

Effects of Illness and Injury on Foraging Among the Yora and Shiwiari: Pathology Risk as Adaptive Problem

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He who has experienced it knows how cruel a companion sorrow is to the man
who has no beloved protectors.

--"The Wanderer" (Anglo Saxon poem)

I. Introduction

Current foraging models concerned with "risk analysis" focus on the ways in which the risk of temporal or spatial resource shortages (i.e. foraging risk), influences human subsistence behavior (e.g., Cashdan, 1985; Kaplan & Hill 1985a; Hames 1990). The impact of pathology risk on adaptations affecting social behavior has received less attention (see, however, Baksh & Johnson 1990; Cashdan 1990; Dettwyler 1991; Kaplan and Hill 1985a; Low 1988; Sugiyama 1996; Trinkaus 1983). Studies that do investigate pathology in foraging populations concentrate primarily on causes of mortality (e.g., Baksh & Johnson 1990; Hill & Hurtado 1996). Yet while both sublethal pathology and mortality risk exert selection pressure for adaptations designed to reduce the risk of their untimely occurrence, a focus on sublethal pathology draws our attention to the selection pressure on, and the design of, adaptations that ameliorate the negative effects of those pathologies that inevitably do occur.

The obvious fitness benefits of avoiding pathological conditions lead one to expect adaptations motivating measured caution in the presence of cues reliably linked with dangerous stimuli over the course of hominid evolution, as well as adaptations dedicated to identifying such cues. A rich body of research supports this hypothesis, indicating the existence of a suite of mechanisms dedicated to the problems of injury and illness. Some examples are cross-cultural human antipathy toward potentially dangerous or noxious stimuli and/or their cues (e.g., snakes, predators, vermin, heights, vomit, puss, feces, and secondary plant toxins [Marks 1987; Profet 1992; Rozin & Fallon 1987; Rozin *et al.* 1986]), pronounced fear of strangers during specific stages of childhood (Bowlby 1969), cognitive algorithms dedicated to reasoning about precautions and threats (Fiddick 1999; Rutherford *et al.* 1996), increased levels of polygynous mating associated with environments of increased pathogen risk (Low 1988), modifying the environment to reduce risk of snakebites (Baksh & Johnson 1990) and anxiety and depression, which have been analyzed as emotional adaptations designed to cope with both social and other sources of threat (Hagen 1999). All of these are strong indicators that humans have adaptations designed to reduce pathology risk. Still other potential risk-aversion adaptations have yet to be fully investigated, such as aversion to animals exhibiting other cues of toxicity or threat (e.g., bright coloring, loud buzzing or hissing, pincers or barbs, direct eye contact, bared teeth).

Obviously these mechanisms are not foolproof: Pathology occurs with considerable frequency across extant, recent prehistoric and earlier Homo populations (e.g., Bailey 1991; Baksh & Johnson 1990; Berger & Trinkaus 1995; Chagnon 1997; Hill & Hurtado 1996; Lambert 1993; Low 1988; Sugiyama, 1999; Trinkaus 1983; Truswell & Hansen 1976; Walker 1989). When it occurs, it poses a number of adaptive problems for its victim. Here we report the effects of physical pathology on the foraging productivity of the Yora and Shiwiar of Eastern Amazonia,

explore the adaptive problems for human social relations posed by pathology risk, and outline how adaptations designed to elicit behavior to mitigate these problems may operate.

II. Study populations

The Yora

The Yora are a hunter/horticulturalist group of Panoan-speaking people who live in the Amazonian lowlands of southeastern Peru near the Mishagua and Manu rivers. The Yora remained relatively isolated until their first peaceful contacts with outsiders in 1984. Within two years, approximately half the population died from introduced diseases (Hill & Kaplan 1989). By the time of this study in the summer of 1990 the population was rebounding and none of the pathology reported herein can be attributed to postcontact epidemics (Sugiyama & Chacon 1993). At that time the Yora were living in three locations: 66 full-time residents lived in the study village of Putaya, 37 persons lived in Cashpajali (as of 1986), and a third group lived in the mission town of Sepahua.

Methods

The authors used three methods to obtain quantitative data on Yora consumption patterns and subsistence activities during a 59 day observation period: scan sampling, focal person follows, and departure/return records. During the study period the population of Putaya varied between 56 and 71 people. From two to six instantaneous scan samples were run on each of 29 days, yielding a total of 100 scans and 6,448 individual behavioral observations (Sugiyama & Chacon 1993, Walker et al. 1998). Data on time allocated to subsistence activities and the relative frequency with which different foods were observed being eaten are based on these observations. Additional data were collected by recording the time that foragers left and returned to the village, the tools taken, and the type and weight of food acquired. The authors also accompanied the Yora on a number of foraging trips (focal person follows). These techniques were used to gather data on hunting and fishing returns for all village residents for 42 consecutive days. Foraging returns are based on this period. Significant illnesses and injuries and their effects on foraging were noted, as were minor injuries brought to the authors' attention throughout their stay in the village.

Yora Foraging

Initial reports suggested that the Yora relied almost entirely on hunting and gathering for their livelihood (Hill & Kaplan 1989). In 1990, however, horticultural products were a major part of their diet (53% of observed consumption) and 50.9% of subsistence activities were devoted to horticulture. None of the Yora cultigens we observed are particularly rich sources of protein. The main garden staple was sweet manioc; both boiled manioc and manioc beer were part of almost every meal and together comprised 21.6% of observed consumption. Plantains were also an important food and accounted for 9.7% of the foods consumed. Other cultigens consumed were sugar cane, jicama, maize, and sweet potatoes (Sugiyama & Chacon 1993; Walker et al. 1998).

