

Implications of Pathology Risk and Disability Care for Human Life History Evolution:

Evidence from Shiwiar Forager-Horticulturalists

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Running Head: Shiwiar Disability and Life history Evolution

Abstract:

Both our long period of juvenile dependency and long lifespan are hypothesized to have co-evolved with (1) health care provisioning, (2) the hominid dietary transition to high quality, difficult-to-acquire foods, and (3) increased investment in learning complex subsistence strategies. These hypotheses are contingent upon pathology risk having exerted significant selection pressure upon our ancestors, and upon health-care provisioning having reduced the effects of this risk. One prediction that follows from these hypotheses is that health-care provisioning reduced juvenile mortality, thereby enabling the evolution of delayed maturity. Evidence to test this prediction may be sought in the fossil record and among extant foraging populations. Here I present evidence from the latter source, reporting on the causes, distribution, and duration of injuries and illnesses suffered by Shiwiar forager-horticulturalists prior to age of first reproduction, based on physical evidence and reported occurrence of pathologies in this population. Results indicate that, consistent with the hypotheses considered, pathology is a recurrent feature in the juvenile lifespan (approximately half of the individuals sampled suffered pathology during their pre-reproductive lifetimes that would be lethal without provisioning), and that these periods are both temporally unpredictable and not primarily attributable to direct impact from the industrial world.

Key Words: human life history, juvenile health, health care, provisioning, pathology, risk, Shiwiar

Introduction

Human forager life is marked by a long lifespan, a long period of juvenile dependency, support of females and their offspring by males and post-reproductive individuals, late achievement of adult foraging competence, and exceptional intelligence coupled with a large capacity for learning. Two current theories seek to explain important features of this pattern. The so-called “grandmother hypothesis” (Hawkes et al. 1998) proposes that the long human lifespan evolved because of the fitness benefits that post-reproductive-age women can provide for their offspring and grand offspring. In contrast, Kaplan et al. (2000) present an integrated model proposing that our extended juvenile dependency and lifespan are the product of the co-evolution of (1) dietary transition to high-quality, difficult-to-acquire foods, (2) increase in life-history investment in the learning of complex subsistence strategies to exploit such foods, (3) increased food sharing and provisioning of conspecifics (particularly juveniles), and (4) health-care altruism. According to this model, as dietary reliance on high-quality, difficult-to-acquire game resources increased, fitness benefits could be realized from lengthening the pre-reproductive period and, hence, the period of foraging skill acquisition. This led to the co-evolution of an increased flow of resources from older individuals to juveniles in order to support this period of learning. This development was problematic in that the fitness benefits of an extended learning period would be reduced by the increased probability of pre-reproductive mortality (due to an increased period of time during which lethal pathology might strike). However, if health-care provisioning effectively reduced mortality risk during the pre-reproductive lifespan, then selection for an extended juvenile period and delayed reproduction could evolve (Kaplan et al.

2000). To date, Kaplan et al. (2000) have presented food-sharing, productivity, and life-history data in support of the life-history and provisioning features of their co-evolutionary theory.

Here, I present data relevant to testing a third component of this model, namely the hypothesis that health-care provisioning significantly reduces juvenile mortality in a human foraging context.

If the increased period of juvenile dependency and human longevity co-evolved with juvenile mortality reduction resulting from health-care provisioning, the following are predicted to have characterized the human lifespan in evolutionary environments: (1) pathology risk was a recurrent force during the pre-reproductive lifespan (even though risk-taking behavior may show facultative lifetime variation); (2) juveniles experienced pathologies that would have been lethal without health-care provisioning; and (3) these pathologies occurred with significant probability and widespread distribution across juveniles, such that (4) health-care provisioning effectively reduced juvenile mortality rates. While paleo-anthropological studies give clues to the extent of selection pressure from pathology risk, they are biased by the kinds of pathological conditions that leave osteological or dental signatures. Surprisingly, quantitative evidence about the degree to which foragers and forager-horticulturalists suffer from prolonged disability requiring sustained health care for survival is sparse. Even less is known about the relative fitness consequences of soliciting and receiving such aid. To date, only suggestive evidence from foraging and forager-horticultural societies exists for predictions about pathology risk and health-care provisioning (e.g., Baily 1991; Gurven et al. 2000; Sugiyama & Chacon 2000; Kaplan et al. 2000).

Evidence of illness and injury is seen among great ape (e.g., Lovall 1990) and prehistoric *Homo sapiens* populations (e.g., Alejandro 1996; Aufderheide & Conrado 1998; Berger & Trinkaus 1995; Bush & Zvelebil 1991; Grauer & Stuart-Macadam 1998; Lambert 1995; Owsley & Jantz. 1994; Rothschild & Martin 1992; Trikaus 1983, 1995; Walker 1990; Webb 1994).

Paleo-anthropological studies of both human and non-human hominids can indicate the extent of selection pressure from pathology risk via mortality and morbidity rates estimated for different phases of human evolution. These estimates can be problematic, however (e.g., Wood et al. 1992). Among other things, not all pathological conditions leave osteological signatures, either because the insult resulted only in soft-tissue damage or because no healing occurred (such as when the condition was lethal). Thus paleo- pathology and demography data may present distorted views of pathology, morbidity, and mortality rates within and across populations, particularly among those showing little evidence of pathology. Further, it is difficult to document juvenile mortality reduction via health-care provisioning *per se* using only the paleo-archaeological record.

Despite calls for an ethno-bio-archaeological synthesis (e.g., Lukacs 2000; Walker et al. 1998), systematic evidence regarding the occurrence and duration of pathology in forager and forager-horticulturalist populations who live without consistent access to Western medicine is limited (Kaplan et. al 2000). In extant foraging and forager-horticulturalist populations for which we do have reports, potentially disabling pathology appears to be common. For instance, Efe foragers of central Africa sought medical attention on 21% of person days observed (Bailey 1991). Lacerations from bamboo-like *cana brava* cost three weeks of work loss per person per year among Machiguenga forager-horticulturalists (Baksh & Johnson 1990). Ache adults sought health clinic care on 6% of person days observed, and children required care on 3.5% of person days observed (Kaplan et al. 2000). Sickness or injury interfered with foraging on approximately 5% of person days among the Yora of Peru overall, while male heads of household suffered illness or injury on 10% of man days (Sugiyama & Chacon 2000). Further, disability may occur

for prolonged periods: among the Yora, one hunter was prevented from hunting for over a month due to a major infection of his arm (Sugiyama & Chacon 2000).

