2005). A strategic taxonomy of biological communication. *Animal Behaviour*, *70*(5), 1155–1170. https://doi.org/10.1016/j.anbehav.2005.02.014

Hurtado, A. M., & Hill, K. (1996). *Ache Life History: The Ecology and Demography of a Foraging People*. Hawthorne, NY: Aldine dee Gruyter.

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

Isaac, G. (1978). The Food-sharing Behavior of Protohuman Hominids. *Scientific American*, *238*(4), 90–109. Retrieved from JSTOR.

Jaeggi, A. V., & Gurven, M. (2013). Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: A phylogenetic meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1768), 20131615. https://doi.org/10.1098/rspb.2013.1615

Janssen, M. A., & Hill, K. (2014). Benefits of Grouping and Cooperative Hunting Among Ache Hunter–Gatherers: Insights from an Agent-Based Foraging Model. *Human Ecology*, *42*(6), 823–835. https://doi.org/10.1007/s10745-014-9693-1

Johnstone, Rufus. A. (1997). The Evolution of Animal Signals. In *Behavioral Ecology: An Evolutionary Approach* (pp. 155–178).

Jones, N. B. (2016). *Demography and Evolutionary Ecology of Hadza Hunter-Gatherers*. Cambridge University Press.

Kane, P., & Zollman, K. J. S. (2015). An Evolutionary Comparison of the Handicap Principle and Hybrid Equilibrium Theories of Signaling. *PLOS ONE*, *10*(9), e0137271. https://doi.org/10.1371/journal.pone.0137271

Kaplan, H., & Hill, K. (1985). Hunting Ability and Reproductive Success Among Male Ache Foragers: Preliminary Results. *Current Anthropology*, *26*(1), 131–133. https://doi.org/10.1086/203235

Kaplan, H., Hill, K., Hawkes, K., & Hurtado, A. (1984). Food Sharing Among Ache Hunter-Gatherers of Eastern Paraguay. *Current Anthropology*, *25*(1), 113–115. https://doi.org/10.1086/203089

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology: Issues, News, and Reviews*, *9*(4), 156–185. https://doi.org/10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7

Kelly, R. L. (2013). *The Lifeways of Hunter-Gatherers: The Foraging Spectrum*. Cambridge University Press.

Kokko, H. (1998). Good genes, old age and life-history trade-offs. *Evolutionary Ecology*, *12*(6), 739–750. https://doi.org/10.1023/A:1006541701002

Koster, J. (2011). Interhousehold Meat Sharing among Mayangna and Miskito Horticulturalists in Nicaragua. *Human Nature*, *22*(4), 394–415. https://doi.org/10.1007/s12110-011-9126-4

Lachmann, M., & Bergstrom, C. T. (1998). Signalling among Relatives: II. Beyond the Tower of Babel. *Theoretical Population Biology*, *54*(2), 146–160. https://doi.org/10.1006/tpbi.1997.1372

Lachmann, M., Számadó, S., & Bergstrom, C. T. (2001). Cost and conflict in animal signals and human language. *Proceedings of the National Academy of Sciences*, *98*(23), 13189–13194. https://doi.org/10.1073/pnas.231216498

Lancaster, J. B. (1978). Carrying and Sharing in Human-Evolution. *Human Nature*, *1*(2), 82–89.

Lee, R. (1979). *The !Kung San: Men, women and work in a foraging society*. Cambridge: The Cambridge University Press.

Lozano, G. A. (1994). Carotenoids, Parasites, and Sexual Selection. *Oikos*, *70*(2), 309–311. https://doi.org/10.2307/3545643

Lyles, B., Hill, K., & Hurtado, A. M. (1990). *Preleminary Quantitative Analyses of Food Sharing Patterns Among the Hiwi of Venezuela*. Department of Anthropology, University of Michigan.

Marlowe, F. (1999). Showoffs or Providers? The Parenting Effort of Hadza Men. *Evolution and Human Behavior*, *20*(6), 391–404. https://doi.org/10.1016/S1090-5138(99)00021-5

Marlowe, F. W. (2003). A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior*, *24*(3), 217–229. https://doi.org/10.1016/S1090-5138(03)00014-X

Marlowe, F. W. (2007). Hunting and Gathering: The Human Sexual Division of Foraging Labor. *Cross-Cultural Research*, *41*(2), 170–195. https://doi.org/10.1177/1069397106297529

Martin, M. A., Lassek, W. D., Gaulin, S. J. C., Evans, R. W., Woo, J. G., Geraghty, S. R., … Gurven, M. D. (2012). Fatty acid composition in the mature milk of Bolivian forager-horticulturalists: Controlled comparisons with a US sample. *Maternal & Child Nutrition*, *8*(3), 404–418. https://doi.org/10.1111/j.1740-8709.2012.00412.x

McGraw, K. J., & Hill, G. E. (2000). Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1452), 1525–1531. https://doi.org/10.1098/rspb.2000.1174

Møller, A. P., Barbosa, A., Cuervo, J. J., Lope, F. de, Merino, S., & Saino, N. (1998). Sexual selection and tail streamers in the barn swallow. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1394), 409–414. https://doi.org/10.1098/rspb.1998.0309

Nolin, D. A. (2010). Food-Sharing Networks in Lamalera, Indonesia. *Human Nature*, *21*(3), 243–268. https://doi.org/10.1007/s12110-010-9091-3

Nur, N., & Hasson, O. (1984). Phenotypic plasticity and the handicap principle. *Journal of Theoretical Biology*, *110*(2), 275–297. https://doi.org/10.1016/S0022-5193(84)80059-4

Panchanathan, K., & Boyd, R. (2003). A tale of two defectors: The importance of standing for evolution of indirect reciprocity. *Journal of Theoretical Biology*, *224*(1), 115–126. https://doi.org/10.1016/S0022-5193(03)00154-1

Patton, J. Q. (2005). Meat sharing for coalitional support. *Evolution and Human Behavior*, *26*(2), 137–157. https://doi.org/10.1016/j.evolhumbehav.2004.08.008

Peterson, J. T. (1981). Game, farming, and interethnic relations in Northeastern Luzon, Philippines. *Human Ecology*, *9*(1), 1–22. https://doi.org/10.1007/BF00887853

Peterson, N. (1993). Demand Sharing: Reciprocity and the Pressure for Generosity among Foragers. *American Anthropologist*, *95*(4), 860–874. https://doi.org/10.1525/aa.1993.95.4.02a00050

Pomiankowski, A., & Iwasa, Y. (1998). Runaway ornament diversity caused by Fisherian sexual selection. *Proceedings of the National Academy of Sciences*, *95*(9), 5106–5111. https://doi.org/10.1073/pnas.95.9.5106

Rivas, J. A. (2001). *The life history of the green anaconda (Eunectes murinus), with emphasis on its reproductive biology.* 1.

Roberts, M. L., Buchanan, K. L., & Evans, M. R. (2004). Testing the immunocompetence handicap hypothesis: A review of the evidence. *Animal Behaviour*, *68*(2), 227–239. https://doi.org/10.1016/j.anbehav.2004.05.001

Schaller, G. B., & Vasconcelos, J. M. C. (1978). Jaguar Predation on Capybara. *Z. Säugetierk*, (43), 296–301.

Sear, R., & Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior*, *29*(1), 1–18. https://doi.org/10.1016/j.evolhumbehav.2007.10.001

Searcy, W. A., & Nowicki, S. (2005). *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press.

Seymour, K. L. (1989). Panthera onca. *Mammalian Species*, (340), 1–9. https://doi.org/10.2307/3504096

Smith, E. A. (1988). Risk and Uncertainty in the "Original Affluent Society": Evolutionary Ecology of Resource-Sharing and Land Tenure. *Hunters and Gatherers*, *1*, 222–251.

Smith, E. A. (2004). Why do good hunters have higher reproductive success? *Human Nature*, *15*(4), 343–364. https://doi.org/10.1007/s12110-004-1013-9

Smith, E. A., Bird, R. B., & Bird, D. W. (2003). The benefits of costly signaling: Meriam turtle hunters. *Behavioral Ecology*, *14*(1), 116–126. https://doi.org/10.1093/beheco/14.1.116

Smith, E. A., & Bird, R. L. B. (2000). Turtle hunting and tombstone opening: Public generosity as costly signaling. *Evolution and Human Behavior*, *21*(4), 245–261. https://doi.org/10.1016/S1090-5138(00)00031-3

Smith, J. M., & Harper, D. (2003). *Animal Signals*. OUP Oxford.

Smith, J. Maynard. (1994). Must reliable signals always be costly? *Animal Behaviour*, *47*(5), 1115–1120. https://doi.org/10.1006/anbe.1994.1149

Smith, John M. (1991). Honest signalling: The Philip Sidney game. *Animal Behaviour*, *42*(6), 1034–1035. https://doi.org/10.1016/S0003-3472(05)80161-7

Sosis, R. (2000). Costly signaling and torch fishing on Ifaluk atoll. *Evolution and Human Behavior*, *21*(4), 223–244. https://doi.org/10.1016/S1090-5138(00)00030-1

Sosis, R. (2002). Patch Choice Decisions among Ifaluk Fishers. *American Anthropologist*, *104*(2), 583–598. https://doi.org/10.1525/aa.2002.104.2.583

Spence, A. M. (1973). Job Markey Signaling. *Quarterly Journal of Economics*, *87*(3), 355–374.