Hunting and fishing provide the bulk of Yora dietary protein. Before contact, men hunted with bow and arrow, either stalking their prey or using hunting blinds. Since first contact, dogs have become prized hunting aids. Of the subsistence activity observed in Putaya, 14.3% was devoted to hunting, and game accounted for 16.5% of observed consumption. The primary prey in the Yora diet were collared peccary (*Tayassu tajacu*), followed by paca (*Agouti paca*), capybara (*Hydrochaeris hydrochaeris*), coati (*Nasua nasua*), agouti (*Dasyprocta* sp.), various primates, tamandua (*Tamandua tradactyla*), and acouchy (*Myoprocta* sp.). A small number of birds and squirrels (*Sciurus* sp.) were acquired as well. Large game was butchered at or near the kill site, and much of it packaged for distribution before returning to the village. Almost all the soft tissue of game animals was eaten, including the tough hide of peccary.

A variety of fish were taken with bow and arrow, cast net, or hook and line, accounting for 22.6% of observed consumption. Among the commonly caught fish were zungaro, carachama, sabado, bocachico, and freshwater stingray. The Yora also eat small quantities of turtle and lizard eggs. Although honey was not eaten during the study period, informants report that it is taken at other times of the year, along with seasonally available wild fruits and nuts. Papayas, chickens, and lemons are recently introduced foods not eaten before contact (Sugiyama & Chacon 1993; Walker et al. 1998).

Because meat is distributed throughout the village, it is usually consumed within a day of the kill, and storage of meat or fish is rare. Although distribution is not equal among households, secondary sharing of meat ensures that all households receive a portion of medium and large game, and even small game is shared widely between households. Fish from overnight fishing trips are also widely shared.

Shiwiar

The Shiwiar are a Jivaroan people who live in the southern Oriente (tropical forest) of Ecuador and northeastern Peru. Shiwiar, often considered a subgroup of the Achuar, number approximately 2,000 individuals occupying the Corrientes River drainage and its tributaries. Although the term Shiwiar also refers to a specific set of politically aligned villages in Ecuador, here we are using the broader cultural/historical usage. Unnavigable rivers form a barrier to colonial incursion into Shiwiar territory from Ecuador. Border conflict with Peru has limited contacts between Ecuadorian Shiwiar and colonists in the southeast since the 1940s. Prior to the 1970s, when Shiwiar began accepting missionary contact, they lived in scattered households linked by marriage ties and the influence of powerful individuals (Descola 1988). Since missionary contact, Shiwiar have made dirt airstrips around which houses now form loose clusters. Although missionary light aircraft provides some access to medical and other facilities outside Shiwiar territory, subsistence is still based on foraging and horticulture. The data presented here were gathered in the community of Alto Corrientes (population 67) during separate field trips by the authors in 1993 and 1994. Additional information from this area was collected by Sugiyama in 1993 from the Achuar/Quichua village of Conambo (population 181), and from 1994-1995 in the Shiwiar village of Kurintza (population 87).

Methods

Focal-person follows and departure/return records were used to record all returns from 133 hunts in Alto Corrientes over the course of 89 days during two field seasons. Injury and

illnesses that occurred during one of these periods were recorded, as were previous injuries and illnesses that could be documented based either on physical evidence or on the corroborated recollection of informants (Sugiyama 1999).

Shiwiar Foraging

Hunting and fishing provide the bulk of Shiwiar dietary protein (Descola 1988). Blowguns, muzzle-loading shotguns, and dogs are used in hunting. Animals such as agouti (*Dasyprocta* sp.) are also killed by hand when cornered in a log or burrow. The terrestrial game taken by Shiwiar is similar to that taken by Yora, the most important being collared peccary (*Tayassu tajacu*), tapir (*Tapirus terrestris*), paca (*Agouti paca*), agouti (*Dasyprocta* sp.), acouchy (*Myoprocta* sp.), deer (*Mazama americana*), and armadillo (*Dasypus* sp.). Although Shiwiar use dogs to pursue animals such as collared peccary (*Tayassu tajacu*), agouti (*Dasyprocta* sp.), and paca (*Agouti paca*), they hunt without dogs relatively more often than do the Yora (Sugiyama 1998). This, combined with a mixed strategy of blowgun and shotgun use, yields a greater percentage of primates (primarily wooley, [*Lagothrix lagothricha*], howler [*Alouatta* sp.], and capuchin [*Cebus*, sp.] monkeys), birds, and small game (e.g., squirrels (*Sciurus* sp.) in the Shiwiar than in the Yora diet (Sugiyama 1998).

Fishing is done either with hooks and line or with fish poisons, baskets, spears, and by hand. In the rainy season the bulk of fish are taken by hooks and line. During the transition to the dry season, emphasis on fishing gradually increases as the rivers become shallow and fishing with one of two cultivated poisons, *timiu* (*barbasco*) or *masu*, becomes increasingly efficient. These dry-season fish poisonings are often village-wide events and can produce a large surplus. Fish and meat not eaten on the day of capture are regularly preserved by smoking them over a fire (Descola 1988; Sugiyama 1998). Average daily per capita protein consumption from fish is not included in the present analysis because complete records of fishing returns were impossible to gather. Nevertheless, game accounts for the majority of protein consumed during the rainy season (when foraging data presented here were collected).

Descola (1988) notes that almost no meat was shared between Achuar households during the 1970s. Even in current, more concentrated Shiwiar communities, smaller game is usually not shared beyond the hunter's household. Medium-size and larger game is shared, but even tapir, the largest game animal taken, is only shared amongst a subset of households in some villages. Several factors may limit meat sharing among the Shiwiar. Smoking meat over the fire provides a storage system that reduces day-to-day variance in its availability, thus reducing one benefit of sharing (Cashdan 1985). Similarly, strategic use of blowguns, hunting dogs, and shotguns means that unsuccessful hunting trips are relatively infrequent, further reducing the risk of temporary shortfalls and the benefit of foraging risk reduction via sharing (Kaplan & Hill 1985; Winterhalder 1990). While Shiwiar failed to acquire any game on only 27% of 133 hunts, Yora failed to acquire any game on 45% of 47 hunts ($p < .013$). Shiwiar do experience high absolute variance in hunting returns between trips—sometimes they return with nothing, other times with a squirrel, and still other times with a 115 kg tapir. Nevertheless, in comparison with the Yora, Shiwiar hunters experience relatively few days when they go hunting and return with no game whatsoever, and smoking the game can effectively preserve it for several weeks.

