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Original Article

Upper-body strength predicts hunting reputation and reproductive success in Hadza hunter–gatherers

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ABSTRACT

Hunting is a characteristic feature of early human subsistence, and many theories of evolution have emphasized the role of hunting in hominization. Still today hunting ability continues to be selected for in extant foragers with better hunters experiencing greater reproductive success. Yet little is known about the traits that comprise a successful hunter traits that are presupposed to also be under selection. Two complementary empirical analyses were conducted to examine this question using data collected from Hadza hunter–gatherers in Tanzania. First, data on upper-body strength, running speed, target precision and visual and auditory acuity were collected to examine the traits that predict hunting reputation in men. Second, interview data were collected from Hadza informants regarding the traits they deem important for hunting. Results from the first study implicate upper-body strength as the strongest and most consistent predictor of men's hunting reputation. Hadza conventional wisdom also accord with these findings. Although informants stressed the importance of non-physical traits, such as "intelligence" and "heart", strong arms were cited as the most important physical trait for hunting. Finally, men with stronger upper-bodies experienced greater reproductive success, a result that is largely mediated by hunting reputation. These findings suggest that selection for hunting ability may have acted on men's upper-bodies. Nevertheless, the importance of effort on strength and hunting success cannot be dismissed. This is also discussed.

1. Introduction

Many important changes related to human origins have been linked to hunting (e.g. Gurven, Kaplan, & Gutierrez, 2006; Kaplan, Hill, Lancaster, & Hurtado, 2000; Washburn & Lancaster, 1968). While early anthropological accounts have highlighted the act of hunting as a prime mover of human evolution responsible for the evolutionary grade shift observed between the genus *Homo* and earlier hominid species including increased encephalization (Washburn & Lancaster, 1968), others have highlighted the importance of increased dietary quality due to meat-eating itself (Aiello & Wheeler, 1995). More recently it has been suggested that the distinctive life-history patterns of humans, including their lengthened juvenile period and long lifespan, evolved in response to the long process of learning needed to acquire the skills necessary to become a productive hunter (Gurven et al., 2006; Kaplan et al., 2000). The evolutionary relevance of hunting is still observed in a number of extant foraging societies where better hunters experience greater reproductive outcomes (for review, Gurven & von Rueden, 2006). Despite the importance of hunting in understanding human origins and the fact that it continues to be a significant part of life in extant hunter–gatherers (Stanford, 2001), little work has examined the physical traits associated with hunting ability, traits that are presupposed to also be important in human evolution. This study explored the role of visual and auditory acuity, running speed, upper-body strength and target precision in predicting men's hunting reputation.

Women value hunting ability in mates (Marlowe, 2005), and the finding that good hunters experience greater reproductive success has now been reported in a number of societies including the Hadza (Hawkes, 2001; Marlowe, 1999), the Ache of Paraguay (Hill & Hurtado, 1996; Kaplan & Hill, 1985) and the !Kung Bushmen (Wiessner, 2002). Prior research with Hadza hunter–gatherers has shown that better hunters also attain more hard-working wives, offering another potential source for the greater disparity between more and less successful hunters (Hawkes, O'Connell, & Blurton Jones, 2001). Debates over how hunting increases men's reproductive success, and relatedly, why men hunt at all, are widespread. While the energetic gains provided by a hunter to his family have long been suggested (Lancaster, 1978), it has more recently been argued that big game hunting plays a relatively small role in the provisioning of family due to the sporadic and unreliable nature of hunting success, the observed communal sharing of a hunter's kill (Hawkes et al., 2001) and the fact that men, on average, tend to contribute less food to the diet than women (Marlowe, 2001). In both !Kung (Howell, 2010) and Hadza hunter–gatherers (Marlowe, 2010) meat constitutes less than 30% of energy consumed. For these reasons, it has been proposed that

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hunting may have evolved for purposes other than provisioning. For instance, it has been suggested that hunting serves as a costly signal used to advertise quality in order to attract mating partners (Hawkes & Bliege Bird, 2002; Smith, 2004) and to establish reputations for generosity (Gurven, Allen-Arave, Hill, & Hurtado, 2000). In short, hunting may serve as a form of competition between men.

Other studies suggest that hunting does have an important role in family provisioning. For instance, Wood (2006) used storyboards to describe hypothetical scenarios of camps with good hunters and camps with poor hunters. He found that Hadza men prefer to join camps with the good hunters, a strategy for familial provisioning rather than competing or showing off. Other research with the Hadza suggests that the caloric returns from men's small-game hunting and foraging are important during critical periods of a woman's reproduction. Specifically, Hadza women experience a reduction in foraging returns when they are nursing, and so their husbands make up this deficit by bringing in more food (Marlowe, 2003). Finally, more recent research suggests that the amount of meat the hunter's nuclear family receives can be substantially higher than other group members, calling into question the idea of hunting as a form of costly signaling (Wood & Marlowe, 2013). Nevertheless, the question remains as to whether payoffs from provisioning, signaling, or both explain why men hunt rather than gather (Gurven & Hill, 2009).