Stearman, A. M. (1989). Yuquí Foragers in the Bolivian Amazon: Subsistence Strategies, Prestige, and Leadership in an Acculturating Society. *Journal of Anthropological Research*, *45*(2), 219–244. https://doi.org/10.1086/jar.45.2.3630335

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory*. Princeton University Press.

Stibbard-Hawkes, D. N. E. (2019). Costly signaling and the handicap principle in hunter-gatherer research: A critical review. *Evolutionary Anthropology: Issues, News, and Reviews*, *28*(3), 144–157. https://doi.org/10.1002/evan.21767

Sugiyama, L. S., & Chacon, R. (2000). Effects of illness and injury on foraging among the Yora and Shiwiar: Pathology risk as adaptive problem. In *Human behavior and adaptation: An anthropological perspective* (pp. 371–395).

Számadó, S. (1999). The Validity of the Handicap Principle in Discrete Action–Response Games. *Journal of Theoretical Biology*, *198*(4), 593–602. https://doi.org/10.1006/jtbi.1999.0935

Számadó, S. (2000). Cheating as a mixed strategy in a simple model of aggressive communication. *Animal Behaviour*, *59*(1), 221–230. https://doi.org/10.1006/anbe.1999.1293

Számadó, S. (2011). The cost of honesty and the fallacy of the handicap principle. *Animal Behaviour*, *81*(1), 3–10. https://doi.org/10.1016/j.anbehav.2010.08.022

Trivers, R. L. (1971). The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology*, *46*(1), 35–57. https://doi.org/10.1086/406755

Trumble Benjamin C., Smith Eric A., O'Connor Kathleen A., Kaplan Hillard S., & Gurven Michael D. (2014). Successful hunting increases testosterone and cortisol in a subsistence population. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1776), 20132876. https://doi.org/10.1098/rspb.2013.2876

Tucker, B. (2004). Giving, Scrounging, Hiding, and Selling: Minimal Food Sharing among the Mikea of Madagascar. In *Socioeconomic Aspects of Human Behavioral Ecology* (pp. 45–68). Emerald Group Publishing Limited.

Tybur Joshua M., & Gangestad Steven W. (2011). Mate preferences and infectious disease: Theoretical considerations and evidence in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1583), 3375–3388. https://doi.org/10.1098/rstb.2011.0136

Veherencamp, S. (2000). Handicap, index, and conventional signal elements of bird song. *Animal Signals : Signalling and Signal Design in Animal Communication*. Retrieved from https://ci.nii.ac.jp/naid/10019825562/

Wiessner, P. (1977). *Hxaro: A regional system of reciprocity for reducing risk among the! Kung San*. University of Michigan.

Wiessner, P. (1996). Leveling the Hunter: Constraints on the Status Quest in Foraging Societies. In *Food and the Status Quest: An Interdisciplinary Perspective*.

Wilson, D. S. (1998). Hunting, Sharing, and Multilevel Selection: The Tolerated-Theft Model Revisited. *Current Anthropology*, *39*(1), 73–97. https://doi.org/10.1086/204699

Winking, J., Gurven, M., & Kaplan, H. (2011). Father death and adult success among the Tsimane: Implications for marriage and divorce. *Evolution and Human Behavior*, *32*(2), 79–89. https://doi.org/10.1016/j.evolhumbehav.2010.08.002

Winking, J., Kaplan, H., Gurven, M., & Rucas, S. (2007). Why do men marry and why do they stray? *Proceedings of the Royal Society B: Biological Sciences*, *274*(1618), 1643–1649. https://doi.org/10.1098/rspb.2006.0437

Winking, J. W. (2005). *Fathering Among the Tsimane of Bolivia: A Test of the Proposed Goals of Paternal Care*. 189.

Winterhalder, B. (1986). Diet choice, risk, and food sharing in a stochastic environment. *Journal of Anthropological Archaeology*, *5*(4), 369–392. https://doi.org/10.1016/0278-4165(86)90017-6

Wood, B., & Hill, K. (2000). A Test of the "Showing-Off" Hypothesis with Ache Hunters. *Current Anthropology*, *41*(1), 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*(2), 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*(3), 280–317. https://doi.org/10.1007/s12110-013-9173-0

Wood, B. M., & Marlowe, F. W. (2014). Toward a Reality-Based Understanding of Hadza Men's Work. *Human Nature*, *25*(4), 620–630. https://doi.org/10.1007/s12110-014-9218-z

Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, *67*(3), 603–605. https://doi.org/10.1016/0022-5193(77)90061-3

Zahavi, Amotz. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, *53*(1), 205–214. https://doi.org/10.1016/0022-5193(75)90111-3

Zahavi, Amotz, & Zahavi, A. (1999). *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. Oxford University Press.

Ziker, J., & Schnegg, M. (2005). Food sharing at meals. *Human Nature*, *16*(2), 178–210. https://doi.org/10.1007/s12110-005-1003-6

# APPENDIX A

# TABLES REPORTING DIFFERENCES BETWEEN SEXES FOR TASK 2 AND FIGURES FROM TASK 3 REGRESSIONS

| Aché Task 2 (Men): Predicting Phenotype Assessment by Prey Traits | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | EFP | | | Strength | | | Fighting Ability | | | Disease Susceptibility | | |
| Standardized predictors | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < |
| Intercept | -0.63 | 0.09 | 0.001 | -0.37 | 0.09 | 0.001 | -0.26 | 0.08 | 0.002 | 0.25 | 0.08 | 0.002 |
| diff. Wt (A – B) | 0.80 | 0.13 | 0.001 | 0.81 | 0.14 | 0.001 | 0.69 | 0.13 | 0.001 | -0.51 | 0.12 | 0.001 |
| diff. HtF (A – B) | -1.52 | 0.14 | 0.001 | -1.32 | 0.14 | 0.001 | -1.05 | 0.13 | 0.001 | 0.82 | 0.12 | 0.001 |
| diff. HtK (A – B) | 1.06 | 0.16 | 0.001 | 1.36 | 0.16 | 0.001 | 1.22 | 0.15 | 0.001 | -0.96 | 0.14 | 0.001 |

**Table 1.** Aché Task 2 predicting phenotypic assessment by prey traits (men). 4 regressions were conducted predicting perceptions of hunter phenotype based on differences between animals killed. For each model, the predictors are standardized differences between the prey killed by hunter A and hunter B in Wt (kg), rank HtF, or rank HtK, and the outcome is predicted preference for hunter A.

| Aché Task 2 (Women): Predicting Phenotype Assessment by Prey Traits | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | EFP | | | Strength | | | Fighting Ability | | | Disease Susceptibility | | |
| Standardized predictors | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < |
| Intercept | -0.48 | 0.10 | 0.001 | -0.04 | 0.10 | 0.640 | 0.03 | 0.09 | 0.716 | 0.05 | 0.09 | 0.567 |
| diff. Wt (A – B) | 0.99 | 0.15 | 0.001 | 0.98 | 0.17 | 0.001 | 0.61 | 0.14 | 0.001 | -0.64 | 0.13 | 0.001 |
| diff. HtF (A – B) | -1.47 | 0.16 | 0.001 | -1.05 | 0.15 | 0.001 | -0.77 | 0.13 | 0.001 | 0.85 | 0.13 | 0.001 |
| diff. HtK (A – B) | 1.22 | 0.18 | 0.001 | 1.33 | 0.17 | 0.001 | 1.20 | 0.16 | 0.001 | -1.05 | 0.15 | 0.001 |

**Table 2.** Aché Task 2 predicting phenotypic assessment by prey traits (women). 4 regressions were conducted predicting perceptions of hunter phenotype based on differences between animals killed. For each model, the predictors are standardized differences between the prey killed by hunter A and hunter B in Wt (kg), rank HtF, or rank HtK, and the outcome is predicted preference for hunter A.

| Aché Task 2 (Men): Predicting Preferred Status by Prey Traits | | | | | | |
|---|---|---|---|---|---|---|
| | Preferred Mate | | | Preferred Social Partner | | |
| Standardized predictors | Beta | std. Error | p < | Beta | std. Error | p < |
| Intercept | -0.85 | 0.10 | 0.001 | -0.88 | 0.10 | 0.001 |
| diff. Wt (A – B) | 0.83 | 0.13 | 0.001 | 0.77 | 0.13 | 0.001 |
| diff. HtF (A – B) | -1.75 | 0.16 | 0.001 | -1.70 | 0.16 | 0.001 |
| diff. HtK (A – B) | 1.16 | 0.17 | 0.001 | 1.12 | 0.17 | 0.001 |

**Table 3.** Aché Task 2 predicting preferred status by prey traits (men). 2 regressions were conducted predicting the preferred status of the hunter based on differences between animals killed. For each model, the predictors are standardized differences between the prey killed by hunter A and hunter B in Wt (kg), rank HtF, or rank HtK, and the outcome is predicted preference for hunter A.

| Aché Task 2 (Women): Predicting Preferred Status by Prey Traits | | | | | | |
|---|---|---|---|---|---|---|
| | Preferred Mate | | | Preferred Social Partner | | |
| Standardized predictors | Beta | std. Error | p < | Beta | std. Error | p < |
| Intercept | -0.35 | 0.10 | 0.001 | -0.42 | 0.10 | 0.001 |
| diff. Wt (A – B) | 1.04 | 0.16 | 0.001 | 0.92 | 0.15 | 0.001 |
| diff. HtF (A – B) | -1.39 | 0.16 | 0.001 | -1.53 | 0.16 | 0.001 |
| diff. HtK (A – B) | 1.16 | 0.17 | 0.001 | 1.36 | 0.18 | 0.001 |