II. Pathology Risk Among Yora and Shiwiar

Yora and Shiwiar engage in many types of behavior found among hunter-gatherers known ethnographically and archaeologically: they live in small kin-based communities in which some foods are shared; they rely on hunting and fishing for most of their dietary fat and protein; they have little easy access to Western medicine; and they depend on relatively simple technology for their livelihood. In these and other ways their living conditions mirror important general features of the environments in which hominids evolved. The hazards of such a life are manifold and come from a variety of sources:

- Lacerations, scrapes, and puncture wounds are common and pose the threat of disability due to serious infections (Baksh & Johnson 1990; Bailey 1991; Sugiyama 1996, 1999).
- Fractures resulting from accidental falls or falling timber cause periods of foraging inactivity and can cause infection which may lead to the loss of limbs (Baksh & Johnson 1990; Chagnon, personal communication; Sugiyama 1996).
- Injuries inflicted by prey are a hazard for hunters. Among the Ache, for example, coati are typically killed by hand and bites are common (Hill & Hurtado 1996). During our study period, one Yora man was bitten on the hand by a coati and another was bitten in the leg by a paca agouti.
- Venomous fauna are ubiquitous. Snake bites can cause tissue necrosis leading to long-term disability, loss of limbs, and death (Baksh & Johnson 1990; Chagnon 1997; Hill & Hurtado 1996; Sugiyama 1999). In a survey of injury and illness among the Shiwiar, thirteen out of twenty-four adults surveyed reported being bitten by a venomous snake at least once. One man reported six months of disability from a snakebite that became infected with gangrene: another man's foot was permanently disfigured (Sugiyama 1999). Yora report that fresh-water stingrays may inflict injuries that prevent foraging for up to a week. The venom from scorpions, wasps, spiders and caterpillars can also be disabling for shorter periods. Some insects lay their eggs beneath the skin; this, as well as insect bites in general, carry the risk of serious and sometimes lethal infections (e.g. Chagnon 1997; Hill & Hurtado 1996; Sugiyama 1996, 1999).
- Yora report injuries and deaths at the hands of Machiguenga enemies. Shiwiar are wounded in feuds by means of gunshot, lance, and booby traps; while fighting they sustain injuries ranging from minor contusions to broken bones (Sugiyama 1999). In club fights, Yanomamö, Machiguenga, and Ache suffer split scalps, fractured skulls, and concussions (Baksh & Johnson 1990; Chagnon 1979b; Hill & Hurtado 1996). Archaeological evidence shows that interpersonal violence was the source of sublethal trauma in prehistoric foraging societies as well (e.g., Lambert 1993; Walker 1989).
- A variety of pathogens and illnesses (e.g., giardia, amoebas, malaria, chickenpox, stroke, tuberculosis, arthritis) can render individuals incapable of foraging for periods ranging from days to years (Sugiyama 1999).

Significant Injuries During the Study Period

Two infections stemming from minor injuries had appreciable effects on foraging during our Yora fieldwork. One man suffered a puncture wound on the medial aspect of his elbow that became infected some weeks prior to the study period. The infection spread throughout his arm and he did no hunting or fishing for the entire 59 day study period, although a year earlier he was one of the most active hunters in the village (Kim Fowler, Summer Institute of Linguistics, personal communication, 1990). For the analysis below we used the conservative figure of 36

days (the time between our arrival and the man's first attempt at garden work) to calculate foraging days he lost due to injury. However, it is clear that he refrained from foraging for a longer period. Without antibiotics provided by a visiting missionary he might have lost the arm or died, consequences not unknown in this and similar societies.¹

Another man suffered a puncture wound at the base of his thumb that became infected eight days before we left the village and prevented him from hunting for at least that length of time. We do not know for how much longer he was debilitated by the infection. Undoubtedly, more cuts, puncture wounds, and insect bites occurred than were observed--injuries too common to have been brought to our attention that nevertheless carry significant risk of infection (Baksh & Johnson 1990; Chagnon 1997; Hill & Hurtado 1996; Sugiyama 1999).

Although this analysis concentrates on foraging activities--predominantly but not exclusively male activities among the Yora and Shiwiar--females are, obviously, not immune to sickness and injury. For example, one Yora woman severed her Achilles tendon with a machete prior to the authors' arrival. Although the wound healed, the tendon remained severed and she had a severe limp. She must have been incapacitated for an extended time after she injured herself. When a woman incurs a debilitating injury, someone must make up for her lost productivity or family subsistence will suffer, particularly if she is disabled for a prolonged period. A child's illness may also adversely impact family subsistence. During a whooping cough epidemic among the Shiwiar witnessed by Sugiyama, one woman had to provide constant care for her infant and could do no gardening or foraging for over three weeks. Her husband took over the gardening and the care of their other children during this period, which he claimed prevented him from going hunting.²

Costs of Injury to Yora Foraging

Repeated periods of injury or illness can have adverse consequences for growth, life-span, cognitive function and fertility. Periods of poor maternal health may also have negative effects on unborn or nursing offspring (e.g., Allen 1984; Buzina *et al.* 1989; Wing & Brown 1980). Such cumulative effects are difficult to assess given the data at hand. Below we consider only the relatively short-term problem of pathology effects on subsistence from foraging. Because long-term negative effects are associated with periods of physical pathology, however, we expect selection to have favored traits that not only enhance ability to survive such periods, but to do so with as little long-term fitness costs as possible.

Within a wide range of values, lowered nutritional intake--particularly of dietary protein and/or fat--entails definite fitness costs. Nutritional decrements have been associated with stunted growth, increased morbidity and mortality, shorter reproductive lifespan, delay of menarche and onset of puberty, fewer offspring, a lower proportion of live births, lower infant survival and body weight, and increased juvenile mortality in a variety of primates (including humans) and other mammals (e.g., Allen 1984; Altmann 1991; Frisch & McArthur 1974; Green *et al.* 1986; Hill & Hurtado 1996; Kohrs *et al.* 1976; Manocha & Long 1977; Prentice *et al.* 1987; Riley *et al.* 1993; Schwartz *et al.* 1988). Although we use here the United States Recommended Dietary Allowance (USRDA) of protein as a convenient benchmark for comparison, it should not be taken as an absolute criterion above or below which nutritional variance is insignificant.