Whatever the reason for why men hunt, it is clear that hunting was an important activity in hominin evolution, with the hunting of large animals for consumption dating as far back as 1.8 Ma (Domínguez-Rodrigo et al., 2013). In fact, the consumption of meat in humans far exceeds that of any non-human primate (Kelly, 1995). Animal foods are not only nutrient-rich but also contain large amounts of fat, digestible proteins and essential amino acids. No other plant source in the African savannah can provide a year round supply of protein, and no single plant source contains all the micronutrients present in meats (Domínguez-Rodrigo et al., 2013). Consequently, it has been argued that without meat and its accompanying nutrients, humans would not have been able to develop their unusually large brains (Milton, 2003).

In addition to increased encephalization, humans have also developed a lengthened juvenile period and extended life span. The existence of these two distinct life history traits has been best explained as a response to our unique foraging niche. Specifically, it has been argued that since hunting is an activity that requires a long period of learning before maximum return rates are achieved, natural selection worked to extend the life span so that payoffs from hunting are realized. In turn, this created pressure for slower growth earlier in life when skills from hunting and food production can be learned (Hill & Kaplan, 1999; Kaplan et al., 2000). Age related changes in hunting productivity have been examined in a number of forager societies, including the Hadza (Blurton Jones & Marlowe, 2002), Hiwi (Kaplan et al., 2000) and Aché (Walker, Hill, Kaplan, & McMillan, 2002). These studies demonstrated that hunting success peaks approximately between the ages of 35 and 50 years, long after physical maturity is reached. Again, these findings suggest that hunting is a learned skill that takes many years to develop and master (Blurton Jones & Marlowe, 2002; Gurven et al., 2006). To be a successful hunter one needs to integrate sensory cues including sounds, smells and knowledge of animals over different and seasonally changing landscapes; all of which can take years to develop and master (Gurven et al., 2006).

While a few studies have examined hunting proficiency and learning time in extant hunter–gatherers (Blurton Jones & Marlowe, 2002; Gurven et al., 2006), associations of physical traits with hunting ability have rarely been investigated. While there is little doubt that meat acquisition via hunting is a skill that requires a long period of learning, there is some evidence that constraints of physical ability may also account for some individual differences in hunting ability. For example, in both Aché foragers (Walker et al., 2002) and Tsimané Amerindians (Gurven et al., 2006), body size predicted men's ability to hit stationary objects using a bow and arrow. Similarly, Blurton Jones and Marlowe (2002) find that body weight, arm diameter and the amount of weight pulled back on bow all predict archery ability in Hadza boys and men, implying an effect of strength. After examining two additional subsistence skills (e.g. digging and tree climbing) Blurton-Jones and Marlowe suggest that differences in subsistence abilities may not be entirely due to practice and learning but rather differences in physical traits, such as strength. Other physical traits have been theoretically linked to human hunting ability. For instance, it has been proposed that both human walking and running capabilities evolved so that humans could more effectively hunt animals (Bramble & Lieberman, 2004). There are, however, many more unexplored physical traits and abilities that could contribute to hunting success, such as sensory acuity. The aim of the current study was to determine the role of physical traits, including hearing and visual acuity, running speed, target precision and upper-body strength, in explaining individual differences in hunting success in adult men, as inferred from hunting reputations. The significance of each of these physical traits was also explored by examining whether they were related to men's reproductive success. A second follow-up study was conducted to explore the traits the Hadza believe are important for being a successful hunter.

2. Methods

2.1. Subjects

The Hadza are nomadic, sleep outside under the stars, and practice neither herding nor agriculture. They are central-place foragers meaning that foraged and hunted foods are brought back to a camp and shared. They live in a savannah–woodland type habitat in Northern Tanzania around Lake Eyasi. They number 1,000, but only 300 or so still subsist by hunting and gathering. Entire camps, which number around 30 individuals, shift location approximately every 8 weeks, usually in response to changes in food and water availability (Blurton Jones, Hawkes, & O'Connell, 2005). Membership in camps is also fluid with individuals moving frequently between camps, but generally confined within larger geographic regions (Apicella, Azevedo, Fowler, & Christakis, 2014).

There is a sexual division of labor in which women collect fruit and dig for tubers and men collect honey and hunt for game. Both hunting and gathering by the Hadza occur without the use of modern tools and equipment. Men hunt for animals using wooden bows and arrows made with either wooden or metal-tips depending on the size of the game to be hunted. Metal tips are generally used for big animals and often contain poison, usually made from the flowering plant panjube (*Adenium obesum*), which, after entering the animal's bloodstream, causes the animal to die (Bartram, 1997). Hunting is usually an individual activity, but men occasionally hunt at night in pairs. Young boys are given bows around the time they start walking and use the bows as a source of play (Crittenden, Conklin-Brittain, Zes, Schoeninger, & Marlowe, 2013). However, they will take aim at mice and birds when opportunities arise.

2.2. Procedures

2.2.1. Study 1

Data on hunting reputations, auditory and visual acuity, running speed, target precision and upper-body strength were collected from fifty-four men living in nine different Hadza camps on the eastern side of Lake Eyasi over a period of approximately six months in 2006. Selection of camps relied on a snowball sampling method whereby occupants of the current camp would direct the researcher to the next closest camp. All adult men over the age of 18 within each camp participated in the study with the exception of very elderly men who no longer hunt. A few participants moved from their camp during data collection and consequently were not measured on every trait.