**Table 4.** Aché Task 2 predicting preferred status by prey traits (women). 2 regressions were conducted predicting the preferred status of the hunter based on differences between animals killed. For each model, the predictors are standardized differences between the prey killed by hunter A and hunter B in Wt (kg), rank HtF, or rank HtK, and the outcome is predicted preference for hunter A.

| Tsimané Task 2 (Men): Predicting Phenotype Rankings by Prey Traits | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | EFP | | | Strength | | | Fighting Ability | | | Disease Susceptibility | | |
| predictor | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < |
| Wt (std) | 1.19 | 0.28 | 0.001 | 0.89 | 0.27 | 0.001 | 0.61 | 0.35 | 0.078 | 1.32 | 0.43 | 0.002 |
| HtF (std) | -0.31 | 0.32 | 0.338 | -0.84 | 0.32 | 0.010 | -0.44 | 0.42 | 0.294 | -0.99 | 0.52 | 0.057 |
| HtK (std) | 0.16 | 0.32 | 0.618 | 0.95 | 0.32 | 0.003 | 1.02 | 0.42 | 0.016 | 0.70 | 0.48 | 0.143 |

**Table 5** Tsimané Task 2 predicting hunter phenotypic rankings from prey traits (Men). This table contains the estimates, standard errors, and p values for each of the independent variables (Wt, HtF, HtK) on each of the dependent variables (EFP, Strength, Fighting Ability, Disease Susceptibility) from the multiple ordinal logistic regressions. Independent variables were standardized. Dependent variables were the ranks assigned by individual informants to prey species.

| Tsimané Task 2 (Women): Predicting Phenotype Rankings by Prey Traits | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | EFP | | | Strength | | | Fighting Ability | | | Disease Susceptibility | | |
| predictor | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < | Beta | std. Error | p < |
| Wt (std) | 1.07 | 0.27 | 0.001 | 1.01 | 0.31 | 0.001 | 0.68 | 0.47 | 0.143 | 0.22 | 0.37 | 0.554 |
| HtF (std) | -0.21 | 0.34 | 0.536 | -0.17 | 0.38 | 0.658 | -0.48 | 0.59 | 0.414 | 0.09 | 0.4 | 0.846 |
| HtK (std) | -0.14 | 0.33 | 0.680 | -0.20 | 0.36 | 0.585 | 0.54 | 0.95 | 0.342 | -0.06 | 0.43 | 0.883 |

**Table 6** Tsimané Task 2 predicting hunter phenotypic rankings from prey traits (Women). This table contains the estimates, standard errors, and p values for each of the independent variables (Wt, HtF, HtK) on each of the dependent variables (EFP, Strength, Fighting Ability, Disease Susceptibility) from the multiple ordinal logistic regressions. Independent variables were standardized. Dependent variables were the ranks assigned by individual informants to prey species.

| Tsimané Task 2 (Men): Predicting Preferred Status by Prey Traits | | | | | | |
|---|---|---|---|---|---|---|
| | Preferred Mate | | | Preferred Cooperative Partner | | |
| predictor | Beta | std. Error | p < | Beta | std. Error | p < |
| Wt (std) | 0.54 | 0.26 | 0.034 | 1.20 | 0.27 | 0.001 |
| HtF (std) | -0.29 | 0.31 | 0.350 | -0.96 | 0.32 | 0.003 |
| HtK (std) | 0.17 | 0.31 | 0.583 | 0.27 | 0.30 | 0.360 |

**Table 7** Tsimané Task 2 predicting preferred status rankings from prey traits (Men). This table contains the estimates, standard errors, and p values for each of the independent variables (Wt, HtF, HtK) on each of the dependent variables (Preferred Mate, Preferred Cooperative Partner) from the multiple ordinal logistic regressions. Independent variables were standardized. Dependent variables were the ranks assigned by individual informants to prey species.

| Tsimané Task 2 (Women): Predicting Preferred Status by Prey Traits | | | | | | |
|---|---|---|---|---|---|---|
| | Preferred Mate | | | Preferred Cooperative Partner | | |
| predictor | Beta | std. Error | p < | Beta | std. Error | p < |
| Wt (std) | 0.97 | 0.28 | 0.001 | 1.88 | 0.30 | 0.001 |
| HtF (std) | 0.03 | 0.33 | 0.920 | -0.44 | 0.34 | 0.193 |
| HtK (std) | -0.29 | 0.31 | 0.358 | -0.54 | 0.34 | 0.111 |

**Table 8** Tsimané Task 2 predicting preferred status rankings from prey traits (Women). This table contains the estimates, standard errors, and p values for each of the independent variables (Wt, HtF, HtK) on each of the dependent variables (Preferred Mate, Preferred Cooperative Partner) from the multiple ordinal logistic regressions. Independent variables were standardized. Dependent variables were the ranks assigned by individual informants to prey species.

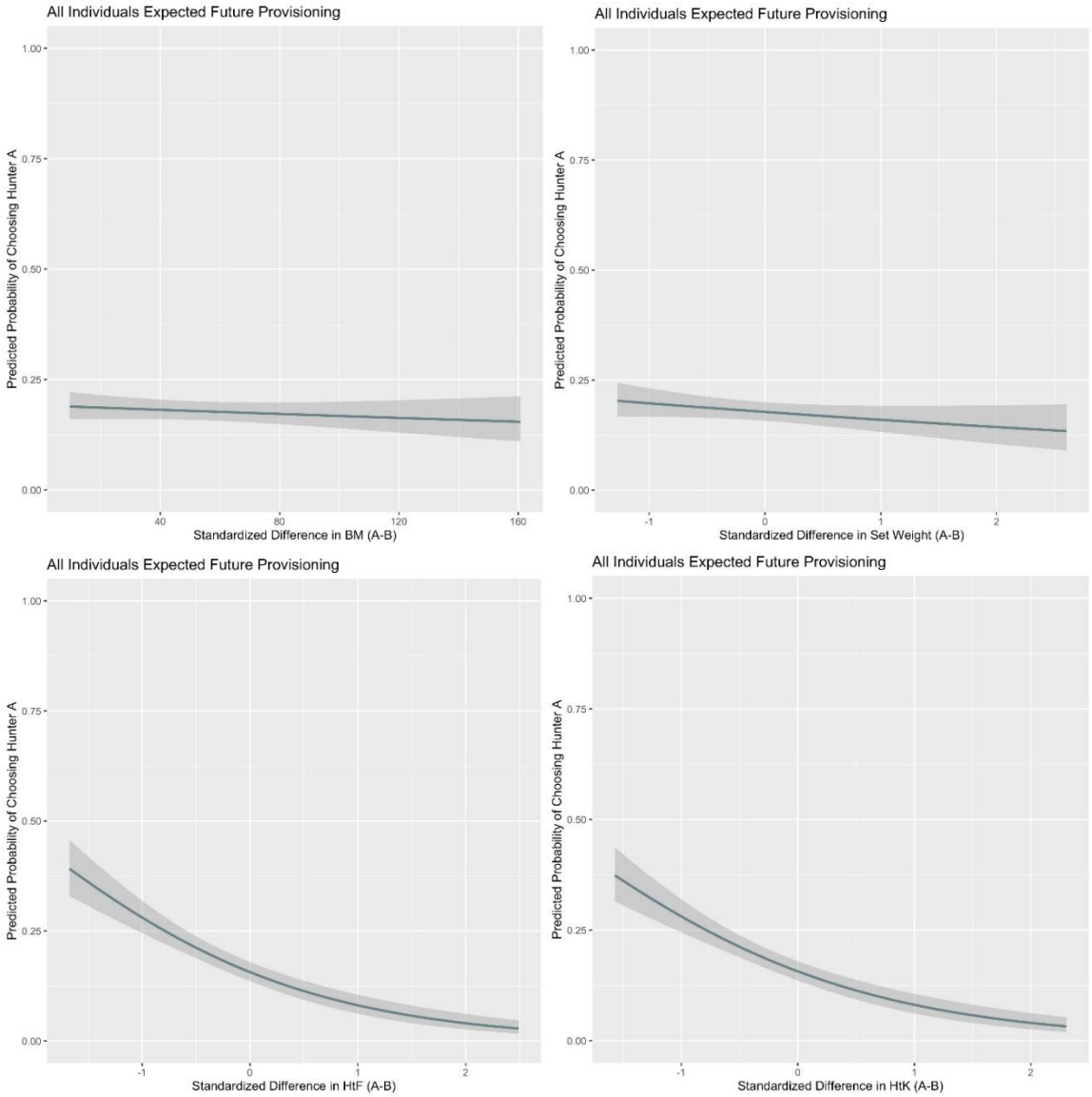



**Figure 1.** Aché Task 3 predicting EFP from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as having greater EFP as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK).

