

# The Hadza and Evolutionary Theory

## *An Introduction*

The Hadza of Tanzania are one of the very few societies anywhere in the world who still live by hunting and gathering. Hunter-gatherers are people who forage for wild foods, practicing no cultivation or animal husbandry. The fact that the Hadza are still foraging makes them invaluable to researchers interested in the lifestyle of our ancestors before agriculture so greatly altered human societies. The Hadza happen to live in East Africa, an area rich in hominin fossils (Figure 1.1). Hominins are all those species (*Australopithecus afarensis*, *Paranthropus boisei*, *Homo erectus*, etc.) that share with us a common ancestor that diverged from the ancestor of our closest living relatives, chimpanzees and bonobos, 6–7 million years ago (mya). Today, we humans are the sole surviving hominin. Humans and their hominin ancestors have occupied East Africa for as long as they have existed. For testing evolutionary hypotheses about past ecological influences and outcomes, it would be difficult to find a living society more relevant than the Hadza. They have been studied extensively, but surprisingly no English-language anthropological book has been published until now.<sup>1</sup>

I began my research with the Hadza in 1995 when I was working on my Ph.D. at UCLA. Since then, I have been back 15 times for a total of about 4 years altogether. Even so, I speak only a little bit of the Hadza

1. In 1958 Kohl-Larsen wrote a book in German, but it has not been translated.



Figure 1.1. Map of East Africa, showing Hadza area in relation to the locations of hominin fossil sites. Inset shows Hadzaland (inside shaded ring) with key locations in a small font and names of neighboring ethnic groups in a large font.

language (Hadzane) because I can communicate with the Hadza in Kiswahili, their second language. My research entails behavioral sampling, measurement of food acquisition and consumption, skills, preferences, anthropometry, demography, and a variety of topics using experiments and interviews. All of this research involves evolutionary theory as a guide to hypothesis testing. I intend this book to serve as a general ethnography of the Hadza, but I also hope to persuade the uninitiated that an evolutionary view is essential for understanding humans. I therefore aim to make the book accessible to readers with little familiarity with evolutionary theory.

Natural selection explains how and why evolution occurs (Darwin 1859). Individuals with certain traits survive and reproduce more successfully than individuals with other traits. The genes involved in producing those successful traits are passed on to the next generation in greater numbers. Darwin did not know about genes, but he knew traits were inherited; the modern theory of selection had to await the rediscovery of Mendelian genetics and the synthesis of Mendel's laws with Darwin's theory by early population geneticists (Fisher 1930, Haldane 1932, Wright 1931). Natural selection leads to adaptation. Genes that promote more optimal use of resources in an environment result in enhanced survival and reproduction of their carriers, and consequently each successive generation becomes more adapted to the environment. When the environment changes, the population will eventually track the changes or go extinct. The environment includes everything: climate, flora and fauna, predators, parasites, and members of one's own species (conspecifics). Conspecifics are especially important among social animals like us because kin and potential rivals, allies, and mates have a strong impact on an individual's reproductive success (RS).

Our bodies and behavior have been shaped by competition between individuals in the past, and we all have inherited our genes from the winners of that competition. Sexual selection is the component of natural selection that deals with reproduction (Darwin 1871). Ultimately, greater RS matters more than longevity because no one lives forever. Even if one lived to be a thousand years old, without reproducing, one's own genes would not be passed on, so one's personal (or direct) fitness would be zero. We can see, therefore, why selection should commonly favor individuals who selfishly exploit resources for their own reproductive benefit (individual selection).

Our understanding of how evolution works greatly expanded when William Hamilton (1964) explained why, despite individual selection, we observe seemingly altruistic behavior in many species. Hamilton's formula tells us when selection should favor one individual helping another. The formula can be expressed as  $C < Br$ , where  $C$  equals the cost to the helper,  $B$  equals the benefit to the beneficiary, and  $r$  equals the degree of relatedness between helper and beneficiary. When the helper and beneficiary are related by 50%, as full siblings are on average, as long as the benefit is more than twice the cost (e.g., benefit = 2.1 and cost = 1), it will pay one sibling to help the other because  $0.5 * 2.1 = 1.05 > 1$ . More precisely, there is positive selection for a gene that promotes helping relatives (nepotism). Hamilton (1964) thus introduced the concept of inclusive fitness. An

individual's inclusive fitness includes the person's own RS (direct fitness) plus his or her effect on others who carry the same alleles by common descent, weighted by the degree of relatedness between them (indirect fitness) (Creel 1991, Hamilton 1964, Lucas, Creel, and Waser 1996).