Besides the immediate problem of surviving a pathological condition once it occurs, juveniles also face fitness costs from lowered nutritional intake when adult providers suffer pathological insults (Sugiyama & Chacon 2000). In humans, this is particularly likely for rich but difficult-to-acquire items such as game, which are key components of the human foraging diet (e.g., Kaplan et al. 2000; Kelly 1995; Sugiyama & Chacon 2000; Tooby & Devore 1987). In a variety of primates (including humans) and other mammals, nutritional decrements are associated with a number of fitness costs, including shorter reproductive lifespan, fewer offspring, delay of menarche and onset of puberty, lower proportion of live births, lower infant body weight, and increased juvenile mortality (see, e.g., Altman 1991; Cromwell et al. 1982; Fritch & McArthur 1974; Green et al. 1986; Hill & Hurtado 1996; Kohrs et al.; Manocha & Long 1977; Prentice et al. 1987; Riley et al. 1993; Schwartz et al. 1988). Among the Yora, prolonged injury to an average hunter resulted in an 18% reduction in average daily per capita protein intake in the village. Injury to the highest producing hunter would result in reduction of average daily per capita protein intake by approximately 37% (Sugiyama 1996; Sugiyama & Chacon 2000). Thus, in foraging contexts with high levels of food transfers, pathology-related disability among adults may severely impact nutrition of all juveniles within the sharing network, not only those whose primary caretaker may be temporarily disabled (Sugiyama & Chacon 2000).

Although these findings suggest that health-care provisioning reduces juvenile mortality among foraging and forager-horticulturalist populations, direct systematic data is lacking. Here I report on the causes, distribution, and duration of injuries and illnesses suffered during pre-reproductive years by Shiwiar hunter-horticulturalists of the Ecuadorian Amazon, based on

physical evidence and reported occurrence of pathologies. This report addresses the following questions: (1) What pathologies do individuals in this population suffer during the pre-reproductive lifespan? (2) With what frequency do these pathological episodes occur? (3) With what frequency and duration do these cases cause disability severe enough to necessitate survival assistance during the pre-reproductive portion of the lifespan? and (4) What are the demographic and fitness effects of individuals having received long-term aid without which they are likely to have died? The data presented were gathered in two communities (67 and 87 persons physically present at time of the study, respectively) during 1994 and 1995.

Study population

The Shiwiar are a Jivaroan speaking people who live in the southern Oriente (tropical forest) of Ecuador and northeastern Peru. Approximately 2000 Shiwiar occupy a region along the Corrientes River and its tributaries in the upper Amazon. Long-term direct contact with non-indigenous populations began in the later 1970s when Shiwiar actively solicited missionary contact. Contact was sought because mortality from raiding and warfare was reduced in missionized areas. Secondly, mission contact provided greater access to industrial goods than previously used trade networks. Prior to this, Shiwiar lived in scattered households linked by marriage ties and the influence of powerful individuals (Descola 1988). Unnavigable rivers, hostility toward outsiders, and border conflict between Ecuador and Peru have limited colonial incursions. Many Shiwiar villages now have cut small dirt airstrips in the forest, around which houses form loose clusters. These airstrips provide some access to medical and other facilities outside of Shiwiar territory via missionary light aircraft; however Shiwiar subsistence is based on

foraging and horticulture, and internal politics are governed by traditional big-man, consanguine- and affine-based alliances.

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 foraging by hunting and fishing for most of their dietary fat and protein, and on plant products for fruits, starch, construction, and tool material. They are closely related to most of the people with whom they have daily interaction in the study area, and come into repeated contact with relatively few people. They have limited everyday access to Western medicine but have a detailed system of indigenous medical knowledge.

Shiwiar grow a wide variety of horticultural products. The predominant starch in the diet is manioc (cassava: *Manihot escalante* and *Manihot elongata*); other roots (e.g., sweet potatoes, yams, papa-china, papa-jivaro) are also important. Each female head of household has between two and four gardens at different stages of production, and on most mornings women go to the garden to harvest, replant, and weed. Gardens are larger than necessary for household consumption, even when need to buffer the risk of losses due to animal and other pests is considered (Descola 1988). Horticultural production provides the foraging equivalent of a highly productive, reliable, and spatially concentrated patch of carbohydrate resources. Large-scale clearing is done via *mingas*, village-wide parties of cooperative labor exchange. Thus, day-to-day investment in horticulture is broadly similar to that of foraging: harvesting and processing the resource.

Both blowguns and muzzle-loading shotguns are used in hunting, although single-shot cartridge shotguns are increasingly used when cash is available for the relatively costly shells. A wide variety of small, medium and large game are taken. Hunting returns are relatively high, and

the day-to-day risk of returning from a hunting trip without game is low (Sugiyama 2000; Sugiyama & Chacon 2000). Further, as one might expect, informants state that increasing use of shotguns has reduced predation by jaguar, compared to earlier periods when shot and powder were less available. Fishing is done either with hooks and line or by using barbascos fish poison (Walker et al. 1998; Sugiyama 2000; Sugiyama & Chacon 2000). Finally, the industrially produced machete is used ubiquitously as an all-purpose cutting, chopping, and digging tool. Metal pots, hooks, axes, and other tools are widely used.

Methods

Participant observation and records of injuries and illness during the study periods provide the ethnographic context for Shiwiar reactions to injury. Formal and informal interviews were conducted between 1993 and 1998 in four Shiwiar and closely related villages to gather genealogical and life history data. Physical examination of nineteen male and twenty female Shiwiar individuals ranging in age from three through fifty was conducted to document scars, broken bones, or other observable signs of past pathological events. This bulk of this data is reported in detail elsewhere (Sugiyama n.d.), and is summarized only briefly here. The examination for evidence of injury or illness proceeded in a standardized way. Beginning with the right foot, the examination proceeded up the right leg as far as was comfortable for the informant, and then down the left leg. The left and right arm were then examined, followed by the front and then rear of the torso and neck, followed by the face and head. Scars and evidence of broken bones were noted on standardized forms depicting front and rear line drawing views of a human form, and enlarged views of the hands and feet. Each pathology recorded was coded as visible, reported (by the informant), current, or some combination of these in order to specify the

evidence upon which the recording of each pathology was based. For each scar or evidence of a broken bone observed, the subject was asked to provide information about the cause, activity being engaged in, and age at which the event occurred. Informants from one of the sample villages (n=17) were also asked the duration of disability if applicable, and this information cross-checked with other informants. A standard set of questions about past illnesses, injuries, and treatment received (either from a shaman or Western medical practitioner) was then administered (Sugiyama n.d.). Disability duration gives a clearer indication of the frequency with which pathology that would have been lethal without health-care provisioning occurred, and thus serves as a means by which juvenile mortality reduction via health-care provisioning can be estimated.