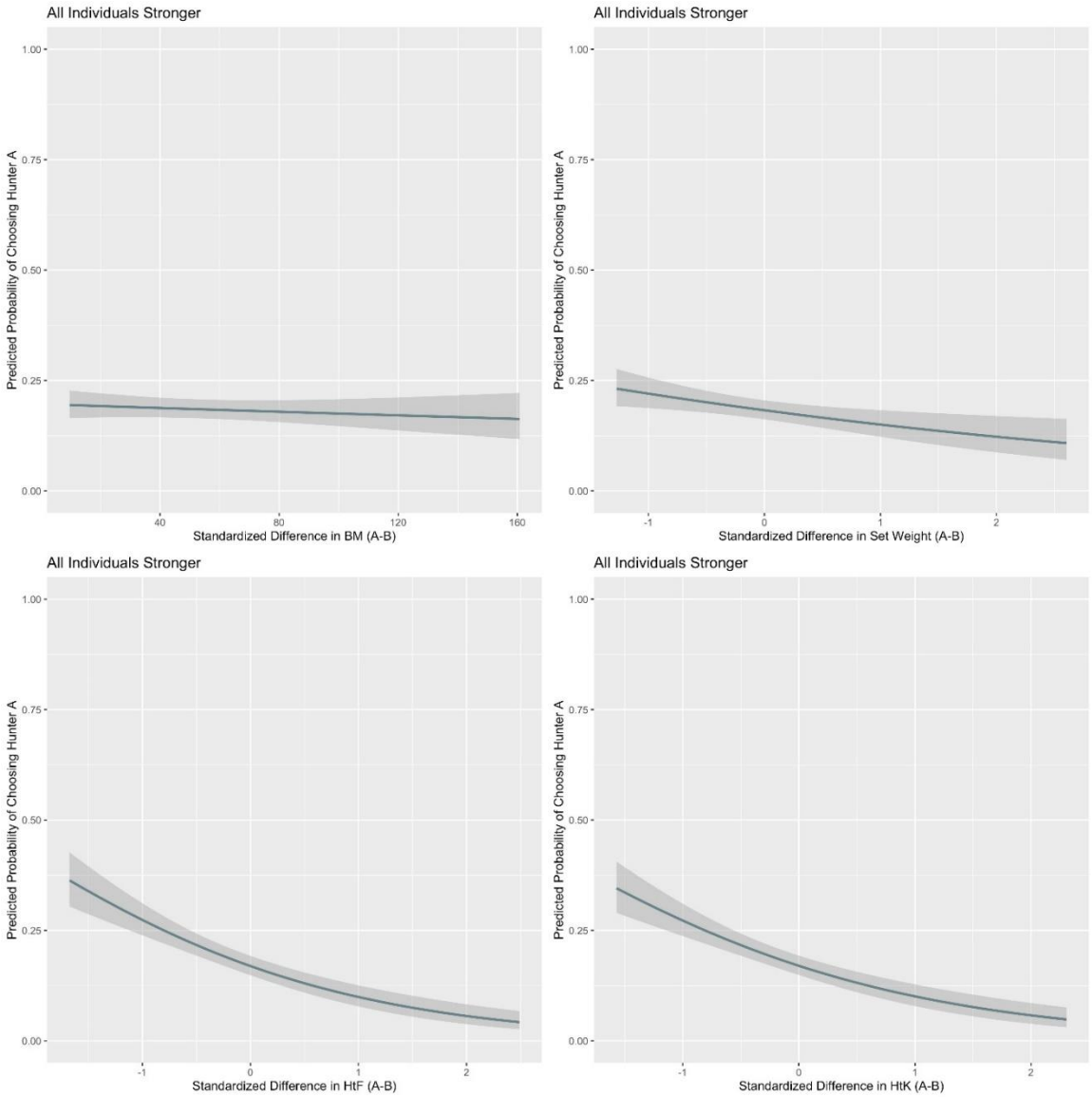



**Figure 2.** Aché Task 3 predicting Strength from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as having greater Strength as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK).

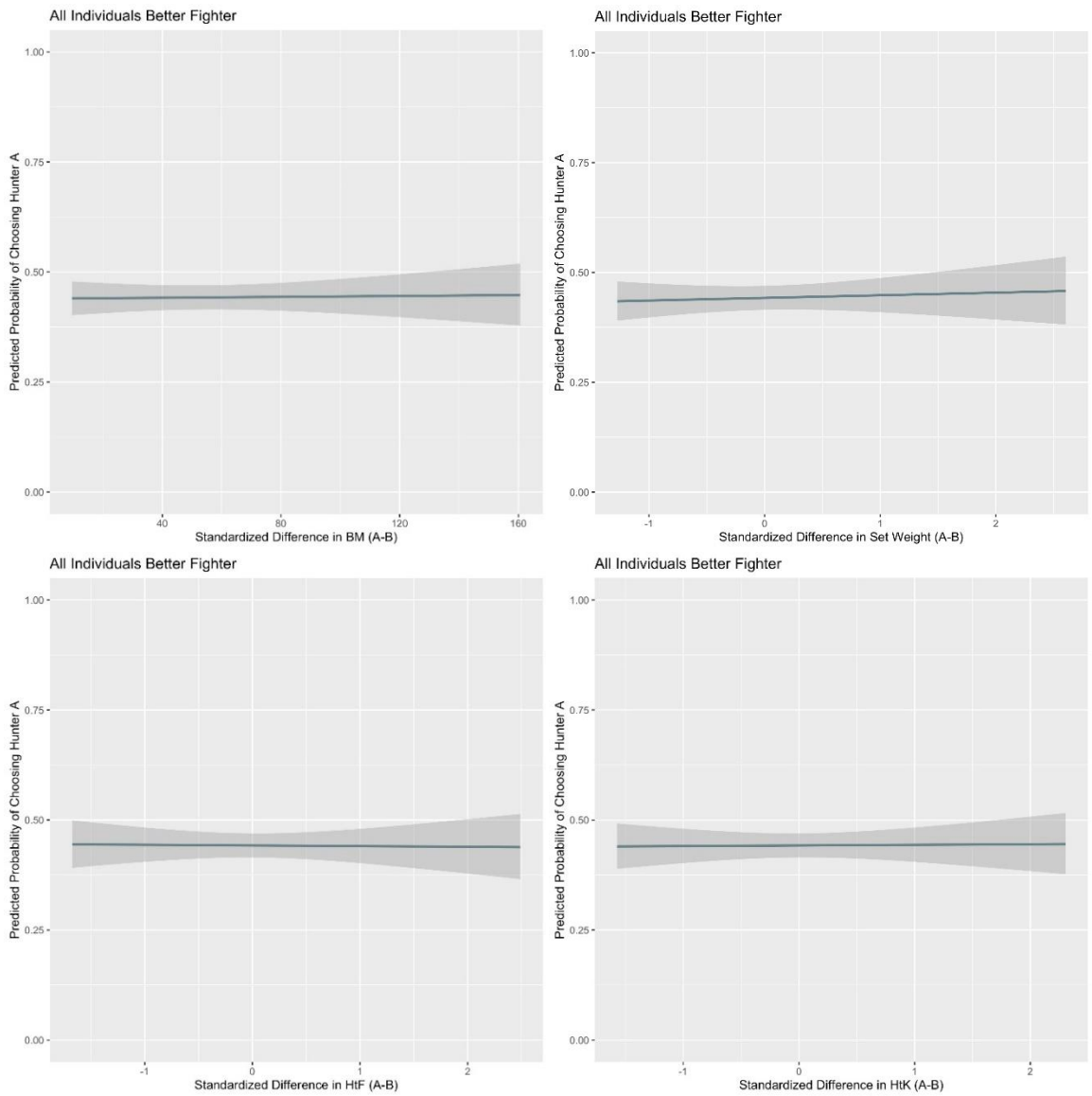



**Figure 3.** Aché Task 3 predicting Fighting Ability from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as having greater Fighting Ability as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK).