The reason Hamilton's paper was such a profound development was that it explained seemingly altruistic behavior without invoking group selection. One proponent of group selection, Wynne-Edwards (1962) had suggested that a population of birds restrains its reproduction to avoid overexploitation of resources and to prevent group extinction. But David Lack's (1966) experiments had already shown that optimal clutch size, rather than maximum clutch size, was favored because a female who laid too many eggs fledged fewer chicks than when she laid the optimal number. G. C. Williams (1966) made the case that Lack's explanation of reproductive restraint was more consistent with basic Darwinian theory because restraint increased the individual mother's RS.

Darwin's natural selection was fundamentally about individuals competing for resources and turning them into more offspring than their rivals had (individual selection). Nonetheless, before Hamilton's seminal paper, one commonly heard group selection arguments like "subordinates defer to dominant individuals" or "the slowest animal gets eaten by the predator" because it is "for the good of the species." Even Darwin himself invoked group selection to explain behavior seen in warfare, saying that those who were bravest, risking death to save their group, would make the best warriors and that self-sacrificing behavior would evolve from their defeating other groups (Darwin 1871). On the other hand, he had no explanation for the existence of sterile castes within bees, wasps, and ants, but recognized that their inability to reproduce posed a potentially fatal blow to his theory of natural selection that depended on reproduction. Hamilton's formula provided an explanation: The sterile workers helped the queen make more sisters for them because given their haplo-diploid genetic system they were more closely related to their sisters ( $r=75\%$ ). This explanation highlighted that it is the gene, not the group or the individual, that is selected. Because genes behave as if they are selfish, individuals sometimes behave unselfishly (Dawkins 1976).

No one ever puzzled over why a mother was willing to risk her life to protect her offspring; they are her genes' vehicles into the future. Helping other kinds of kin can be favored for the same reason, even though the path to the next generation is less direct. Hamilton's rule tells us that even a mother will sometimes fail to help her offspring. Her interests and those of her offspring do not overlap perfectly because she shares only

50% of her genes with each one. She should weigh the gains of helping one offspring against the costs to her future offspring. In other words, we can expect parent-offspring conflict (Trivers 1974). A mother shares 50% of her genes with each of her two children, so she wants to help both equally. On the other hand, the child shares 50% of its genes with its full sib, which is only half of the 100% in its own genome. The child will prefer to get more help from mother than is in the mother's best interest or the interest of the other sib. The ages of individuals will also affect the calculus because a very young sib may not be capable of helping its older sib, while the elder may be able to help the younger.

It is inclusive fitness that determines a gene's success in succeeding populations, more precisely, the success of particular variants of the genes called alleles. There may be a brown or blue allele occupying the site of the gene coding for eye color. Often one allele is so successful that it spreads throughout the population and replaces all alternatives, at which point it is "fixed." By influencing the individual's behavior in ways that cause them to get passed on, genes affect their own representation in the gene pool. From the perspective of the allele, any behavior that helps make copies in others is advantageous, even if it causes its host to behave in an unselfish, even self-destructive way, so long as this leaves the greatest number of copies in the next generation. However, since genes in the individual's genome share their fate and will all die together, they tend to work well together; otherwise they are less likely to be passed on. For this reason, genes tend to promote a considerable degree of self-regarding behavior in individuals. Dawkins (1976) used the metaphor of rowers in a boat; they go nowhere if they do not paddle in concert and in the same direction.