While the methods used provide systematic data collection on past and present illness and injury, they do entail some problems. All scars on the skin of young individuals can be easily observed, but the skin of older individuals has been subject to so many lacerations, abrasions, and infections that only the most prominent or most recent can be accurately recorded. Therefore, numbers of injuries recorded for older adults reflect mainly the most recent or most serious injuries. For individuals below approximately 25 years of age, complete recording of pathology leaving visible evidence was possible. However, methods used were time consuming, and informants no doubt differed in levels of patience and quantity of details they were willing to supply. While these problems could not be entirely solved, any systematic effect is likely to result in under-reporting or missing data. Independent means of cross-checking information suggest that overestimation or false reporting was highly likely to be exposed. Physically observable evidence was the principle source of data on the occurrence of a pathological event; reports of broken bones were verified both by tactile examination for evidence of healed fracture and by verifying reports with other informants. For both disability data and pathologies leaving

no direct physical evidence, informant reports were cross-checked with informants who were present at the time of the injury/illness or knowledgeable about the incident in question. Incidents causing significant disability were known by multiple informants, and the most significant were common knowledge.

Results

Age/Sex Distribution of Sample

As of 1998, 410 Shiwiar living in six villages (1 outside officially designated Shiwiar territory) were in the core study area, with an additional eighty-seven siblings or offspring of core area individuals living in surrounding villages. Usual resident population in the two villages from which pathology data was collected was 63 and 103, respectively. The sample of forty individuals represents 24% of the total population in these villages, and 10.25% of the population of the core study area. The seventeen-person disability sample represents 16.5% of the population of Village 2 and includes individuals from ten of the twelve households in the village. Residents of the additional two houses in that village were not present while data was being collected. Table 1 shows the age/sex distribution of the Shiwiar individuals included in the overall sample from which data on pathologies during the pre-reproductive lifespan are drawn. One of the males included in the 31-40 year old age cohort was not examined during the study because he was not present in the village. However, all critical information regarding a near-lethal snakebite was available from previous interviews, so it was included in the analysis. The Kruskal Wallis test shows no significant differences between the ages of males and females in the sample overall ($X^2=28.6$, $df=28$, $p=.42$) or by ten-year age cohorts ($X^2=1.514$, $df=4$, $p=.82$). Removing the aforementioned individual from the sample does not significantly change this result.

Insert Table 1 about here

Frequency of Pathological Conditions Suffered

A total of 678 injuries and illnesses were recorded throughout the lifetime of the forty individuals examined and, as expected, significant differences were observed in the relative frequencies with which different types of pathologies were observed (Table 2). The most commonly observed incidents were lacerations, followed by infections (including infectious disease), bites and stings, puncture wounds, abrasions, pain (either chronic or periodic), broken bones, and burns ($\chi^2=1861$, $df=16$, $p<.000$). Some pathology does not fit neatly into one category. As a guiding principle I categorized pathology type according to the proximate cause of the condition with regard to its potential for causing disability. For instance, pathology was recorded as laceration if the wound did not result in infection, but as infection if it did, because infection subsequent to laceration has the potential to cause disability far in excess of most observed lacerations. Similarly, insect bites that resulted in subsequent minor skin infection were recorded as infections, because such infections may become severe as other ectoparasites infect the wound. Finally, pathology was only recorded as pain when it occurred beyond simultaneous occurrence of another condition. For example, although snakebite causes extreme pain, at the time of the bite it is the venom and not the pain which poses the greatest threat of disability and death. Thus, pain of this type is recorded as snakebite. However, subsequent nerve or tissue damage can cause pain and limitations on mobility, which can last long after the threat from venom is past. Accordingly, pain of this type is reported as pain, not snakebite. Table 2 provides an overview of the relative frequency of different classes of pathology by sex of victim. Sugiyama

(n.d.) provides detailed overall analysis of frequency, definition, and distribution of pathologies by type, cause, and sex of victim.

Insert Table 2 about here

Data on pathological conditions suffered during the pre-reproductive phase of the lifespan were extracted from the larger sample in two ways. Twenty-two individuals, ten females and twelve males (aged 3-25), had not yet begun reproduction at the time of the study and all pathologies they suffered were therefore included. Eighteen individuals, nine females and nine males, had begun reproduction at the time of the study. For these adult informants, pathologies for which an age of occurrence or phase of lifetime (e.g., childhood) was reported were examined for cases occurring prior to the individuals' age at first reproduction. Together, these yielded 456 cases of pathology occurring prior to first reproduction. The Kruskal-Wallis test indicates that there is no significant age difference between the sexes within either the pre-first-reproduction or post-first-reproduction sub-samples, either overall ($\chi^2=15.546$, $df=14$; $p=.34$; $\chi^2=13.22$, $df=15$, $p=.585$ respectively) or by five-year age cohort ($\chi^2=2.03$, $df=3$, $p=.566$; $\chi^2=9.633$, $df=7$, $p=.21$ respectively).

As with the larger sample overall, significant differences were observed in the relative frequencies with which different types of pathologies were observed in the pre-reproductive lifespan ($\chi^2=819.37$, $df=11$, $p<.000$). Table 3 shows the frequency of pathology occurring prior to first reproduction. Lacerations were the most frequently observed pathology, and were observed significantly more frequently than bites and stings, the second leading cause of pathology ($\chi^2=4.281$, $df=2$, $p=.039$). Although the frequencies of bites/stings and infections (the

third leading cause of pathology) do not significantly differ ($\chi^2=1.664$, $df=1$, $p=.197$), both were significantly more common than puncture wounds ($\chi^2=36.91$, $df=1$, $p=.000$ for comparison of infection with puncture wounds). Thus all other pathology types occur with significantly lower frequency than infections.

Insert Table 3 about here

Sex differences in pathology suffered

Males generally suffer disproportionately more illness and injury than females, a fact attributed both to higher male behavioral risk-taking and susceptibility to disease. As expected, males in the overall sample suffered significantly more pathologies than females ($\chi^2=48.855$, $df=1$, $p<.000$). This was true for all pathology types with sample sizes over 30, including lacerations ($\chi^2=21.68$, $df=1$, $p<.000$), infections ($\chi^2=6.94$, $df=1$, $p=.008$), bites/stings ($\chi^2=13.08$, $df=1$, $p<.000$), puncture wounds ($n=40$, $\chi^2=6.4$, $df=1$, $p=.011$), and abrasions ($\chi^2=6.53$, $df=1$, $p=.011$). Males also suffered more burns than females, though the difference was not quite statistically significant by conventional standards ($\chi^2=3.77$, $df=1$, $p=.052$). Males and females did not differ in number of broken bones ($\chi^2=.059$, $df=1$, $p>.8$), contusions ($\chi^2=.2$, $df=1$, $p=.655$), scars of unknown cause ($\chi^2=.077$, $df=1$, $p=.782$), or incidence of severe chronic or acute pain ($\chi^2=1.64$, $df=1$, $p=.2$ [Table 2]), but sample sizes for these were small.