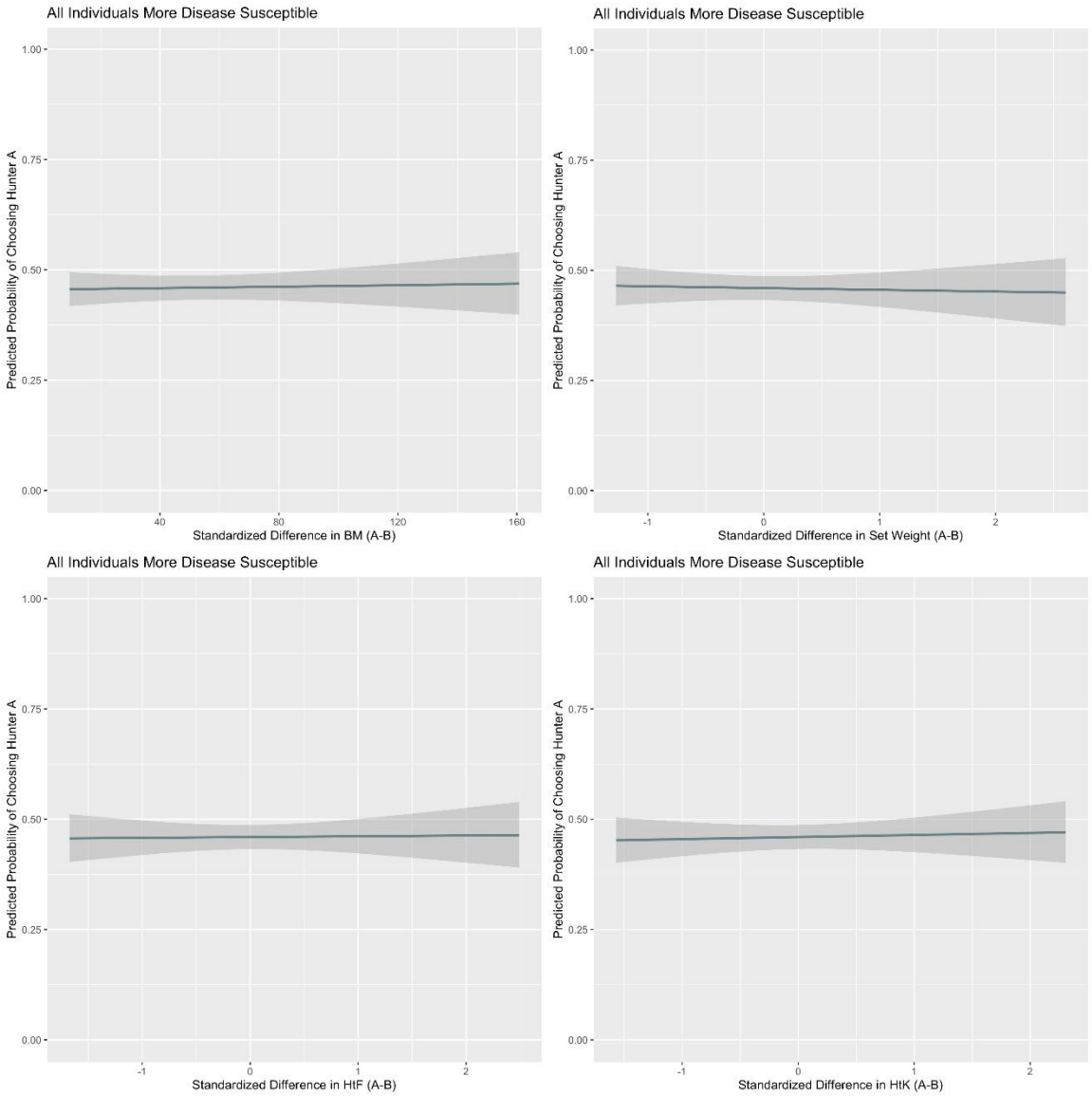



**Figure 4.** Aché Task 3 predicting Disease Susceptibility from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as having greater Disease Susceptibility as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK).

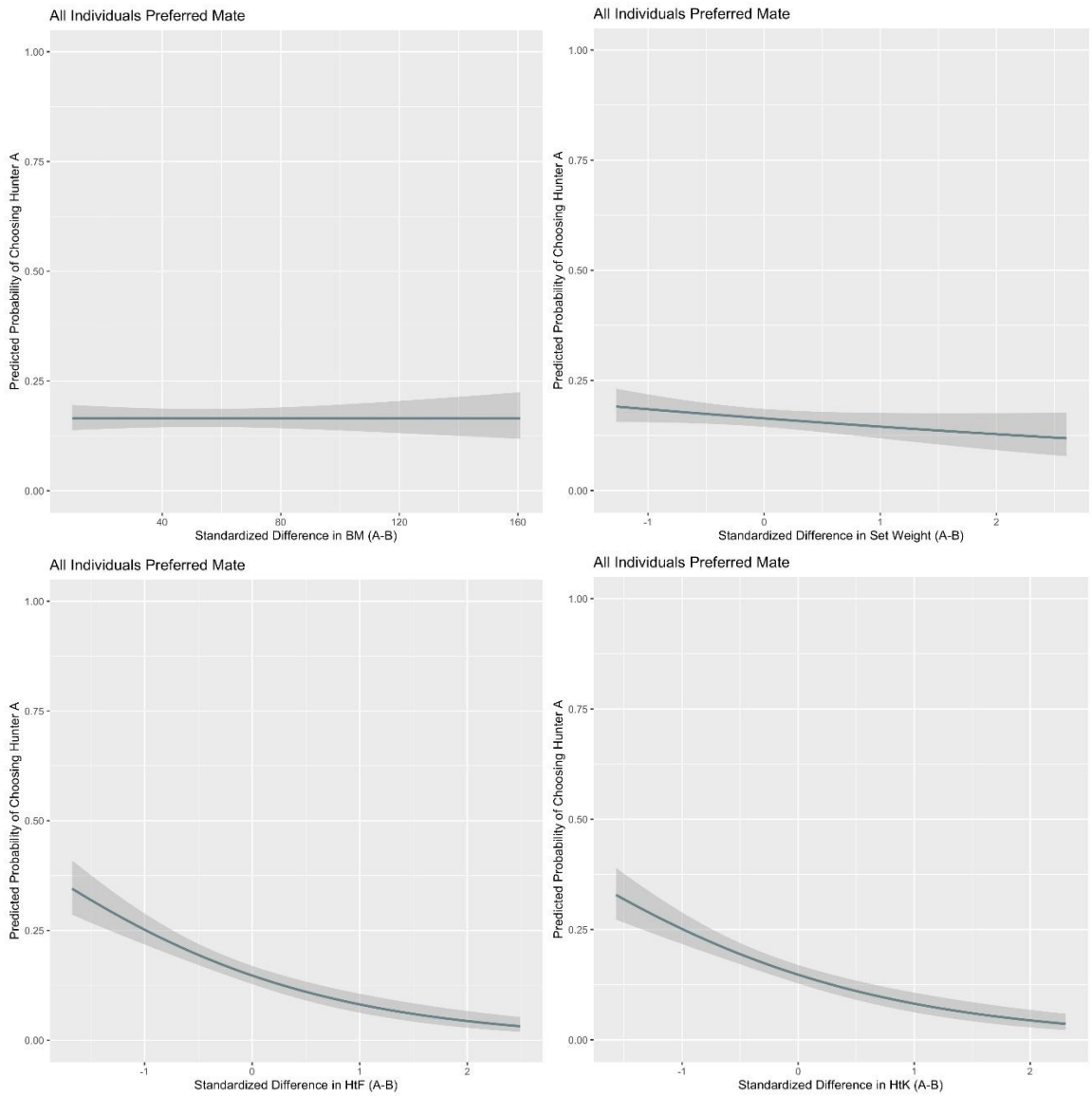



**Figure 5.** Aché Task 3 predicting preferred Mate status from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as a Preferred Mate as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK).

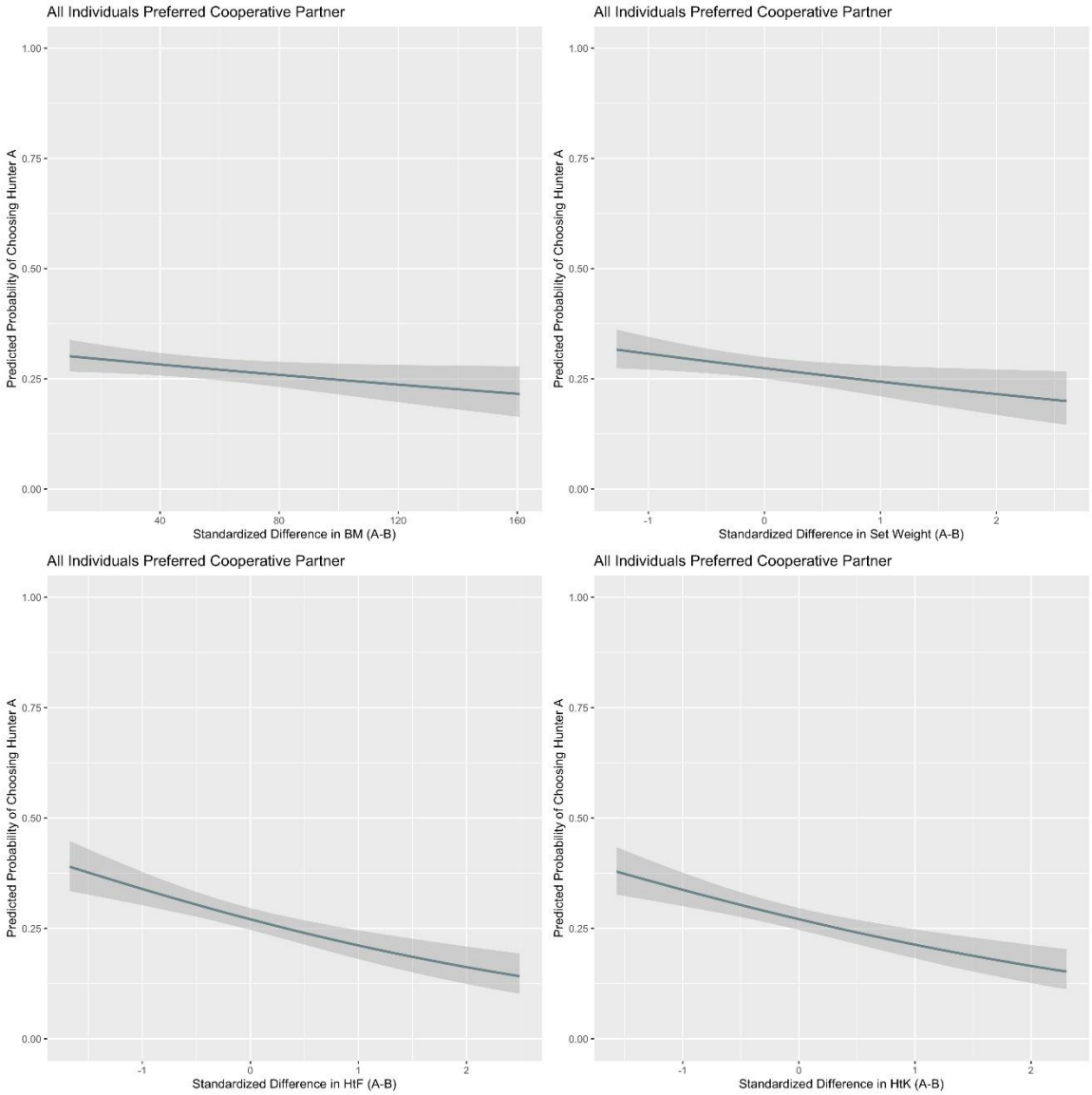



**Figure 6.** Aché Task 3 predicting preferred Cooperative Partner status from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as a Preferred Cooperative Partner as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK).