How animals meet their energetic and nutritional requirements is the focus of optimal foraging theory (OFT). OFT assumes that individuals will seek to minimize costs and maximize benefits in their foraging behavior. That means they will usually not waste time or energy going after low-yield foods when higher-yield foods are available. They should be efficient in harvesting energy, and energy is used as a proxy for fitness. However, the individual always faces many constraints. The first constraint is the diet itself; committed carnivores cannot live on plant foods and herbivores on meat. Other important questions include the proper currency to use (kilocalories vs. protein) and the primary goal (maximize average rate of energy intake vs. minimize risk of shortfall) (Stephens and Krebs 1986). OFT models, like models of morphological evolution, are essentially engineering problems. With a given availability

TABLE 1.1. PAYOFF MATRIX FOR  
HAWK-DOVE GAME

	H	D
H	$(\text{prob. win} * \text{value of food}) +$ $(\text{prob. lose} * \text{cost of injury})$ $(0.5 * 50) + (0.5 * -100) =$ $25 - 50 = -25$	$(\text{prob. win} * \text{value of food})$ $(1 * 50) = 50$
D	$(\text{prob. win} * \text{value of food})$ $(0 * 50) = 0$	$(\text{prob. win} * \text{value of food}) +$ $(\text{prob. lose} * \text{cost of display})$ $(0.5) * (50 - 10) +$ $(0.5) * (-10) = 20 - 5 = 15$

NOTE: Payoffs shown are for the player listed in the row.

of food A and food B, each with a different nutritional value and a required search and handling time, how much of A vs. B should a forager take? But in life there are always competitors, and we need to consider their effect. Game theory is ideally suited for this.

Game theory treats individuals as different strategies, lets them play against each other in a game with specified payoffs for certain outcomes, and then sees which strategy wins. In the hawk-dove game, two strategies are employed with regard to a food source. A hawk is willing to fight and risk injury to get the food. A dove only displays, which goes on a while against another dove, but gives up quickly against a hawk. When dove meets dove, each gets the food half the time. If the value of the food is worth a gain of 50 points, the cost of a dove's long display is a loss of 10 points, and the cost of injury in a fight is a loss of 100 points, we can calculate the outcome (Table 1.1). When doves meet, each has a 50-50 chance of getting the food, so each receives an average of 25 minus the cost of display ( $25 - 10 = 15$ ). When a hawk meets a dove, hawk gets the food and 50 points. When two hawks meet, they each have the same chance of winning their fight and getting the food but also the same chance of being injured. That gives each an average of 25 for getting the food and -50 for getting injured; thus their average payoff is -25.

In each instance, the hawk beats the dove, which means hawks can always invade a population of doves and do very well (+50). However, when there are too many hawks, they do poorly (-25). Doves do better against each other (+15); even against a hawk, doves get 0, which is better than two hawks against each other (-25). This means that no pure strategy is stable. With the payoffs specified here, there will be a mixed

strategy with an equilibrium frequency of 0.58 hawk and 0.42 dove. This might consist of a population of 58% hawks and 42% doves, or individuals who play the hawk strategy 58% of the time and the dove strategy 42% of the time. The strategy that does best against other strategies and against itself, and therefore cannot be invaded by other strategies, is called an evolutionarily stable strategy (ESS) (Maynard Smith 1982). A strategy called “bourgeois,” in which one defends food if there first or if closest to the food, is an ESS because it avoids fights against other bourgeois by using a simple, salient rule—proximity or priority—yet does not cause one to relinquish food like a dove does against a hawk (Maynard Smith 1982).

Genetic selection leads to adaptive behavior across environments, but because optimal solutions vary in different environments and different circumstances (different games), so too does behavior. Although we do not know precisely how alleles at genetic loci translate into specific behaviors, we can assume behavioral strategies, or decision rules (which do not imply conscious decisions), have been favored by selection to create adaptive phenotypes. This assumption of a link between heritability and phenotype, known as the phenotypic gambit (Grafen 1984, Smith and Winterhalder 1992), allows us to make predictions about behavioral outcomes. That is, we expect to see individuals modify their behavior in ways that tend to enhance their inclusive fitness. Just as our bodies tell us to seek water to quench our thirst, so our emotions tell us to flee an enemy, recruit allies, or seek a mate. Behavioral ecologists tend to measure behavior directly to test predictions about fitness outcomes. For this reason, they have mostly studied simpler societies (Borgerhoff Mulder 1988a, Winterhalder and Smith 2000), not necessarily foragers, but at least natural fertility (non-contracepting) societies, where there is still a direct link between behavior and RS.