An estimate of the cost of injuries in terms of lost foraging returns was calculated in the following manner. The number of days in the observation period that each independent hunter was present and not injured was divided by the number of times he went hunting. The mean of

the resulting values for all independent hunters yielded the average period between hunts for these individuals. The number of days potentially lost to foraging include only those periods for which the duration of an injury or illness was longer than the average period between hunts, or for which a foraging trip was aborted due to injury. This figure was divided by the average period between hunts to arrive at an estimate of foraging days lost to injury. This estimate was multiplied by the average returns per hunt in the village (i.e., total returns in the village divided by total number of hunts observed during the study period) to get an estimate of lost hunting returns. The same calculations were then made for fishing. Visits between villages caused village size to vary throughout the study period; these fluctuations were taken into account and visitors were included as both foragers and consumers for the analysis.³ One man foraged infrequently and complained repeatedly of pain that limited his movement, but because the cause of the discomfort and its effect upon foraging could not be definitively established, we did not count the time he did not forage as pathology-related. He was however, included among active hunters.⁴ Young men who fished independently and consistently but did not hunt independently or consistently were calculated in fishing but not in hunting data.

Men who hunted independently were clearly prevented from foraging due to injuries on at least 47 man-days, which represents approximately 10.6% of all man-days observed for independent hunters. On average, individual hunters hunted once every 5.27 days with average returns of 7.65 kg per hunt. The average time between hunts for individual hunters ranged between 2.6 and 7 days. On average, those central to fishing productivity went fishing once every 4.85 days with average returns of 3.35 kg per trip. An estimated total of 8.92 hunts and 9.69 fishing trips were foregone due to pathologies that we can confidently determine, but again this is a conservative estimate.

Figure 17-1 presents average per capita Yora protein consumption from meat and fish.⁵ The horizontal axis indicates the USRDA of protein for people of the Yora's stature. Bar 1 presents observed average per capita protein consumption during the study period. Even though injuries interfered with some foraging, protein consumption during this time remained above the USRDA (48.14 g). Bar 2 presents estimated per capita protein consumption had there been no injuries during the study period (58.55 g) to give an idea of the cost of observed injuries--that is, an estimate of what returns would have been had no hunters been injured and were there no change in average rate of foraging. Thus, we estimate an 18% reduction in average per capita protein consumption due to pathologies based on the assumption that observed injuries affected a statistically average hunter.

However, hunting frequency and returns vary across hunters. Kaplan and Hill (1985a) suggest that members of Ache foraging bands might extend greater than average solicitude to the best hunters (and their dependents) when they are injured because group members are loath to lose this important source of meat. If injury prevented the best Yora hunter from foraging, average time between successful hunts in the village would go from an estimated .77 days to 2.8 days. More importantly, without the best hunter, estimated average per capita protein consumption would drop 37%, from 58.55 g to 36.77 g (Bar 3)--that is, from well above to below the USRDA of protein for people of this weight and stature. Other group members certainly do benefit from the best hunter's subsistence contributions and will suffer nutritional declines if he is injured.

The best hunter and his dependents will also suffer such declines when injured. One way to buffer this risk may be to maintain a sufficient number of sharing partners to provide aid during times of disability. Analysis shows that, indeed, protein intake diminishes a further 7% if

the village has even one less hunter of average abilities (and his dependents) while the best hunter is injured (Bar 4, 32.71 g).⁶

One could ask whether the pattern of pathology effects on subsistence described above is an idiosyncratic feature of a short period of time in Yora history or is widespread among similar societies. A study of the Shiwiar documenting significant lifetime injuries and illnesses suggests the latter conclusion: minor injuries are ubiquitous and significant injury and illness are not uncommon within this population (Sugiyama, 1999). Reports of similar injury and disability among other groups further support this hypothesis (e.g., Baily 1991; Baksh & Johnson 1990; Hill & Hurtado 1996; Truswell & Hansen 1976). In the following section, we examine Shiwiar foraging data to see whether effects of pathology on Shiwiar subsistence would exhibit a pattern similar to that found among the Yora.

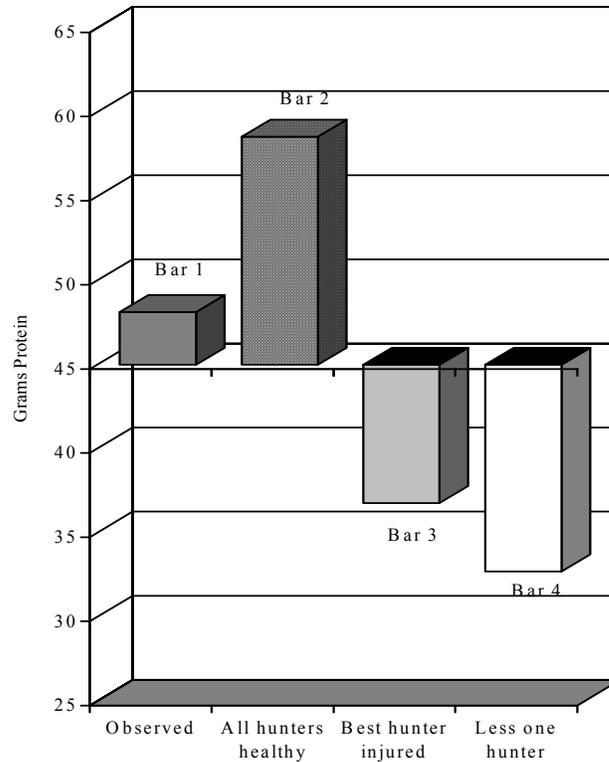


Figure 17-1: Yora Daily Per Capita Protein Intake from Game and Fish

Costs of Injury To Shiwiar Hunting

Figure 2 (Bar 2) presents data on Shiwiar average daily per capita protein intake from game from two periods (42 and 47 days, respectively) in which hunting returns were recorded for

contiguous days. We then asked the hypothetical question, What would happen if the Shiwiar experienced the same number of injuries experienced by the Yora over a similar period of time?⁷ Calculations and estimates were conducted in the same manner as with Yora data.