As in the larger sample, males suffer significantly more pathology than females in the pre-reproductive years ($\chi^2=74.24$, $df=1$, $p<.000$ [Table 4]). Analysis by pathology type indicates that prior to age at first reproduction, males were more frequent victims of laceration ($\chi^2=32.24$, $df=1$, $p<.000$), infection ($\chi^2=12.374$, $df=1$, $p<.000$), bites/stings ($\chi^2=17.93$, $df=1$, $p<.000$), and

puncture wounds ($\chi^2=8.53$, $df=1$, $p=.003$) than females. Males and females did not differ in number of abrasions ($\chi^2=2.91$, $df=1$, $p=.088$) or scars of unknown cause ($\chi^2=.000$, $df=1$, $p=1.0$). Contusions, fractures, and pain did not occur with sufficient frequency for statistical tests to be meaningfully performed. In addition, only males suffered burns.

Insert Table 4 about here

Causes of pathology suffered in the pre-reproductive years

The specific cause of each pathology was recorded at the time of data collection. Table 5 shows the frequency with which the thirty-seven specific causes of pathology observed occurred during the pre-reproductive lifespan. There are clear significant overall differences in the relative frequency with which these causes of pathology occur ($\chi^2=1720$, $df=36$, $p=.000$). The most frequently observed specific cause of pathological conditions was bites from vampire bats ($n=98$), followed by machete wounds ($n=75$), encounters with plant tissue (e.g., puncture by spines, laceration from branches, logs [$n=70$]), and insects (mostly ectoparasites [$n=60$]). Together these account for 66.4% of all pathology observed, and all causes of pathology occurring with significantly greater frequency than expected. Nevertheless, the frequencies with which the four most common causes of pathology occur differ significantly ($\chi^2=10.25$, $df=3$, $p=.017$) due to the difference between the highest frequency cause--vampire bat bites--and the least frequent--insects ($\chi^2=9.14$, $df=1$, $p=.003$). Falls, lance wounds, varicella, snake bites, malaria, axe wounds, leishmaniasis, and burns from cooking fires occur repeatedly but

significantly less frequently than the first set of causes ($\chi^2=30.26$, $df=1$, $p=.000$ for insect vs. fall).

Of particular interest when considering pathology in evolutionary perspective is comparison of those causes of pathology directly attributable to industrial technology and those that arise from non-industrial causes. Conclusions become problematic if most pathology is due to direct influences of industrialized technology. Machete cuts are highly prevalent. However, chi-square tests reveal that when industrial causes of pathology (i.e., wounds by machete, axe, knife, injection, and shotgun) are compared to all other causes of pathology, the absolute number of the latter is significantly higher than the former ($\chi^2=128.85$, $df=1$, $p=.000$). It is possible that the significantly higher frequency of pathology caused by natural versus industrial agents is a reflection of limited contact with pathological causes associated with industry, as thirty-two of the thirty-seven observed causes of pathology in the sample were not directly related to industrialized tools. However, when expected frequencies are adjusted to account for this fact (86.5% of 407 = 352.06 for non-industrial and 13.5% of 407 = 54.95 for industrial-related, respectively), natural causes are still more frequently observed causes of pathology than industrially produced tools ($\chi^2=.24.405$, $df=1$, $p<.000$).

Insert Table 5 about here

Within pathology type, some vectors are more frequent causes of pathology in the pre-reproductive lifespan than others (Table 6). Vampire bats are by far the most frequently observed cause of animal bites and stings that do not lead to infection ($\chi^2=621.68$, $df=8$, $p<.000$). While these do not in and of themselves cause disability or death, in 1998 rabies was

reported in areas north of the study area. Without Western medicine, provisioning will not aid rabies victims; however, preventive measures such as enclosing the sleeping area can be effective in reducing the number of bat bites. Infections stemming from a wide variety of causes affect people in this sample, and overall they differ significantly in the frequency with which they cause infection ($\chi^2=381.76$, $df=14$, $p<.000$). Mild skin infection as the result of insect bites that are scratched and become infected occurs with highest frequency. Frequencies with which different causes result in lacerations also differ significantly ($\chi^2=339.86$, $df=10$, $p<.000$). Among these, machete wounds account for the highest frequency of lacerations, followed by plant wounds ($\chi^2=16.96$, $df=1$, $p<.000$, machete wounds compared to plant-caused lacerations) and lance wounds ($\chi^2=13.56$, $df=1$, $p<.000$). Significant differences are also found in the frequency of puncture wound causes, with punctures from branches and sticks the most frequent kind ($\chi^2=29.27$, $df=6$, $p<.000$).

Insert Table 6 about here

Disabling pathology

Informants from one sample village were asked the duration of disability associated with each pathology reported, and this information was then cross-checked with other informants. The Kruskal Wallis test indicates that the sex composition of this sub-sample, including eight males and nine females, does not differ significantly from the rest of the larger sample ($\chi^2=.100$, $df=1$, $p=.725$) although it does contain an older age cohort (comprised mostly of individuals over fifteen [$\chi^2=14.31$, $df=1$, $p=.000$]). Disability was defined as the informant suffering a condition preventing him or her from leaving the house to engage in foraging or garden work (see Sugiyama

2001 for discussion of Shwiar values and disability). Informants usually reported disability duration estimates in even units of days, weeks, and months; these were converted to number of days for comparison. In this sub-sample, 215 cases of pathology were recorded; eighty-six (40%) resulted in disability lasting a day or longer that could be confidently established, sixty-six (30.7%) resulted in disability lasting a week or longer, fifty-one (23.7%) lasted fourteen days or longer, and twenty-eight (13%) lasted approximately a month or longer (Table 7). In addition, four chronic conditions resulted in periodic disability of varying unspecified duration. These disabilities were widely distributed across individuals in the sub-sample: sixteen of seventeen individuals suffered disability of seven days or longer (94%), fifteen suffered disability of fourteen days or longer (88%), and eleven suffered disability of approximately thirty days or longer (64.7%) (Table 11).