Evolutionary psychology focuses on the mind and the mechanisms that selection has favored to execute adaptive behavior (Hagen 2003). Such mechanisms are assumed to be universal across humans, by and large. This means humans anywhere are appropriate subjects. Much depends on the trait, however. Some traits, like fear of snakes or desire for sex, may have changed little over the last several million years, while others, such as tribal identification and loyalty or the value placed on fatness in potential partners, may have changed significantly even over the past few hundred years.

The Environment of Evolutionary Adaptedness (EEA) (Bowlby 1969) refers to the sum total of environments hominins have occupied since

they diverged from the ancestor of chimpanzees and bonobos 6–7 mya. It is within this time period that all hominin traits that were not present in the last common ancestor must have evolved. These are called derived traits; ancestral traits are those that were present in the last common ancestor. The EEA obviously includes a wide range of different environments, and different ones are relevant for different traits. The relevant environment for the evolution of our lungs dates back to the Devonian about 400 mya, for bipedalism to the end of the Miocene 6–7 mya, and for our peculiarly enlarged brain to about 2.5 mya. Lactose tolerance (the ability to digest milk in adults) dates to only about 7,000 years ago, and only in certain populations (Bersaglieri et al. 2004). Given that the relevant period varies with the trait in question, it makes more sense to think in terms of the Adaptively Relevant Environment (ARE) (Irons 1998).

Culture is obviously an important component of the human environment. When we talk about different environments, we are not simply contrasting desert with rain forest, but forager camp with inner-city neighborhood, societies where marriage is arranged by parents with those where people pick their own mates, and societies where food is scarce with societies in which food is guaranteed by a welfare program. Humans have created such varied cultural environments that it is often culture, rather than the physical habitat, that determines which behaviors enhance fitness. Ignoring culture can leave us without a clue (Laland, Odling-Smee, and Feldman 2000). However, there is something unsatisfying about an explanation of one cultural trait by reference to another without any attempt to explain how the first trait came about. For example, people often attribute sexual chastity in some cultures to adherence to religious doctrine. Religion may well be a proximate explanation, but why did a strict religious doctrine evolve in one population and not in another? Here, I attempt to see how much we can understand by reference to the habitat and mode of subsistence. Since among foragers each person must spend much time looking for and processing foods, it is easier to link behavior to the habitat and ecology.

The novel environments we have created can give rise to maladaptive behavior. Maladaptive does not mean bad, only fitness-reducing. This can occur when there has not been sufficient time for selection to produce the appropriate cognitive processing of the new environmental cues. Thus, individuals cannot calibrate the appropriate behavioral response that would maximize inclusive fitness (Richerson and Boyd 2005). It is important to appreciate that decision rules need not be conscious to work, and often it

would be inefficient if they were. Imagine a truck coming at you; it is best if you do not have to consciously deliberate and decide whether to jump out of the street. When past selection produced adaptive behavior that is no longer fitness-enhancing in the present, it is called a mismatch. To cite one example, a study found that wealthier men in Montreal did not have more children, though they did have more sexual partners (Perusse 1994). Before contraception, more sexual partners would likely have resulted in more children. Note that what was selected for in the past was desire for sexual partners, not desire for siring offspring. Still, selection never ceases. As long as some people do want to have some children someday (and most people do), reproductive competition continues.

Mismatch is less of an issue among foragers because they are still living in an environment without so many novel cues, and we can expect mostly adaptive behavior from them (Symons 1987, Tooby and Cosmides 1990). There is still much to learn from foragers like the Hadza. Because they live in an area our hominin ancestors inhabited for as long as they existed, where the flora and fauna have not changed much since the Pliocene began 5.3 mya, their ecology is relevant for a long period of human evolution. Mortality risks, energy expenditure, and growth, as we will see in Chapter 6, are probably not so different from what they were 10–20,000 or more years ago. Because the Hadza live outdoors, most of what they do is in full view, which means their behavior can be measured directly. The foods they acquire can be weighed and, with effort, traced to the person who consumes them. We can see what sort of help a parent can give that might impact survivorship or growth. There are few books that report on quantitative behavioral studies carried out in foraging societies (Hewlett 1991, Hill and Hurtado 1996, Howell 1979, Lee 1984). We now have a record of the Hadza going back to the late 1950s, with some continuity back to the 1930s and even a bit earlier. A book-length treatment of Hadza research is long overdue.

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