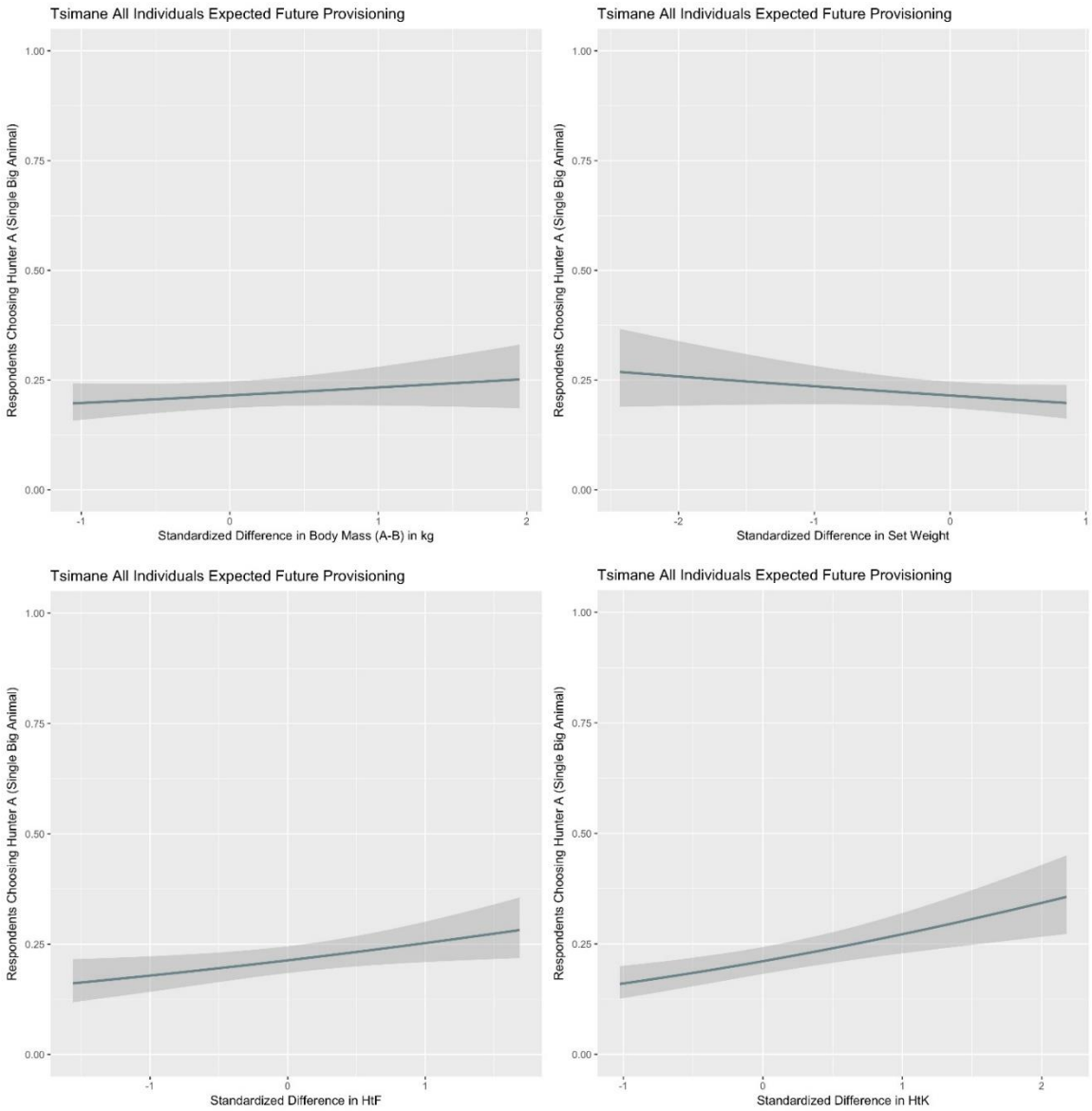



**Figure 7.** Tsimané Task 3 predicting EFP from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as having greater EFP as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK). Only HtK and HtF are significantly associated with the choice of hunter A.

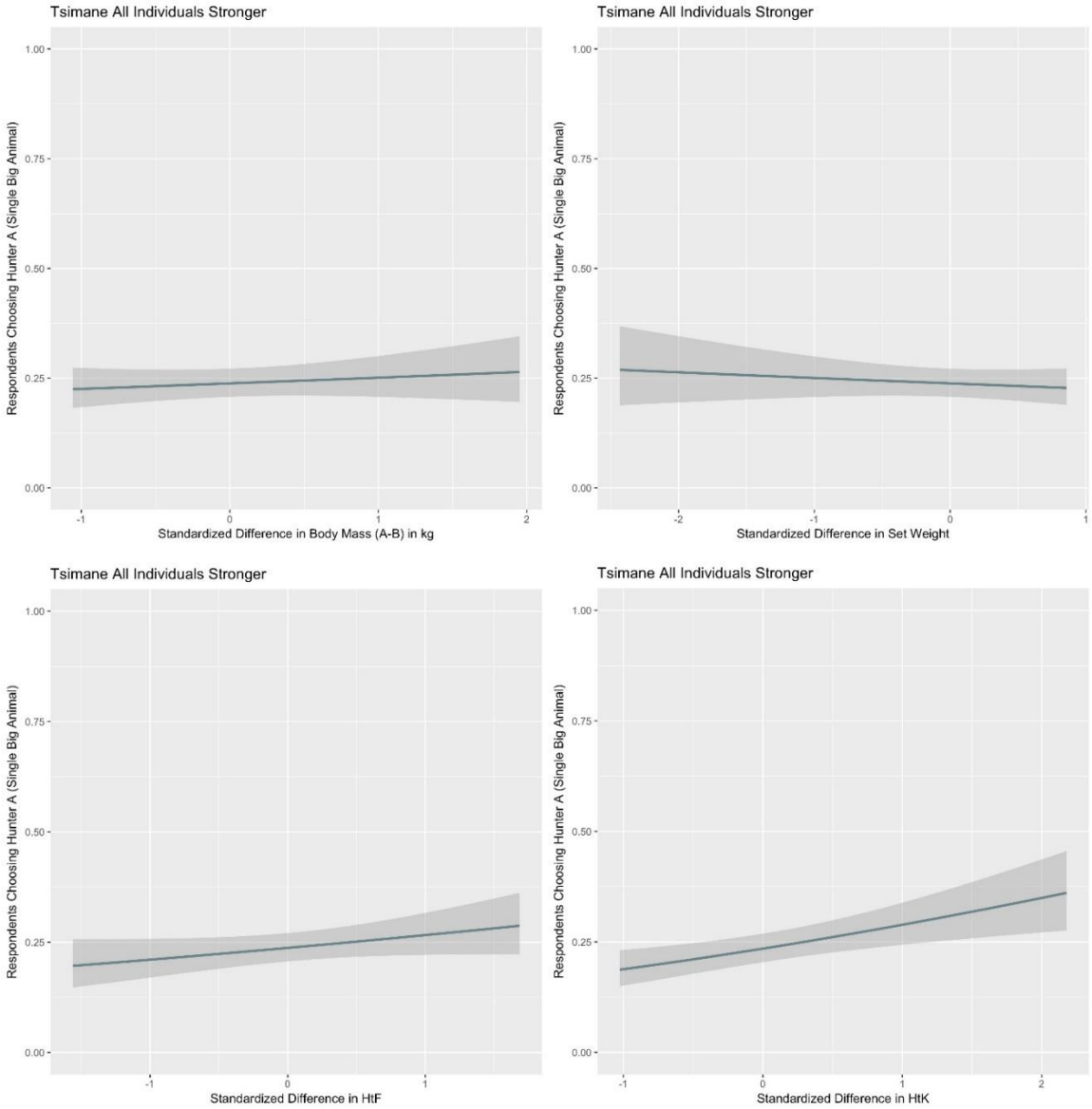



**Figure 8.** Tsimané Task 3 predicting Strength from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as stronger as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK). Only HtK is significantly associated with the choice of hunter A.