Insert Table 7 about here

Twenty-eight infections (13.02% of total cases in sub-sample), fifteen bites (6.97%), thirteen cases of debilitating pain (6.05%) , eleven broken bones (5.12%), ten lacerations (4.65%), four stings (1.86%), and one burn, one puncture wound, one case of postpartum bleeding, and one case of multiple simultaneous contusions of unknown origin (attributed to shamanistic attack) accounted for the disabilities observed in the sub-sample. Without health-care provisioning individuals suffering disability for extended periods are unlikely to survive because they can not gather food for themselves. Here I assume that without provisioning, disabilities approaching thirty days in duration would be highly likely to prove lethal. In this sample, those

pathologies causing disability of thirty days or longer include ten infections, eight bites, four fractures, three lacerations, one multiple contusion, and one case of debilitating pain (Table 8).

Insert Table 8 here

Once they occur, some types of injury/illness are significantly more likely to cause disability than expected (for pathologies resulting in disability, $X^2=20.06$, $df=9$, $p=.018$). Table 9 shows the observed and expected frequency of disability by type of pathology for the sub-sample, as well as results of relevant chi-squared tests for disabling conditions that could contribute to the overall effect. As one would expect, once they occur, fractures are significantly more likely to result in disability than expected by their prevalence in the sub-sample ($X^2=11.438$, $df=1$, $p=.001$). Conversely, lacerations are less likely to cause disability than expected ($X^2=5.675$, $df=1$, $p=.017$). This is probably because many minor lacerations nevertheless leave scars. Further, given the prevalence of lacerations in the sample, few become infected (due largely to indigenous medical skill). Similarly, techniques for preventing blood loss from lacerations are also effective. Neither infections nor pain result in significantly more or less disability than expected by their prevalence in the sub-sample ($X^2=1.986$, $df=1$, $p=.159$; $X^2=.693$, $df=1$, $p=.405$, respectively).

Of the bites observed, snakebite is highly likely to cause long-term disability. Ten cases for which duration of disability is estimated and was cross-checked were recorded. In four of these instances, antivenin was administered. Eight of the ten cases accounted for a combined 502 days of disability, with one case resulting in permanent disfigurement of the victim's foot. This and another case resulted in major tissue necrosis and gangrene, resulting in disability of a year

and six months, respectively. The foot disfigurement resulted in a lifelong reduction in mobility due to a pronounced limp, as well as ancillary pain during travel. Interviews and observation indicate that this limp resulted in an impaired gait and curtailment of activities for which quick movement is necessary (e.g., felling large trees, pursuit of game with hunting dogs), as well as limiting the victim's ability to carry heavy loads and to walk long distances at normal speed without pain.

Insert Table 9 about here

Either specific age of occurrence, or whether the incident occurred before or after first reproduction, was determined for 131 of the 215 pathological conditions recorded in the sub-sample. Fifty-nine of these were cases in which disability was observed. Comparing age of disability occurrence with genealogical data thereby allows calculation of the probable effects of disability on reproduction and mortality. Thirty-three of fifty-nine (55.9%) cases of disability affected individuals prior to first reproduction (Table 10). Duration of these cases ranged from one to 365 days, with twelve of the thirty-three pre-reproduction cases (22%) causing disability of one month or longer. The twelve pre-reproduction incidents were distributed among nine of the seventeen individuals (52.94%) for which data was available. If provisioning is required for individuals to survive disability of thirty days or longer, then without provisioning, over half of the sub-sample would have died during their pre-reproductive years (Table 11). In addition, fourteen post-first-reproduction incidents causing disability of one month or longer were distributed among five of the twelve individuals in the sub-sample who had begun reproduction at

the time of the study (42%). Overall, then, without health-care provisioning, eleven of seventeen individuals in the sub-sample (64.7%) would likely have died prior to the study period.

Insert table 10 about here

Using age of disability occurrence in combination with genealogical data also makes it possible to calculate the number of surviving offspring and grand-offspring that would likely not have been born without health-care provisioning to their direct ancestors in the village 2 sample. Fifty-four offspring and twenty-eight grandchildren were born to individuals in the sample (children/grandchildren born to parents/grandparents who are both in the sample were counted only once), although only two members of the sample had completed or were approaching probable completed fertility. Strategic health-care altruism can have large effects on subsequent generations and the population structure as a whole. Forty-six out of fifty-four (82%) of the first descending generation, and twenty-seven out of twenty-eight (96.4%) of sample individuals were born after a direct ancestor in the sample survived an incident likely to be fatal without health-care provisioning. Further, three sample individuals (ID numbers 2, 11, and 13) who survived pathology likely to be lethal without health-care provisioning are either the parent or grandparent of the twenty-seven second-generation descendants. Together, these three individuals are either parent or grandparent of 45% of sub-sample village residents, and 11.5 % of the Shiwiar population in the study area. One (ID number 13), is the parent or grandparent of 23% of the village 2 sample and 5% of the Shiwiar population block. Another, (ID number 2) is the direct ancestor of 14.5% of the village and 3.6% of the population (Table 11).

Insert Table 11 about here

Discussion

To date, only suggestive evidence existed for the hypothesis that health-care provisioning reduces juvenile mortality in forager and forager-horticulturalist societies. No systematic data has been available on the degree to which individuals in such societies suffer injury/illness of sufficient duration to interfere with foraging. The data presented in this paper addresses these questions more directly. As expected pathology risk is a significant force during the pre-reproductive lifespan in the sample population. Pathological conditions are frequently encountered and widely distributed across individuals in the sample both overall and during the pre-reproductive lifespan. During their pre-reproductive lifespan, over half the individuals in the disability sub-sample suffered pathology expected to be lethal without provisioning, indicating that health-care provisioning is effectively reducing juvenile mortality.

Further, it is clear that Shiwiar population structure is predicated on the existence of health-care provisioning to temporarily disabled individuals. Of fifty-four offspring born to informants in the sub-sample, over 80% were born after a parent included in the sample suffered injury or illness likely to be fatal without extended provisioning. Of twenty-eight individuals in the second descending generation of informants in the sub-sample, over 95% were born after a direct ancestor in the sample survived an incident likely to be fatal without provisioning. Findings presented here also bolster the related prediction that humans engage in evolutionary stable strategies for garnering health-care altruism (e.g., Gurven et al. 2001; Sugiyama 1996; Sugiyama & Chacon 2000). Additional work must be done to extend these findings, particularly through increasing sample size and constructing life-history and mortality tables for the Shiwiar, so that

the degree of mortality reduction via health-care provisioning can be estimated. Comparative studies among extant foraging societies living with little access to Western medical care are also critical.