Figure 17-2 indicates that when all hunters are active, returns from game alone are well over minimum requirements for a population of this stature (Bar 2, 56 g). Injuries to a hunter of average ability would reduce estimated protein consumption from meat alone by 18%, to just over USRDA minimum requirements (Bar 1, 46 g). If the best hunter were to be injured, however, hunting returns would drop 32%, to below minimum requirements (Bar 3, 38 g). And if a hunter of average ability were to leave the group (taking his family with him) while the best hunter were injured, there would be a further nutritional decrement of 4% (Bar 4, 36 g). For at least one other Amazonian group, then, a similar pattern obtains to that found among the Yora.⁸ As one might expect in a group with less foraging risk, more food storage, less food sharing and a tradition of scattered settlement, the effect of losing a village member appears to be slightly less detrimental for the Shiwiar than for the Yora.

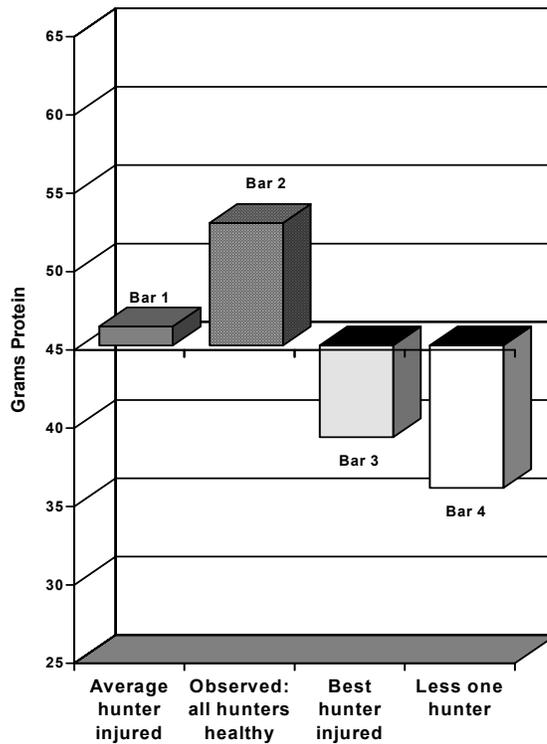


Figure 17-2: Shiwiar Per Capita Protein Intake from Game

V. The adaptive problem posed by pathology risk

For a given individual, disability due to pathology may last much longer than periods of "bad luck" in foraging. Among the Yora, one hunter did not hunt for eight weeks, more than a

month of which was unambiguously due to injury. Baksh and Johnson (1990) estimate that up to 10% of male Machiguenga lose from one to four weeks each year due to cuts from *cana brava* (a plant resembling bamboo with thorns at the joints) alone. Compared with day-to-day variance in hunting success, the effects of pathology on foraging returns can be quite large. Kaplan et al. (1990) estimate that without food sharing a foraging Ache family (in which 67% of calories consumed are from game) would fail to acquire 50% of their necessary calories three weeks in a row due to bad luck only once in seventeen years. In the absence of injury, illness, or natural disaster (e.g., catastrophic climatic fluctuations), then, five weeks of unsuccessful hunting will be rare and three to six months of unsuccessful hunting (as seen in the Shiwiar cases of snakebite) will be virtually unknown. Further, unlike seasonal variation and some types of spatial variation in resources, illness and injury are, for a given individual and within a wide range of parameters, temporally unpredictable. More importantly, unlike those who are experiencing a temporary slump in foraging returns, those who are severely ill or injured are physically unable to defend themselves and their interests.

One of the critical adaptive problems pathology risk presents, then, is the insurance of an adequate source of support and protection should disability occur. Two complementary explanations have been advanced to explain the evolution of “altruism”—that is, adaptations motivating individuals to provide fitness benefits to others at a fitness cost to themselves: kin selection and reciprocal altruism. A consideration of these explanations highlights the problems that adaptations designed to buffer pathology risk must effectively solve.

Kin Selection

Kin selection theory posits that adaptations designed to provide fitness benefits to others at a cost to their bearers could evolve when the cost to the “altruist” is less than the benefit to the recipient discounted by the probability that they share genes in common (Hamilton 1964). In ancestral populations, however, such factors as migration, high mortality rates, abduction of females, and residence patterns associated with mating would have led to situations in which some individuals lived among people to whom (in comparison to the average degree of relatedness between the other group members) they were only distantly related (e.g., Chagnon 1975, 1979a, 1979b). Over the course of human evolution this circumstance would have been a recurrent problem for some individuals. A trait that, on average, buffers pathology risk for individuals who lack close, coresident consanguineal kin should therefore spread relative to one that buffers pathology only for those who do not lack such kin.

The decision to aid a disabled relative is further complicated by the fact that the probability that aid to an injured relative will yield inclusive fitness benefits to their provider is increasingly diminished in relation to the likelihood that the injured individual will not recover. This, in turn, increases the relative potential gain from investing in others instead of the injured party. As death of the injured individual becomes increasingly certain, withdrawal and reallocation of aid may become the prudent choice for the potential benefactor, as both evolutionary logic and ethnographic evidence bear out (e.g., Freuchen 1961; Hill & Hurtado 1996; Tooby & Cosmides 1996).

Reciprocal altruism

Reciprocal altruism theory posits that traits designed to provide benefits to others at a fitness cost to their bearers can evolve when there is sufficient probability that compensatory benefits will be received (Trivers 1971). Trivers (1971) suggests that the potential benefit from extending aid increases as the need of the recipient increases, because expected compensation for providing the aid will be higher. Herein lies the problem posed by pathology risk: as the need of the injured party increases past critical levels, the probability that the disabled person will live to provide compensatory benefits to the altruist diminishes, and with it the potential benefit of extending aid to him or her.