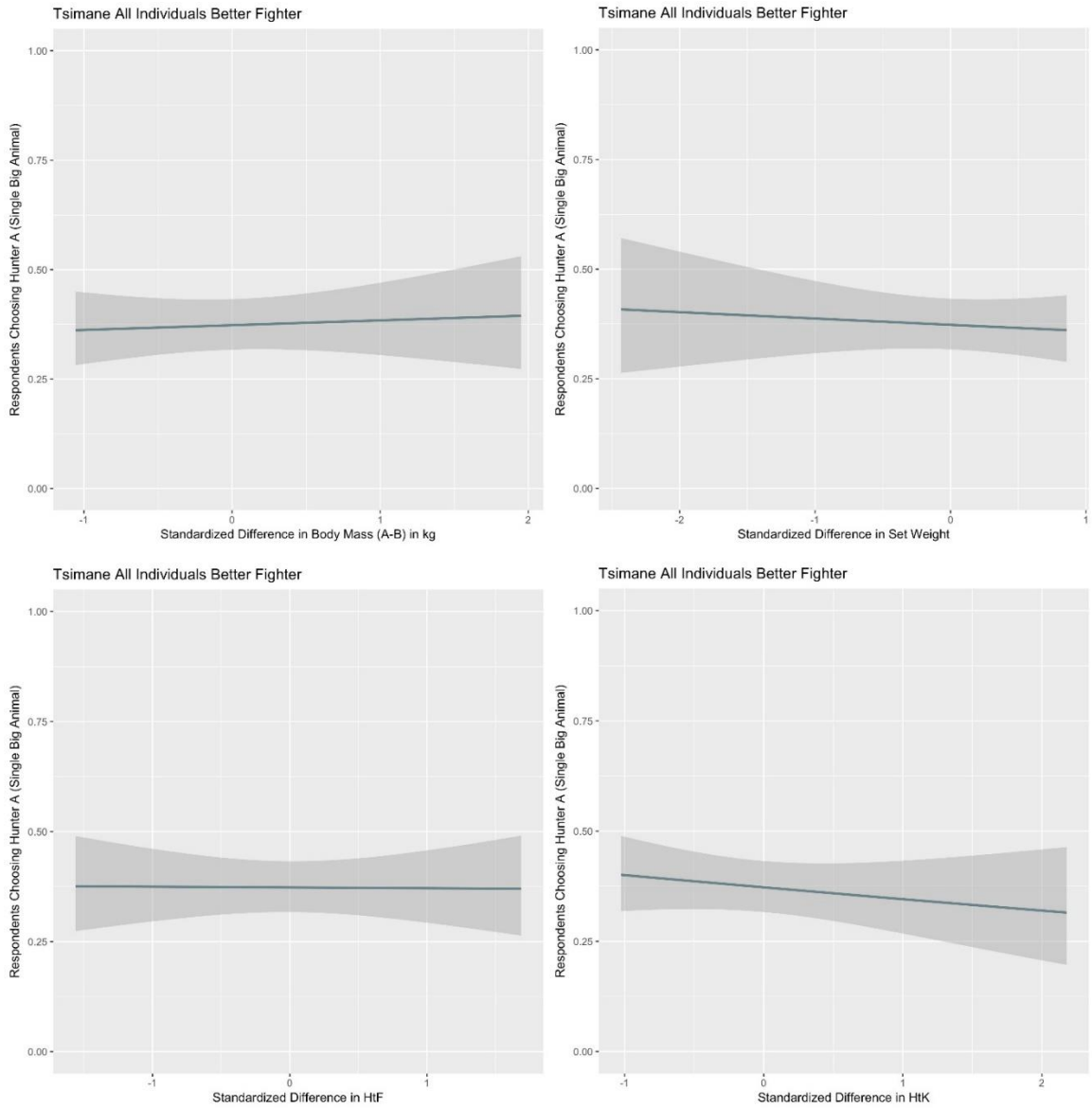



**Figure 9.** Tsimané Task 3 predicting Fighting Ability from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as having greater fighting ability as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK). None of the predictors is significantly associated with informant choice of hunter A.

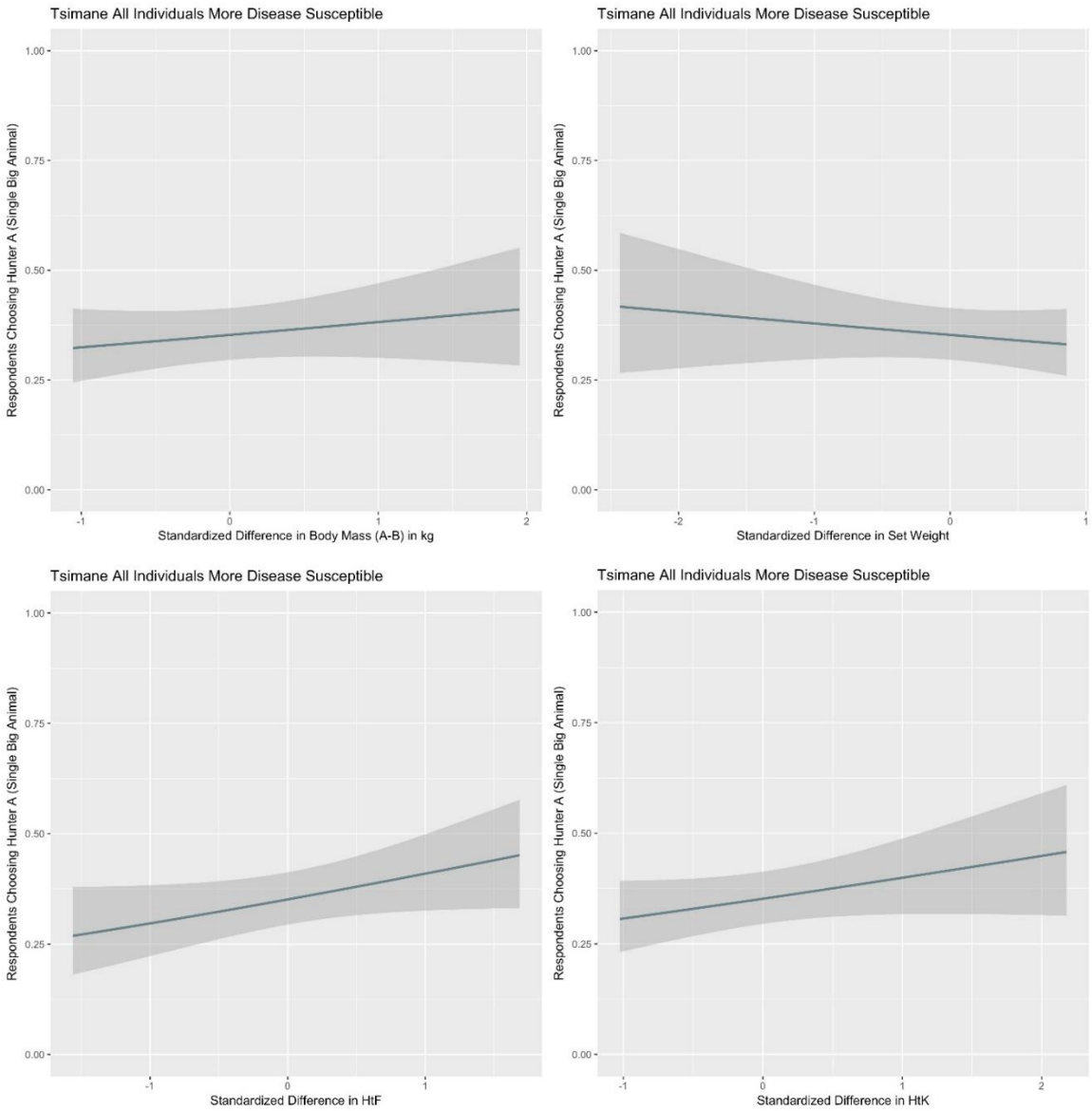



**Figure 10.** Tsimané Task 3 predicting Disease Susceptibility from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as having greater disease susceptibility as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK). None of the predictors is significantly associated with informant choice of hunter A.

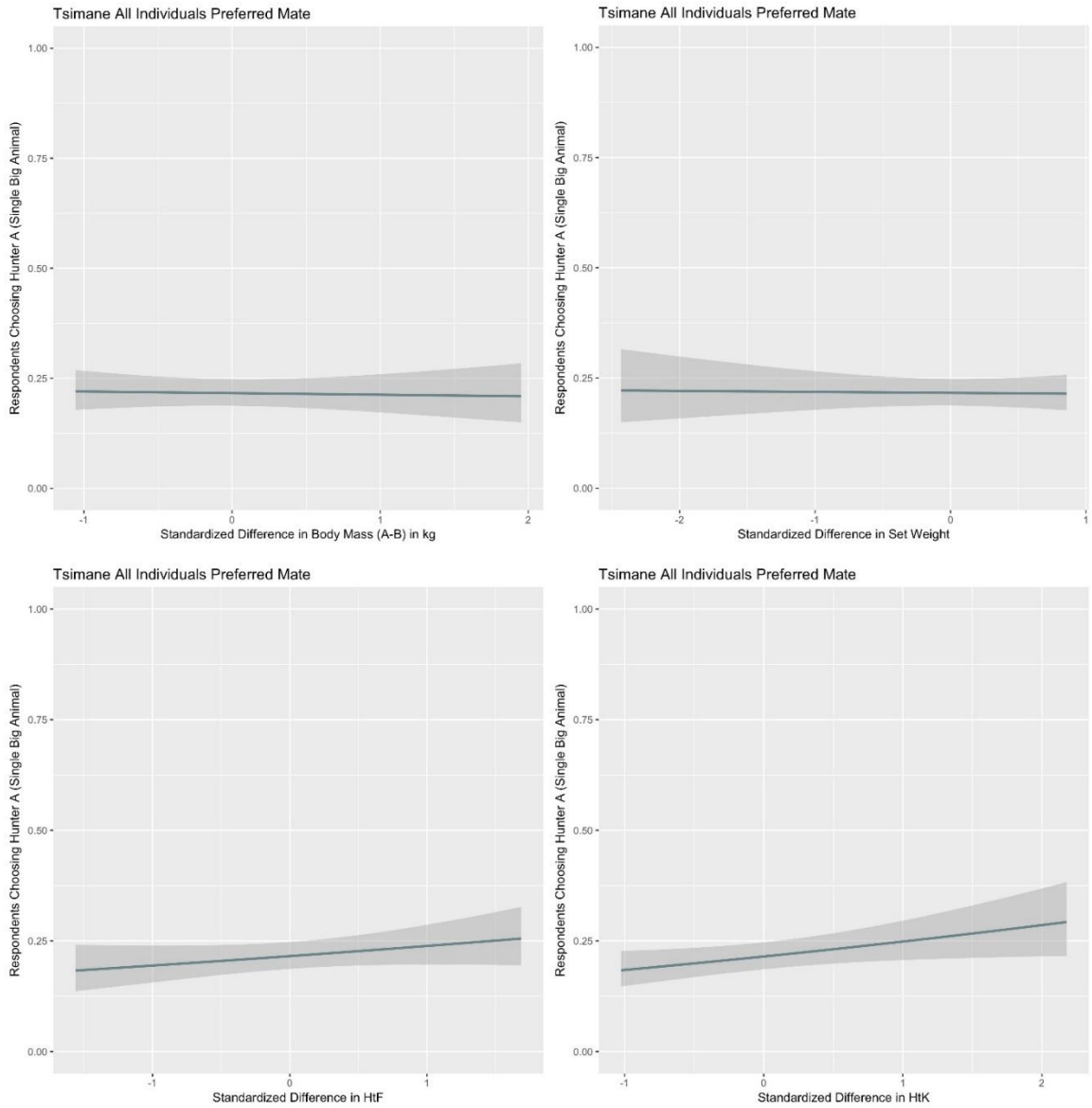



**Figure 11.** Tsimané Task 3 predicting preferred Mate status from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as a preferred mate as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK). Only HtK is significantly associated with the choice of hunter A.