Although data supporting each component of the Kaplan et al. (2000) co-evolutionary model of human life-history evolution now exists, other adaptationist theories for elements of human life-history evolution have been proposed. These include the Hawkes et al. (1998, 2000) “grandmother” hypothesis mentioned in the Introduction; the “machiavellian intelligence” hypothesis, which posits that the evolution of large brains and high intelligence is a consequence of an increasing intra-specific arms race for social intelligence (e.g., Whiten & Byrne 1997); and Miller’s (2000) hypothesis that increased human intelligence is largely the consequence of runaway sexual selection. Blurton-Jones and Marlowe (1999) challenge the widely-held assumption that adult foraging competence requires an extended period of learning, arguing that the reason Hadza children do not achieve adult levels of foraging competence is that they have insufficient size and/or strength to do so. Among Miriam Island foragers, children are reported to achieve adult foraging rates for some skill-intensive fishing techniques well before they achieve adult rates for techniques requiring less skill but greater size, speed or strength (Bliege-Bird et al. 1995). Although each of these hypotheses appears to have valid elements, uni-dimensional theories are unlikely to explain the complex complement of human traits ultimately at issue: (1) long pre-reproductive period and lifespan; (2) high levels of social and technical intelligence; (3) cultivation of a foraging niche based on acquisition of difficult-to-acquire, high-quality foods; (4) extended investment in offspring and in the learning of complex social and foraging strategies; and (5) conspecific provisioning of injured/ill individuals and of females and their offspring. Co-

evolutionary models positing interacting evolutionary feedback loops appear necessary to explain these intersecting phenomena.

Regardless of one's position with regard to these theories, the data reported here illustrate a fairly clear point. If pathology and disability risk among the Shwiar are within the normal range of those associated with a foraging lifeway, then whichever explanation of these phenomena one wishes to advance, the evolution of pathology/mortality risk reduction via health-care provisioning appears to be a necessary feature that must be incorporated into one's model, either as a pre-adaptation or co-evolutionary condition for the emergence of these features of the human "cognitive niche" (Tooby & DeVore 1987?). Without risk reduction through health-care provisioning, features of the human lifeway associated with long juvenile period, long lifespan, and long period of cognitive development are unlikely to have evolved, because the fitness costs of extending the lifespan in the absence of health-care provisioning are overwhelmingly great.

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Tables

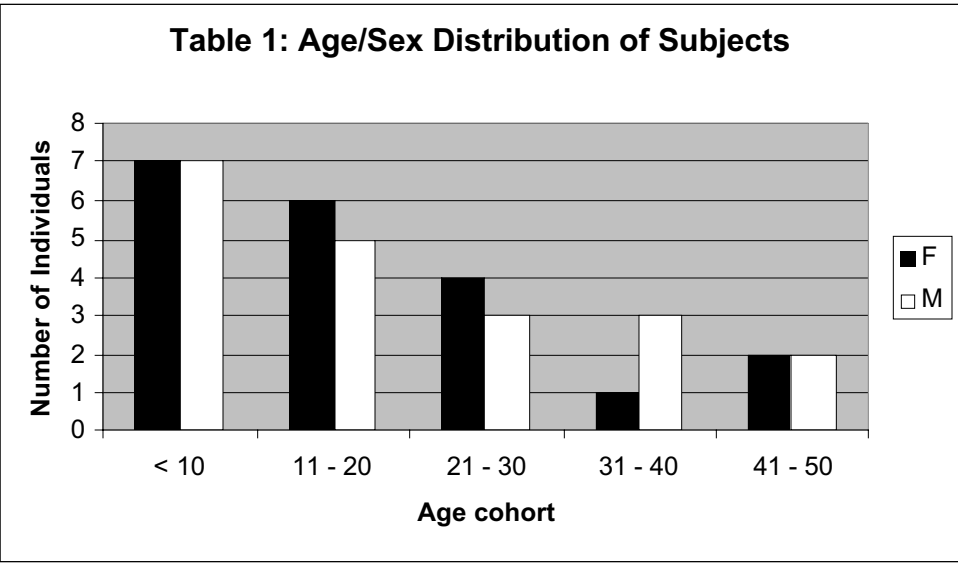


Table 2: X^2 Tests, Frequency of Pathology by Type and by Sex of Victim

Pathology	Female		Male		X ² for sex differences			Total: column X ² =1861, df=16, p<.000	
	Obs.	Exp.	Obs.	Exp.	X ²	df	p-value	Tot. Obs.	Tot. Exp.
Laceration	77	113	148	113	*21.68	1	.000	^a 226	39.9
Infection	62	78.5	95	78.5	*6.94	1	.008	^{a, b1, c} 157	39.9
Bite/sting	52	74	96	74	*13.08	1	.000	^c 148	39.9
Puncture wound	12	20	28	20	**6.4	1	.011	40	39.9
Abrasion	8	15	22	15	**6.53	1	.011	30	39.9
Pain	14	11	8	11	1.64	1	.2	^{b2} 22	39.9
Fracture	8	8.5	9	8.5	.059	1	.8	^{b2} 17	39.9
Burn	3	6.5	10	6.5	3.77	1	.052	^{b2} 13	39.9
Scars unknown	6	13	7	13	.077	1	.782	^{b2} 13	39.9
Contusion	2	2.5	3	2.5	.2	1	.655	5	39.9
Arthritis	1		0		^d			^{b2} 1	39.9
Bleeding	1		0		^d			^{b2} 1	39.9
Blisters	0		1		^d			^{b2} 1	39.9
Concussion	0		1		^d			^{b2} 1	39.9
Irritation	1		0		^d			^{b2} 1	39.9
Sprain	0		1		^d			^{b2} 1	39.9
Swelling	0		1		^d			^{b2} 1	39.9
Total	248		430	339	*48.45	1	.000	678	678

^a X²=50.568, df=1, p<.000

^{b1 vs b2} X²=50.568, df=1, p<.000

^c X²=.859, df=1, p=.354

^d expected frequency less than 5, no X² test performed

* significant at p<.01 level

** significant at p<.05 level

Table 3: Frequency of Pre-First Reproduction Pathology by Type

Pathology	Observed N	Expected N	Residual	Percent
laceration	^a 152	38.0	114.0	33.3
bite/sting	^{a, b} 118	38.0	80.0	25.9
infection	^{b, c} 99	38.0	61.0	21.7
puncture	^c 30	38.0	-8.0	6.6
abrasion	22	38.0	-16.0	4.8
scars unknown	10	38.0	-28.0	2.2
fracture	9	38.0	-29.0	2.0
burn	6	38.0	-32.0	1.3
contusion	4	38.0	-34.0	.9
pain	4	38.0	-34.0	.9
blisters	1	38.0	-37.0	.2
irritation	1	38.0	-37.0	.2
Total	456			100.0

Overall: $\chi^2=819.368$, $df=11$, $p<.000$

^a $\chi^2=4.281$, $df=2$, $p=.039$

^b $\chi^2=1.664$, $df=1$, $p=.197$

^c $\chi^2=36.91$, $df=1$, $p<.000$

Table 4: Sex differences in Pre-first-reproduction Pathology Frequency by Type

Pathology	Male Observed	Male Expected	Female Observed	Female Expected	Total	χ^2	df	p-value
abrasion	15	11.0	7	11.0	22	2.91	1	.088
bite/sting	82	59.0	36	59.0	118	*17.93	1	.000
blisters	1		0		1	a, b		
burn	6	6.0	0	0	6	a, b		
contusion	3	2.0	1	2.0	4	1.00	1	.317
fracture	5	4.5	4	4.5	9	b	1	.739
infection	67	49.5	32	49.5	99	*12.37	1	.000
irritation	0		1		1	a		
laceration	111	76.0	41	76.0	152	*32.24	1	.000
pain	2	2.0	2	2.0	4	b		
puncture	23	15.0	7	15.0	30	**8.53	1	.003
scars	5	5.0	5	5.0	10	.00	1	1.00
unknown								
Overall Total	319	228	135	228	456	*44.24	1	.000

* Significant at p<.00 level, 2 sided.

** Significant at p<.01 level, 2 sided.

a This variable is constant. Chi-Square Test cannot be performed.

b Expected cell frequency less than 5. Chi-Square Test not performed.

Table 5: Frequency of Pathological Causes For Pathology Occurring Prior to Age of First Reproduction

Cause	Observed	Expected	Residual	Percent
bat	a, b 98	12.0	86.0	21.5
machete	a 75	12.0	63.0	16.4
plant	a 70	12.0	57.7	15.3
insect	a, b, c 60	12.0	48.0	13.2
na	49	12.0	37.0	10.7
fall	c 13	12.0	1.0	2.9
lance	11	12.0	-1.0	2.4
varicella	11	12.0	-1.0	2.4
snake	8	12.0	-4.0	1.8
malaria	7	12.0	-5.0	1.5
ax	6	12.0	-6.0	1.3
leishmaniasis	6	12.0	-6.0	1.3
fire	5	12.0	-7.0	1.1
injection	4	12.0	-8.0	.9
hit	3	12.0	-9.0	.7
knife	3	12.0	-9.0	.7
measles	3	12.0	-9.0	.7
assault	2	12.0	-10.0	.4
fingernail	2	12.0	-10.0	.4
pertusis	2	12.0	-10.0	.4
scorpion	2	12.0	-10.0	.4
amoebae	1	12.0	-11.0	.2
ant	1	12.0	-11.0	.2
bee	1	12.0	-11.0	.2
blisters	1	12.0	-11.0	.2
bot fly	1	12.0	-11.0	.2
collision	1	12.0	-11.0	.2
dog	1	12.0	-11.0	.2
ear piercing	1	12.0	-11.0	.2
fight	1	12.0	-11.0	.2
fish spine	1	12.0	-11.0	.2
harpoon	1	12.0	-11.0	.2
howler monkey	1	12.0	-11.0	.2
oncherosiasis	1	12.0	-11.0	.2
person	1	12.0	-11.0	.2
pirana	1	12.0	-11.0	.2
shotgun	1	12.0	-11.0	.2
Total	456			100.0

Overall: $\chi^2=1720$, $df=36$, $p=.000$

a $\chi^2=10.25$, $df=3$, $p=.017$

b $\chi^2=9.14$, $df=1$, $p=.003$

c $\chi^2=30.26$, $df=1$, $p=.000$

Table 6: Frequency of Cause by Pathology Type Prior to First Reproduction

PATHOLOGY	PCAUSE	Obs. N	Exp. N	Residual	χ^2	df	p=
abrasion	branch/stick/log	7	4.4	2.6			
	fall	3	4.4	-1.4			
	fingernail	2	4.4	-2.4			
	na	5	4.4	.6			
	spine	5	4.4	.6			
abrasion Total		22	a		3.455	4	.485
bite/sting	ant	1	13.1	-12.1			
	bat	98	13.1	84.9			
	bee	1	13.1	-12.1			
	dog	1	13.1	-12.1			
	insect	6	13.1	-7.1			
	person	1	13.1	-12.1			
	pirana	1	13.1	-12.1			
	scorpion	2	13.1	-11.1			
	snake	7	13.1	-6.1			
bite/sting Total		118	b		*621.678	8	.000
blisters	blisters	1					
blisters Total		1	j				
broken bone	branch/stick/log	2	1.8	.2			
	collision	1	1.8	-.8			
	fall	3	1.8	1.2			
	fight	1	1.8	-.8			
	na	2	1.8	.2			
broken bone Total		9	c		1.566	4	.817
burn	fire	5	3	2			
	shotgun	1	3	-2			
burn Total		6	d		2.667	1	.102
contusion	assault	1	1	0			
	branch/stick/log	1	1	0			
	fall	1	1	0			
	hit	1	1	0			
contusion Total		4	e		.000	3	1.00
infection	ameoba	1	6.6	-5.6			
	bot fly	1	6.6	-5.6			
	branch/stick/log	1	6.6	-5.6			
	ear piercing	1	6.6	-5.6			
	injection	4	6.6	-2.6			
	insect	54	6.6	47.4			

	leishmaniasis	6	6.6	-6.6			
	machete	2	6.6	-4.6			
	malaria	7	6.6	-2.6			
	measles	3	6.6	-3.6			
	na	3	6.6	-3.6			
	onchorsoriasis	1	6.6	-5.6			
	pertusis	2	6.6	-4.6			
	spine	2	6.6	-4.6			
	varicella	11	6.6	4.4			
infection Total		99			*381.758	14	.000
irritation	na	1					
irritation Total		1					
laceration	assault	1	13.8	-12.8			
	axe	6	13.8	-7.8			
	branch/stick/log	29	13.8	15.2			
	fall	5	13.8	-8.8			
	hit	2	13.8	-11.8			
	howler monkey	1	13.8	-12.8			
	knife	3	13.8	-10.8			
	lance	8	13.8	-5.8			
	machete	73	13.8	59.2			
	na	22	13.8	8.2			
	spine	2	13.8	-11.8			
laceration Total		152			*339.86	10	.000
pain	na	3	2				
	snake	1	2				
pain Total		4					
puncture	branch/stick/log	13	4.3	8.7			
	fall	1	4.3	-3.3			
	fish spine	1	4.3	-3.3			
	harpoon	1	4.3	-3.3			
	lance	3	4.3	-1.3			
	na	3	4.3	-1.3			
	spine	8	4.3	3.7			
puncture Total		30			*29.267	6	.000
scars unknown Total		10					
Grand Total		456					

a 5 cells (100.0%) have expected frequencies less than 5. The minimum expected cell frequency is 4.4.

b 0 cells (.0%) have expected frequencies less than 5. The minimum expected cell frequency is 13.1.

c 5 cells (100.0%) have expected frequencies less than 5. The minimum expected cell frequency is 1.8.

d 2 cells (100.0%) have expected frequencies less than 5. The minimum expected cell frequency is 3.0.

e 4 cells (100.0%) have expected frequencies less than 5. The minimum expected cell frequency is 1.0.

f 0 cells (.0%) have expected frequencies less than 5. The minimum expected cell frequency is 6.6.

g 0 cells (.0%) have expected frequencies less than 5. The minimum expected cell frequency is 13.8.

h 2 cells (100.0%) have expected frequencies less than 5. No Chi-square test performed.

i 7 cells (100.0%) have expected frequencies less than 5. The minimum expected cell frequency is 4.3.

j This variable is constant. No Chi-square test cannot be performed.

* Significant at p=.000 level.

Duration/days	Frequency	Percent	Cumulative Percent	Percentage above
0	129	60.0	60.0	40.0
1	8	3.7	63.7	36.3
2	8	3.7	67.4	32.6
3	2	.9	68.4	31.6
4	1	.5	68.8	31.2
6	1	.5	69.3	30.7
7	12	5.6	74.9	25.1
10	1	.5	75.3	24.7
11	1	.5	75.8	24.2
12	1	.5	76.3	23.7
14	7	3.3	79.5	20.5
15	4	1.9	81.4	18.6
17	1	.5	81.9	18.1
20	1	.5	82.3	17.7
21	5	2.3	84.7	15.3
23	1	.5	85.1	14.9
30	17	7.9	93.0	7.0
45	4	1.9	94.9	5.1
60	4	1.9	96.7	3.3
90	1	.5	97.2	2.8
180	1	.5	97.7	2.3
365	1	.5	98.1	1.9
chronic	4	1.9	100.0	0.0
Total	215	100.0		

Table 8: Frequency of Disability Duration by Pathology

Pathology	Duration in days	Total Cases
bite/sting	1	5
	3	1
	7	3
	21	2
	30	2
	45	1
	60	2
	90	1
	180	1
365	1	
bite/sting Total		19
bleeding Total	30	1
fractures	7	1
	14	3
	15	1
	20	1
	21	1
	30	3
45	1	
fractures Total		11
burn Total	7	1
concussion Total	3	1
contusion Total	30	1
infection	1	3
	2	1
	6	1
	7	4
	10	1
	12	1
	14	2
	15	3
	21	2
	30	7
45	2	
60	1	
infection Total		28
laceration	4	1
	7	3
	11	1
	14	1
	23	1
	30	2

	60	1
laceration Total		10
pain	2	7
	17	1
	30	1
chronic		4
pain Total		13
puncture Total	14	1
Grand Total		86

Table 9: Chi-Squared tests for Frequency of Disability by Pathology

	Observed N	Expected N	Residual	Chi-Square	df	p=
bite/sting	19	18.0	1.0			
bleeding	1	.4	.6			
fracture	12	4.9	7.1	*10.858	1	.001
burn	1	.4	.6			
concussion	1	.4	.6			
contusion	1	.8	.2			
infection	27	30.7	-3.7	.693	1	.405
laceration	10	19.2	-9.2	*5.675	1	.017
pain	13	9.0	4.0	1.986	1	.159
puncture	1	2.0	-1.0			
Total	86			*20.060	9	.018

Test Statistics

a 6 cells (60.0%) have expected frequencies less than 5. The minimum expected cell frequency is .4.

* indicates statistically significant at the $p < .05$ level

Table 10: Frequency of Disability by Duration and Age of Occurrence in the Reproductive Lifespan																
Duration/days	Age															Total
	juvenile	21	22	23	24	25	26	27	28	30	35	37	39	41	43	
1	4							1								5
2	1															1
3			1										1			2
4				1												1
6	1															1
7	6				1		1		1		1			1		11
10															1	1
14	2	2					1			1					1	7
15	3	1														4
17	1															1
20	1															1
21	2			1												3
30	7						1		1			1			1	11
45	2		1													3
60	1			1		1						1				4
90	1															1
180			1													1
365	1															1
Total	33	3	3	3	1	1	3	1	2	1	1	2	1	1	3	59

Table 11: Frequency of Disability by Individual, Duration, and Reproductive Success

ID	Age	Sex	Frequency of disability duration (days)				RS (Descending generations)				Descendants % Population	
			total	7-13	14-29	30+	1st	2nd	total	in village	% village	% tot. pop
1 ^{a, b}	22	m	4	2	0	2	2	0	2	2	1.94	.40
2 ^{a, b, c}	43	f	10	2	3	5	10	8	18	15	14.56	3.6
3 ^{b, c}	36	m	1	na	na	1	3	0	3	3	2.91	.60
4 ^b	37	m	3	2	1	0	5	1	6	6	5.83	1.20
5 ^a	18	f	8	2	3	2	0	0	0	0	0	0
6 ^a	25	f	1	0	0	1	0	0	0	0	0	0
7 ^b	24	m	7	1	5	0	3	0	3	3	2.91	6.0
8	16	f	2	1	1	0	0	0	0	0	0	0
9 ^b	43	m	3	2	0	0	9 ^d	5 ^f	14	7 ^d	6.80	2.82
10 ^{a, b}	18	f	3	0	1	1	2	0	2	2	1.94	.40
11 ^{a, b}	37	f	4	1	0	3	9 ^d	5 ^f	14	7 ^d	6.80	2.82
12 ^{a, b, c}	29	f	14	1	1	4	8 ^e	0	8	8 ^e	7.78	1.61
13 ^{a, b}	50	m	8	1	1	3	11	14	25	24	23.30	5.03
14 ^b	34	m	1	0	0	0	9 ^e	0	9	9 ^e	8.74	1.81
15 ^a	15	m	5	0	3	2	0	0	0	0	0	0
16 ^{a, b, c}	27	f	6	0	1	3	2	0	2	2	1.94	.40
17	7	m	2	0	2	0	0	0	0	0	0	0
Total			82	15	22	27	54*	28*	82*	73*	70.87*	16.49*

^a individuals who suffered pathology likely to be lethal without provisioning before age of first reproduction.

^b individuals who had begun reproduction by time of the study.

^c individuals who suffered pathology likely to be lethal without provisioning after age of first reproduction (during socially recognized adulthood).

^d represents identical individuals: offspring of a married couple both included in the sample.

^e 8 of these 9 are identical individuals: offspring of a married couple both included in the sample.

^f represents identical individuals:

*Totals calculated based on descendants of a couple both of whom are included in the subsample only once.