Further, the ability to recognize and punish cheaters (i.e., exchange partners who do not reciprocate) or exclude them from future exchanges is a necessary feature for the evolution of adaptations arising via the pathway of reciprocal altruism (Axelrod & Hamilton 1981; Trivers 1971; Cosmides & Tooby 1992). Yet disabled individuals lack the physical formidability necessary to compel past exchange partners to reciprocate, and detection of cheaters at the time of injury is of no value to the injured party if he or she dies. Moreover, individuals who are sensitive to current probable payoffs have incentive to renege on exchange commitments to a disabled exchange partner when they are most in need: there is no profit to be gained by investing in someone who cannot reciprocate now and is unlikely to be able to do so in the future (Tooby & Cosmides 1996). Withholding aid further decreases the likelihood that the injured party will recover, making him or her an even worse investment. Although an individual who refused to recompense his disabled exchange partner might face negative repercussions should the injured party recover (i.e., reprisals, loss of reputation, loss of other exchange partners), what constitutes adequate aid in these circumstances can not be well specified: an individual could simply proffer nominal aid—sufficient to dampen possible future reprisals but insufficient to sustain the disabled party until he or she recovers. Adaptations arising from reciprocal altruism, particularly the subset based on contingent social exchange, therefore appear to be problematic solutions to the problem of pathology risk. In a world where only the logic of kin selection and reciprocal altruism operate, there comes a point at which abandonment of a sick or injured individual becomes the rational choice for potential benefactors. Traits motivating individuals to behave in a way that shifts this critical decision point, causing potential benefactors to provide aid at relatively greater levels of pathology, should be selected for as long as such aid effectively resulted in survival in some proportion of cases.

Pathology risk thus poses three major adaptive problems in the human social arena: (1) how to subvert the short-term cost-benefit psychology of potential aid sources such that they are more rather than less likely to invest, even though, all else equal, the current probable payoff of doing so is low relative to other potential uses of the investment; (2) how to stimulate this investment at a time when one lacks the ability to defend one's own interests; and (3) how to do so in a way that circumvents the temporally unpredictable nature of pathological events.

Despite these obstacles, individuals do receive care adequate to survive extended periods of disabling pathology, a phenomenon that arose at least by the time of *Homo Neandertalensis* (Trinkaus 1983; Dettwyler 1991).⁹ We suggest that a suite of adaptations designed to solve these problems has arisen.

The Best Hunter Solves the Pathology Risk Problem

Our data suggest that when an average Yora or Shiwiari hunter suffers significant injury, a buffer exists such that, although there is a notable nutritional decline, protein consumption

remains adequate. If the best Yora hunter is injured, however, nutritional declines are dramatic and a high-quality source of nutrition is jeopardized. This effect is similar but less pronounced among the Shiwiari. If the best hunter becomes temporarily disabled and group size is low, then the best hunter and his family (as well as other band members with whom he shares meat) will suffer additional nutritional decrement. During such times, the best hunter may benefit from living amongst larger groups of people even though sharing with them may be costly during times when he and his fellow foragers are healthy (see, e.g. Blurton Jones 1984, 1987; Hawkes 1990, 1991; Kaplan & Hill 1985a, 1985b). If the requisite aid can be dispersed amongst a larger group, then the per capita cost of providing the aid is also reduced. Because periods of incapacitation due to disability regularly last much longer than slumps in foraging due to day-to-day variation in returns, estimations of optimal group size or sharing networks based on the latter may well underestimate the degree of risk that must be buffered by these groups, thereby resulting in observations of larger group sizes than predicted by these models (for a review of other such factors see Sugiyama 1996).

These findings suggest that the risk of relatively infrequent periods of long-lasting disability and debilitation is likely to have constituted a selection pressure affecting individual decision-making psychology about the desired size of social groups and social networks. Specifically, pathology risk may select for adaptations motivating their bearers to live in social groups both large enough and motivated enough to provide aid effectively in times of need. The apparent link between depression and lack of sufficient social support seen in modern contexts may be a manifestation of one part of this psychological complex (Hagen 1995). The critical question remains unanswered, however: How are potential sources of aid motivated to become reliable sources of aid when one suffers severe physical pathology?

As noted above, Kaplan and Hill (1985a) have suggested that among the Ache, good hunters may receive preferential treatment when they are sick or injured because other band members benefit from maintaining access to the meat these hunters provide. Because pathology risk is temporally unpredictable, for good hunters to garner this solicitude they would have to provide meat to others consistently, or risk becoming incapacitated at a time when interest in their continued presence in the band has waned. Indeed, good hunters may not only share game with more individuals than would otherwise be optimal, but may consistently provide more meat to others than they receive in return (e.g., Blurton Jones 1984, 1987; Hawkes 1990; Kaplan & Hill 1985a, 1985b, 1990; Sugiyama 1996). If lack of aid could spell death to the injured party (as seen among other primates) and increased morbidity and mortality risk for any dependents (Chagnon 1997; Hill & Hurtado 1996), and if widespread meat sharing buffers this risk, then adaptations designed to produce consistent widespread sharing may be, within wide parameters, largely impervious to the day-to-day costs of doing so, even if they never yield these benefits during the lifetime of any given individual providing them.

Consistent asymmetric provisioning of meat also provides a strong cue to recipients that, should the hunter become ill or injured, the flow of such benefits will resume if and when he recovers. In other words, because the benefits provided are uncoupled from the psychological framework of social exchange by being made available in the absence of associated cues that reciprocity is expected or desired, then others may treat receipt of the benefits as a consistent byproduct of living with the good hunter, for which they pay no direct costs. Those who acquire such benefits should therefore be highly motivated to retain access to them.

For the hypothesized system to work, not only must the absolute value of the best hunter's contributions be sufficiently high that the loss of these benefits constitutes a significant

fitness cost to the recipients, but the cost of acquiring the same benefits elsewhere must also be sufficiently high. As Tooby and Cosmides (1996) point out, one feature of an optimal circumstance is reached when there are no readily available alternative sources for replacing the benefits—that is, when they are irreplaceable. When this is the case, the fitness of the group members receiving the benefits is inextricably tied to the ability of the provider to deliver them, and they should therefore be willing to pay high short-term costs to retain access to the source of these benefits. Just how a system that bypasses the pathways of kin selection and reciprocal altruism could evolve has been discussed in detail by Tooby and Cosmides (1996). With regard to the data at hand, however, it is sufficient to note that among the Yora, injury to the best hunters does have a comparatively large adverse subsistence impact. To replace the benefits provided by the best hunter in these groups would entail large time and energy costs associated with resettlement, intervillage politics, or increased foraging by other band members. Among the Shiwiari, the relative benefits provided by the best hunter appear to be fewer, and the apparent costs of losing the best hunter may be further buffered by returns from fishing, particularly in the dry season. In this case aid to injured individuals may be provided by fewer individuals, or predicated upon an individual's conferral of other important benefits to others (see below).

An apparent problem with the preceding analysis is that it leaves open a common goods problem: even though individual social group members may have an intense interest in retaining access to a highly productive hunter, if one individual is willing to pay the costs necessary to effect recovery, then others might profitably refrain from doing so. If all use this reasoning, then no one will provide aid and the injured person will die. While this may be the reason why extended aid to injured conspecifics is rare in the animal world, we think humans solve the problem in the following way. When consistent asymmetric provisioning yields benefits that are difficult to replace, the individual providing them increases others' interest in his or her continued ability to provide these benefits above what they would otherwise be (due, for example, to kin selection). Depending on their own abilities, social networks, and degree of relatedness to the hunter, some of the best hunter's potential benefactors will benefit more by his provisioning than others, and will have more to lose if he dies. Because individuals with the most interest in the best hunter's survival are not themselves injured, they can apply pressure to others to provide aid, thereby shifting the cost-benefit balance of others for doing so. As Tooby and Cosmides (1988) illustrate in an analysis of enforcement problems inherent in the evolution of coalitional aggression, if backed by sufficient credible threat, those who stand to gain most may even get others to incur all the costs of collective action, as well as any costs of enforcement. Humans appear to have cognitive adaptations specifically designed to reason about threats and can compute second-order effects of behavior such as triangular awareness (Rutherford *et al.*; Brown 1991). All else equal, differential targeting of benefits to those most able to influence the behavior of others may be expected.

Irreplaceable Benefits and Social Niche Differentiation

Although this discussion arises from a consideration of the effects of pathology on hunters and their contributions to others' fitness, the same adaptive logic should hold for individuals who consistently provide other costly-to-replace benefits to their social group. While there may not be as many positions of status in egalitarian bands as there are people to fill them, there certainly are other social roles besides being a good hunter that provide difficult-to-replace benefits, and we therefore expect a proliferation of social niche differentiation as circumstances

allow. These roles are not fixed but, rather, dependent on opportunity and circumstance. In fact, when differences between the hunting returns of the best and other hunters are low, when returns from foraging uniformly exceed needs by large margins, when game is shared because it has begun to have diminishing marginal returns for the hunter and his family--i.e., when sharing appears to be due to "tolerated theft" (Blurton Jones 1984)--or when food storage techniques allow individuals to survive long periods of disability without subsistence aid, then being a more successful hunter may not provide irreplaceable benefits or yield higher-than-average solicitude (although subsets of the social group may be highly dependent on a given hunter and therefore motivated to aid him).

Clearly, then, an adaptation specifying that each individual attempt to become the best hunter in his or her group will not solve the pathology risk problem. The solution is dependent upon the evolution of a number of adaptations, including mechanisms that (1) evaluate the abilities of their bearers, (2) identify the important needs of others (or have knowledge of recurrent needs), (3) compare their bearers' ability to provide those needs with the abilities of others, (4) identify the needs that their bearers are most qualified to provide and are not well provided by others, and then (5) cultivate abilities in this area such that they confer needed benefits in a manner that (6) convincingly signals to others that provision of the benefit is a consistent product of living with their provider. Such a system requires the evolution of complementary adaptations designed to recognize important benefits, identify individuals who consistently provide these benefits at no apparent cost to the recipient, and motivate behavior that preserves access to these benefits (for example, by extending aid to individuals who provide uniquely valuable benefits--see Tooby & Cosmides 1996 for psychological mechanisms that appear to operate in this fashion).

Further, because the functional payoff for a behavioral pathway expected to confer unique benefits may never be needed, or may be needed only rarely, there exists a degree of uncertainty that a given niche will indeed provide the benefits, to others and eventually to self, that it is ultimately designed to deliver. For solution, this problem requires a complementary, contingent set of mechanisms: one activated in the specialist condition, designed to assess an interim system of reliable cues confirming that a given behavioral path is indeed providing uniquely valuable benefits, and another activated in the beneficiary condition, designed to provide such signals to uniquely valuable individuals.¹⁰ One signal of the degree to which an individual fills a beneficial social niche for which we might find anthropological evidence is the prestige accorded to the individual who fills it, or the esteem in which he or she is held. Significantly, in a cross-cultural analysis of two social niches that convey special benefits to others (oratory skill and specialized craft production), prestige does indeed appear to be associated with unique ability (Sugiyama & Scalise Sugiyama 1997).

Shiwiari society provides a case in point, exhibiting both the cultivation of social niche differentiation and the benefits that derive from it. For example, juunt (elders or, literally, big men), are the central figures around which settlement, politics, and warfare are organized. Their qualities of leadership, bravery, and strategic decisionmaking make them important individuals throughout society, particularly to men allied with them (Descola 1988; Hendricks 1993; Patton, this volume). Another important role in Shiwiari society is that of the shaman. The most powerful shamans are also juunt, and while feared and hated by their enemies, they are respected and essential parts of their alliance groups and they spend long years in training and practice to attain this role. Notably, a critical benefit they provide is directly related to pathology risk: the curing of sick and injured people. When they cannot or will not fulfill this role, their value is nullified

and interest in their continued well-being largely evaporates (Sugiyama, unpublished recordings of a Shiwiar political meeting). When they are successful and aid their social allies without hesitation, their lives and interests are well guarded. For instance, a locally powerful shaman in an alliance of 7 Shiwiar villages promised, at what is considered a potentially life-threatening cost to himself, to focus his activities on curing and to forego retaliatory attacks against other shamans (which were interpreted as having unintended negative repercussions for some members of the alliance). He has since been provided an armed escort to protect him from ambush whenever he leaves the vicinity of his village. As of 1998 this security service had been in effect for three years. Conversely, another local shaman who was less generous with his services felt compelled to leave his village of residence in haste when it was made clear that he would receive no support if raiders came to kill him.

Other Shiwiar men are well known for the exceptional quality of the blowguns they make, and they derive trade and positive social connections from this specialized skill. Since accepting contact with missionaries, the roles of local health promoter and preacher have been cultivated by individuals with certain skills. Finally, some people are valuable not for any particular skill but, rather, because they are recognized as being particularly likely to aid their fellows during communal work parties, to share what game they have, or to support their fellows in conflicts (Sugiyama 1996). One might think of this service as something akin to the loyal deputy--not skilled in a particular craft, but eminently dependable and willing to contribute to the interests of others in their social group.

If an individual's success at filling a uniquely valuable role is contingent on there being no one else to readily fill it, attempts by more than one individual to cultivate an occupied niche may be expected to provoke resentment, resistance, even conflict (Tooby & Cosmides 1996). The behavior observed in the study populations suggests that this is indeed the case. Shamans, for example, wage spiritual warfare against each other in battles for status that are a chronic feature of Jivaroan life. Such competition is not limited to the role of shaman, however. In the Achuar/Quichua village of Conambo, for example, intense social tension developed when an opportunity to train as the village health promoter arose. Two people had the requisite skills to take the course, and conflict arose over who should be selected. The fact that one person was Quichua and the other Achuar made matters worse because village residents saw the issue in terms of their own vested interests, which broke down largely along ethnic lines: the Quichua thought an Achuar promoter would bias distribution of aid toward the Achuar, while the Achuar thought a Quichua promoter would bias the distribution of benefits toward the Quichua.¹¹

Conclusions

Whatever the faults of the foregoing analysis, we believe we have identified an important intersection of subsistence and social phenomena: (1) group sizes may be larger than what foraging theory predicts; (2) the best hunters often hunt far more than it "pays" in any of the short-term "currencies" that have previously been examined; (3) debilitating illness and injury are a ubiquitous feature of life among hunting peoples, including the populations studied; (4) subsistence costs of injury and illness, and the fitness costs they entail, are substantial; (5) when the contribution of the best hunter is subtracted from the net take of the groups studied (as it would be whenever he is injured), per capita protein intake drops below the minimum USRDA; and (6) when group size includes one less hunter and his dependents, protein intake drops further. The injury data presented here suggest that temporary disability has been a sufficiently

frequent and formidable problem to cause the selection of psychological adaptations dedicated to its solution, and that a suite of these adaptations will be dedicated to solving the problems for social relations that pathology risk entails. The universal striving among people of all ranks to acquire a distinct, acknowledged, and irreplaceable social role may have its roots in the continuous risk that illness and injury posed throughout the lives of our foraging ancestors. Among the Yora, excellence at hunting coupled with consistent widespread sharing of game coincide with the pattern of behavior expected to buffer that risk.

Summary

1. Both severe or repeated pathology and lower protein and fat intake are associated with a variety of indicators of lowered fitness. Potentially severe pathologies are ubiquitous in extant, recent prehistoric, and early Homo foraging populations. The nutritional costs of pathologies observed for the Yora and estimated for the Shiwiari are substantial.
2. Pathology risk formed a substantial adaptive problem. One part of this problem was how to ensure high levels of aid in times of disability. Traits which motivated their bearers to behave in ways that solved this problem are expected to have conferred significant fitness benefits upon their bearers. However, as the probability that a sick or injured person will die increases, so too does the probability that any investment in him or her will be lost, making that individual an increasingly bad investment for potential benefactors.
3. This problem may be solved to the extent that individuals provide honest signals that (1) increase the perceived probability that by providing aid potential benefactors will reap future fitness benefits, (2) increase the expected probable size of those future fitness benefits well in excess of any costs of providing extended aid, and (3) reduce the expected cost that each potential benefactor must incur to reap those benefits.
4. Debilitating pathology occurs in a temporally unpredictable manner. Behavior generated by adaptations designed to elicit aid during periods of disability must therefore be engaged in consistently, even when disability aid is not currently needed.
5. Recipients of valuable benefits should be interested in retaining access to them, particularly when they cannot be obtained from another source. An individual can thus increase the aid he/she garners when ill/injured by consistently providing valuable and costly-to-replace benefits to others when able to do so.
6. Behavior of the best hunters among the study groups appears consistent with the criteria for solving the pathology risk problem outlined above:
 - a) The fitness benefits provided to others by the best hunters in the study populations, particularly among the Yora, are large and by their very magnitude difficult to replace.
 - b) Consistent asymmetric provisioning by the best hunters provides a powerful cue or “honest signal” to recipients that provisioning will continue if and when the provider recovers.
 - c) If the groups studied were to have one less hunter and his family while the best hunter was injured, per capita protein intake would further decline. Living in larger groups than

might be otherwise desirable reduces the per capita cost of providing adequate aid to a disabled group member. Conversely this suggests that increased sources of aid when injured may be one benefit that good hunters reap from living and sharing with more people than otherwise optimal.

7. There are other social niches that deliver difficult-to-replace benefits to others besides being an exceptional hunter and sharing meat widely. We therefore expect a proliferation of social niche differentiation where circumstances allow, with prestige or esteem being accorded those who fill such roles, and conflict or tension arising when two or more individuals attempt to fill the same niche. Ethnographic evidence from the Shiwiar and cross-cultural data on status, oratory skill and craft specialization is consistent with these predictions.

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