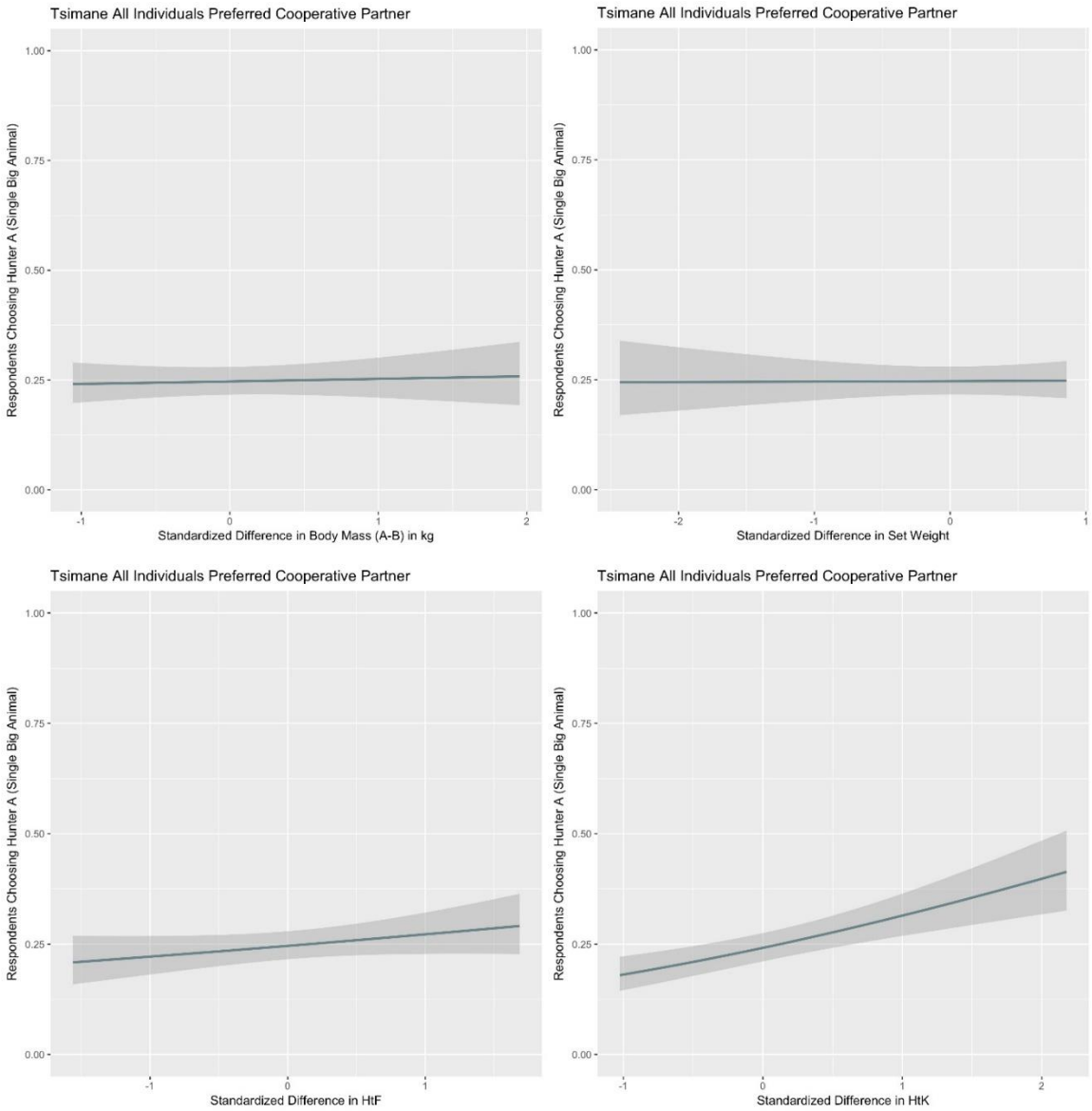



**Figure 12.** Tsimané Task 3 predicting preferred Cooperative Partner status from prey traits. Univariate logistic regressions examining the likelihood that hunter A will be chosen as a preferred cooperative partner as a function of four prey set traits (Differences in Wt, Set Weight, HtF, HtK). Only HtK is significantly associated with the choice of hunter A.

# APPENDIX B

## IRB HUMAN SUBJECTS RESEARCH APPROVAL

ASU Knowledge Enterprise Development

APPROVAL: EXPEDITED REVIEW

Kim Hill
Human Evolution and Social Change, School of (SHESC)
-
Kim.Hill@asu.edu

Dear Kim Hill:

On 9/23/2014 the ASU IRB reviewed the following protocol:

| | |
|---|---|
| Type of Review: | Initial Study |
| Title: | Intertidal foraging, Sociality and Culture |
| Investigator: | Kim Hill |
| IRB ID: | STUDY00001593 |
| Category of review: | (7)(b) Social science methods, (7)(a) Behavioral research |
| Funding: | Name: John Templeton Foundation; |
| Grant Title: | |
| Grant ID: | |
| Documents Reviewed: | • Child assent form.pdf, Category: Consent Form;<br>• Project 4 - Templeton CONSENT FORM.pdf, Category: Consent Form;<br>• Project 4 - Templeton Parental-Consent.pdf, Category: Consent Form;<br>• Project-Hill-Templeton-2014IRB-503a (2).docx, Category: IRB Protocol;<br>• Project 4 - Interview 1 Economics.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 1A Costly Signaling.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 4 Specialization.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Marine foraging observation.pdf, |

| | |
|---|---|
| | Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 2 Interaction networks.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 3 Cooperation.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 5 Reproductive helping.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 6 Cultural learning.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• 48952_evolutionary_foundations_of_human_uniqueness_recovering_patterns_of_cognition_cumulative_culture_and_cooperation.pdf, Category: Sponsor Attachment; |

The IRB approved the protocol from 9/23/2014 to 9/22/2015 inclusive. Three weeks before 9/22/2015 you are to submit a completed "FORM: Continuing Review (HRP-212)" and required attachments to request continuing approval or closure.

If continuing review approval is not granted before the expiration date of 9/22/2015 approval of this protocol expires on that date. When consent is appropriate, you must use final, watermarked versions available under the "Documents" tab in ERA-IRB.

In conducting this protocol you are required to follow the requirements listed in the INVESTIGATOR MANUAL (HRP-103).

Sincerely,

IRB Administrator

cc: Lindsay Mullen
Andrew Bishop

ASU Knowledge Enterprise Development

APPROVAL: MODIFICATION

Kim Hill
Human Evolution and Social Change, School of (SHESC)
-
Kim.Hill@asu.edu

Dear Kim Hill:

On 4/28/2015 the ASU IRB reviewed the following protocol:

| | |
|---|---|
| Type of Review: | Modification |
| Title: | Intertidal foraging, Sociality and Culture |
| Investigator: | Kim Hill |
| IRB ID: | STUDY00001593 |
| Funding: | Name: John Templeton Foundation |
| Grant Title: | None |
| Grant ID: | None |
| Documents Reviewed: | • Project 4 - Interview 3 Cooperation.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Templeton Parental-Consent.pdf, Category: Consent Form;<br>• Project 4 - Marine foraging observation.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Interview 1A (1).pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 6 Cultural learning.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project-Hill-Templeton-2014IRB-503a (2).docx, Category: IRB Protocol;<br>• Project 4 - Interview 2 Interaction networks.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Templeton CONSENT FORM.pdf, |

| | |
|---|---|
| | Category: Consent Form;<br>• Child assent form.pdf, Category: Consent Form;<br>• Project 4 - Interview 1A Costly Signaling.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 1 Economics.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>•<br>48952_evolutionary_foundations_of_human_uniqueness_recovering_patterns_of_cognition_cumulative_culture_and_cooperation.pdf, Category: Sponsor Attachment;<br>• Project 4 - Interview 5 Reproductive helping.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Interview 1B (2).pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions);<br>• Project 4 - Interview 4 Specialization.pdf, Category: Measures (Survey questions/Interview questions /interview guides/focus group questions); |

The IRB approved the modification.

When consent is appropriate, you must use final, watermarked versions available under the "Documents" tab in ERA-IRB.

In conducting this protocol you are required to follow the requirements listed in the INVESTIGATOR MANUAL (HRP-103).

Sincerely,

IRB Administrator

cc: