Illness, Injury, and Disability Among Shiwiar Forager-Horticulturalists: Implications of Health-Risk Buffering for the Evolution of Human Life History

Lawrence S. Sugiyama*

Department of Anthropology and Institute of Cognitive and Decision Sciences, University of Oregon, Eugene, Oregon 97403

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Human life history is distinguished by long lifespan, delayed reproduction, intergenerational asymmetric benefit transfers from adults to juveniles and between adults, and a large brain able to engage in unprecedented levels of learning, reasoning, and insight. The evolution of these traits depends on relatively low human mortality. Understanding why humans have low mortality is therefore critical for understanding the evolution of key human traits. One explanation is that the evolution of food provisioning during periods of health crisis reduced mortality. This hypothesis turns on health risk having posed a significant adaptive problem that could be effectively buffered by healthcare provisioning. Unfortunately, the frequency, duration, and fitness effects of temporary disability are difficult to estimate based on osteological evidence alone, and systematic ethno-biological research on these issues among extant small-scale societies with

little access to Western medical care is lacking. Here I present data on 678 injuries and illnesses suffered by 40 Shiwiar forager-horticulturalists, based on physical evidence and informant reports. A subsample of 17 individuals provided data on incidence and duration of disability for 215 pathological incidents. Results indicate that injury and illness occur frequently across the lifespan. Most living individuals have suffered temporarily disabling health crises likely to have been lethal without provisioning. The fitness effects of surviving these episodes are high, suggesting that the Shiwiar population structure and lifeway are dependent on infrequent extended provisioning to temporarily disabled individuals, and that provisioning of aid during healthcare crises effectively lowers mortality in this small-scale society. Am J Phys Anthropol 123: 371–389, 2004. © 2004 Wiley-Liss, Inc.

Life-history theory examines how natural selection produced age-related allocation of resources between somatic (growth and maintenance) and reproductive (fertility, mating, and parenting) effort (e.g., Charnov, 1993; Charnov and Schaffer, 1973; Hawkes et al., 1997; Hill and Hurtado, 1996; Hill and Kaplan, 1999; Kaplan et al., 2000; MacArthur and Wilson, 1967; Schaffer, 1974; Williams, 1966). Four distinctive features of human life-history traits are long lifespan, delayed reproduction, intergenerational and asymmetric benefit transfers from adults to juveniles and between adults, and a large brain able to engage in unprecedented levels of learning, reasoning, and insight (e.g., Bryne, 1997; Geary and Flinn, 2001; Hawkes et al., 1998, 2000; Hewlett, 1992; Hill, 2002; Hill et al., 2001; Hill and Hurtado, 1996; Hill and Kaplan, 1999; Kaplan et al., 2000; Tooby and DeVore, 1987). The evolution of each of these features is dependent on humans experiencing relatively low mortality rates. Understanding why humans experience low mortality may therefore "hold the key for understanding a variety of evolved human features and . . . the evolutionary history of our species" (Hill and Kaplan, 1999, p. 413).

This study examines health insults and their consequences among Shiwiar forager-horticulturalists of Ecuadorian Amazonia to present quantitative data on health risk among a small-scale population with little ready access to Western medicine, and to determine whether the ethno-biological evidence from this population suggests that care for sick and injured individuals is likely to be a significant factor in lowering human mortality under evolutionarily

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^{*}Correspondence to: Lawrence S. Sugiyama, Department of Anthropology, University of Missouri, Columbia, MO 65211-1440. E-mail: sugiyamal@dark_wing.uoregon.edu

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relevant conditions (e.g., Hill and Kaplan, 1999; Kaplan et al., 2000). Specifically, I present data on the incidence and cause of 678 injuries and illnesses suffered by 40 individuals from two communities (resident populations of 67 and 87, respectively), based on physical evidence and reported occurrence of pathologies. A subsample of 17 individuals provided data on the incidence and duration of disability for 215 cases. Together, these are used to determine: 1) what health insults this population suffers; 2) with what frequency they occur; 3) with what frequency and duration they cause disability severe enough to interfere with subsistence activities and necessitate survival assistance over the course of the lifespan; 4) an indication of the fitness effects of individuals having received long-term aid without which they are likely to have died; 5) an indication of whether healthcare provisioning is likely to be a significant cause of mortality reduction; and 6) the possible intensity of selection pressure from health risk in a society with limited access to Western medicine.

BACKGROUND

Humans exhibit a longer juvenile period (the period between weaning and first reproduction; Pagel and Harvey, 1993) than other primates, including other hominoids (e.g., Hawkes et al., 1998; Hill et al., 2001; Hill and Kaplan, 1999; Kaplan et al., 2000; Pereira, 1993; Pagel and Harvey, 1993). For instance, female chimpanzees begin reproduction at about age 13-15 years (Boesch and Boesch, 2000; Nishida et al., 1990; Pusey, 1990), whereas in foraging societies, human females begin reproduction at about 17-20 years (Hawkes et al., 1998; Hill and Hurtado, 1996; Kaplan et al., 2000). The evolution of delayed maturity calls for explanation because, all else being equal, it increases the probability of death prior to reproduction, thus causing an average decrease in age-specific reproductive value (e.g., Kaplan et al., 2000; Pagel and Harvey, 1993; Pereira and Fairbanks, 1993; Williams, 1966).

Humans also have a longer lifespan than their closest living relatives. For instance, while only about 9% of wild chimpanzees live to age 50 years, 42% of Ache foragers reached 50 prior to contact with outsiders (Hill et al., 2001). Chimps senesce about 20 years earlier than humans, indicating that the differences in average lifespan are due to long histories of selection as well as to higher observed rates of extrinsic mortality (Hill et al., 2001). Evolution of long lifespan calls for explanation because, all else being equal, selection operates more strongly earlier in life when the reproductive payoff of each additional year of survival is higher than at the end of the lifespan (Fisher, 1958; Hamilton, 1966; Medawar, 1952; Williams, 1957).

In addition, human forager life is marked by high degrees of inter- and intragenerational support and cooperation. Postreproductive aged females support the reproduction of younger women and their offspring (e.g., Hawkes et al., 1997, 1998, 2000), and males contribute resources to mates, other adults, and juveniles (Hawkes et al., 2001; Hewlett, 1992; Hill and Hurtado, 1996; Kaplan et al., 2000; Marlowe, 1999, 2001; Winterhalder, 1996). Humans also exhibit exceptional intelligence, complex social skills, and a large capacity for developmental learning (e.g., Byrne, 1997; Bogin, 1999; Geary and Flinn, 2001; Hill and Kaplan, 1999; Kaplan et al., 2000; Tooby and DeVore, 1987). Kaplan et al. (2000) and others argued that human adult foraging competence requires long periods of skill or knowledge acquisition (e.g., Bock, 2002; Hill and Kaplan, 1999; Kaplan et al., 2000; Walker et al., 2001). Although this claim is currently debated and the degree to which juvenile foragers contribute to their own subsistence varies (e.g., Bird and Bird, 2002a,b; Blurton-Jones and Marlowe, 2002), humans are nevertheless distinguished by a long period of juvenile dependence (e.g., Bird and Bird, 2002b; Blurton Jones et al., 1994; Bogin, 1999; Hawkes et al., 2001; Hewlett, 1992; Hill and Kaplan, 1999; Kaplan et al., 2000). Lengthy juvenile dependence entails an increased vulnerability to loss of parental investment (e.g., Chagnon, 1992; Hagen et al., 2001; Hill and Hurtado, 1996). Again, evolution of these traits calls for explanation because, all else being equal, they decrease the probability that a juvenile will reach reproductive age.

Mortality reduction allows evolution of delayed maturation and long lifespan

Three basic factors are used to explain delayed maturity and long lifespan: demographic factors, skill and/or knowledge acquisition, and invariant patterns of allometric growth (Pagel and Harvey, 1993). The demographic perspective emphasizes that reproductive age and lifespan are largely the function of extrinsic mortality rates. Species with high juvenile mortality tend to be faster maturing, smaller, and shorter-lived, because they cannot afford the mortality risk of not reaching maturity (e.g., Horn, 1978; Rose, 1983; Williams, 1957). Species with lower juvenile mortality have later maturation, and can therefore grow larger. Delayed maturity can evolve when the increased risk of prereproductive mortality it entails is offset by the acquisition of fitness-enhancing benefits during the juvenile period. Thus, long juvenile lifespan is seen as a time in which a second factor comes into play, the acquisition of knowledge or skills (e.g., social, parental, aggressive, or foraging) that either enhance later fertility and/or reduce later mortality (Bogin, 1999; Geary and Flinn, 2001; Harvey and Zammuto, 1985; Hill and Hurtado, 1996; Hill and Kaplan, 1999; Kaplan et al., 2000; Pagel and Harvey, 1993; Pereira and Altman, 1985; Pereira and Fairbanks, 1993; Promislow and Harvey, 1990). For this life-history pattern to evolve, the acquisition of skills and/or knowledge that yield fitness payoffs during the adult lifespan must offset increases in prereproductive

mortality risk. Longer adult lifespan allows more time for these payoffs to be realized. Therefore, adult mortality rates covary with age at maturity and fecundity, such that investments in the juvenile period are compensated for by higher lifetime fitness. Decreased adult mortality is expected to allow increased age at maturity, a longer period of skill or knowledge acquisition, and longer lifespan (Hill and Kaplan, 1999; Kaplan et al., 2000; Pereira, 1993).

The third factor in explanations of long lifespan and delayed maturity focuses on invariant patterns of allometric growth: the larger an animal's mature size, the greater its ability to produce energy, but the later the animal will begin reproduction because it takes longer to grow to adult size (e.g., Bonner, 1965; Charnov, 1993; Charnov and Berrigan, 1993; Lindstedt and Swain, 1988). This approach assumes a tradeoff between time spent growing and time spent reproducing. Within a lifespan, the longer it takes to reach reproductive age, the shorter the period in which reproduction can take place (Charnov, 1993). The relative time devoted to each is an invariant function. What varies is the length of lifespan and the probability of reaching reproductive age, both of which are set by levels of extrinsic mortality. According to this view, human maturational timing fits the pattern expected, based on the length of the human lifespan (e.g., Alvarez, 2000; Hawkes et al., 1998), and therefore evolution of delayed maturation requires "no special explanation" (Blurton Jones and Marlowe, 2002, p. 201). It is a byproduct of long lifespan. However, invariant patterns of growth do not account for all of the variance in life-history traits across primates (e.g., Harvey and Clutton-Brock, 1985; Harvey and Zammuto, 1985; Lindstedt and Swain, 1988; Pereira, 1993; Watts and Pusey, 1993); an explanation of long human lifespan is still required.

The "grandmother hypothesis" (Hawkes et al., 1998, 2000, 2001; Williams, 1957) claims that long human lifespan is the result of selection favoring the provisioning of benefits by senior women to descendent generations. Hawkes et al. (1998) argued that as humans entered a feeding niche based on difficult-to-acquire foods (e.g., hard-to-extract tubers and nuts), juveniles could no longer efficiently support themselves. Mothers then faced the choice of foraging where weaned offspring could efficiently forage for themselves (at some foraging cost to the mother), or foraging for richer, difficult-to-acquire resources and provisioning their weaned offspring. Once provisioning evolved, others could enhance their fitness by provisioning genetically related juveniles. The long postreproductive lifespan of women (and with it, long human lifespan) was in turn selected for because at some point, the fitness benefits of provisioning grandchildren outweighed the benefits of continued reproduction (e.g., Hawkes et al., 1998, 2000, 2001; Williams, 1957). Selection for the grandmother effect requires that women lived long enough to realize the benefits of provisioning grandchildren; therefore, relatively low mortality across the lifespan forms one basis for the evolution of grandmothering (e.g., Hawkes et al., 1998; Kaplan et al., 2000).

Kaplan et al. (2000) integrate insights from the demographic, grandmothering, and skill-acquisition perspectives. They propose that our extended juvenile dependency and long lifespan coevolved with 1) the dietary transition to high-quality, difficult-to-acquire foods (in this case, game animals), 2) an increased investment in learning complex subsistence strategies to exploit such foods, 3) increased food sharing and provisioning of conspecifics, and 4) healthcare altruism, resulting in lower mortality. In this view, as hominid dietary reliance on high-quality, difficult-to-acquire game resources increased, fitness benefits were realized from a longer prereproductive period of foraging skill and/or knowledge acquisition. This led to the coevolution of an increased flow of resources from older individuals to juveniles in order to support this period of learning. The increased mortality risk of a longer juvenile period and lifespan was countered by the coevolution of mortality reduction via provisioning to sick and injured individuals (Kaplan et al., 2000).

A central feature of these models is that lower extrinsic mortality increases the likelihood that hypothesized benefits from the evolution of delayed maturity, long lifespan, exceptional intelligence and learning capability, and/or intra- and intergenerational resource transfers can be realized (e.g., Alvarez, 2000; Blurton Jones and Marlowe, 2002; Charnov, 1991, 1993; Hill and Hurtado, 1996; Hill and Kaplan, 1999; Janson and Von Shaik, 1993; Kaplan et al., 2000; Pagel and Harvey, 1993). Understanding why humans experience relatively low mortality is therefore central for understanding human evolution and an important set of basic evolved human traits (Hill and Kaplan, 1999). Possible explanations include decreased extrinsic mortality stemming from 1) a reduction in predation among our hominid ancestors via increasingly effective use of weapons and/or coalitional defensive tactics (Hill and Kaplan, 1999), 2) slow growth and adult protection that insulates juveniles from foraging competition, 3) slow growth and adult protection that insulates juveniles from potentially lethal mating competition with adults (e.g., Bogin, 1999; Janson and van Shaik, 1993), 4) increased investment in immune function, and pathogen and parasite resistance (Aiello and Wheeler, 1995; Hill and Kaplan, 1999), and/or 5) care and provisioning for sick and injured individuals (Dettwyler, 1991; Gurven et al., 2000; Hill and Kaplan, 1999; Kaplan et al., 2000; Sugiyama and Chacon, 2000). Here I present ethno-biological data addressing the latter explanation.

Role of ethno-bioarchaeological evidence for investigating mortality reduction via healthcare provisioning

Obviously, health risk is not an evolutionarily novel problem, and bio-archaeological evidence of illness and injury is seen among prehistoric *Homo* sapiens populations (e.g., Alejandro, 1990; Aufderheide and Rodriguez-Martin, 1998; Berger and Trinkaus, 1995; Bush and Zvelebil, 1991; Grauer and Stuart-Macadam, 1998; Lambert, 1993; Martin and Frayer, 1997; Owsley and Jantz, 1994; Rothschild and Martin, 1993; Steckel et al., 2002; Trinkaus, 1983; Walker, 1989; Webb, 1995). Paleoanthropological studies can give an indication of the selection pressure from health risk, and whether or not individuals may have survived health insults that would have temporarily interfered with foraging (e.g., Berger and Trinkaus, 1995; Dettwyler, 1993; Trinkaus, 1983). They are limited in that not all health insults leave osteological signatures, either because the insult affected only soft tissue or because no healing occurred (e.g., when the condition was lethal). While chronic conditions are likely to be well-represented because of their observable effects on skeletons, acute infectious diseases, for instance, are likely to be underrepresented (Steckel et al., 2002). The paleo-pathological evidence thus presents a potentially biased view of pathology prevalence within a population, particularly among those showing little evidence of pathology (e.g., Wood et al., 1992). This "osteological paradox" means that we may find fewer observable signs of pathology in populations suffering high mortality than in those with higher survival rates, at least in cases of rapid changes in health status (e.g., Steckel et al., 2002). Other biases arise because of differences in preservation according to age and sex, with older, very young, and female individuals likely to be underrepresented (Hoppa, 2002).

Further, it is difficult to assess the effects of health insults on behavior simply from osteological or dental evidence. For instance, osteological evidence of degenerative joint disease is not clearly related to whether or not the individual experiences disability (Steckel et al., 2002). The duration of disability (if any) is also difficult to estimate based on osteological evidence alone. People engage in arduous work while suffering from injuries that would appear debilitating in the fossil record (e.g., deformed foot, severe arthritis, loss of limbs; Sugiyama, 1996; Sugiyama and Chacon, 2000), and we do not know the relative frequency with which health insults leaving only soft-tissue (i.e., osteologically invisible) damage occurred in prehistoric populations, the probability that these would cause disability, or the duration of disabilities that did occur. Without this information, it is difficult to know whether or not an individual required provisioning to survive a given health insult.

Ethno-bioarchaeological data from small-scale egalitarian societies have proven useful for testing assumptions about the meaning of bio-archaeological data for understanding behavior and for providing insight into problems that are paleo-anthropologically intractable (e.g., Lukacs and Pastor, 1988; Walker and Hewlett, 1990; Walker et al., 1998). Suggestive evidence does indicate that health insults severe enough to prevent food acquisition occur in present foraging and forager/horticulturalist populations (Bailey, 1991; Gurven et al., 2000; Sugiyama and Chacon, 2000), and that individuals may survive these periods only via relatively costly provisioning by others (e.g., Gurven et al., 2000; Sugiyama and Chacon, 2000). Yet little is known about the frequency and duration of disabling illness and injury among forager and forager-horticulturalist populations who live without consistent access to Western medical attention (but see Bailey, 1991: Baksh and Johnson, 1990; Chagnon, 1975, 1979, 1992; Gurven et al., 2000; Hill and Hurtado, 1996; Kaplan et al., 2000; Sugiyama and Chacon, 2000; Truswell and Hansen, 1976). We do not know how many individuals suffer such events, how they are caused, how long they last, how often they occur across the lifespan, what the effects of surviving these adaptive bottlenecks might have on individual fitness, or the probable effects of care and provisioning on the survival of sick and/or injured individuals (Hill and Kaplan, 1999). Without such data, it is difficult to assess the probable effects of healthcare provisioning on mortality or the probable strength of selection pressure for the evolution of healthcare provisioning. What follows is intended to provide this kind of detailed data for one particular smallscale society.

STUDY POPULATION

The Shiwiar are Upper Amazonian, Jivaroanspeaking people of eastern Ecuador and northeastern Peru. Approximately 2,000 Shiwiar occupy a region along the Corrientes River and its tributaries. Unnavigable rivers have impeded colonial incursion into Shiwiar territory from the west (Ecuador). Shiwiar hostility toward outsiders has deterred colonization dating back at least to the time of the Incas. Border conflict between Ecuador and Peru has limited contact between the Ecuadorian Shiwiar and colonists in the southeast since the 1940s. Prior to the 1970s, Shiwiar lived in scattered households linked by marriage ties and the influence of big men (Descola, 1988). Since seeking missionary contact in the 1970s, Shiwiar have cleared dirt airstrips around which houses now form loose clusters. Although these airstrips provide some access to medical and other facilities outside of Shiwiar territory via missionary aircraft, Shiwiar subsistence remains based on foraging and horticulture, and they have severed ties with evangelical missionaries.

Shiwiar 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 plant products for fruits, starch, construction, and tool material; they have little easy access to Western medicine; and they depend on relatively simple technology for their livelihood. Shiwiar also grow a wide variety of horticultural products, the most important being manioc, plantains, yams, sweet potatoes, and maize. Each female head of household maintains and harvests 2-4 gardens at different stages of production. When she is disabled, her daughters, husband, or close female relatives take over garden tasks. For example, when one woman fell victim to an illness from which she eventually died, two informants reported that they jointly maintained her gardens for 3 months, but stopped when they could no longer sustain the work necessary to do so and adequately maintain their own gardens as well. Widowers may maintain their own gardens, but prior to contact, these men would have been given new wives.

Both blowguns and muzzle-loading shotguns are used in hunting, although single-shot cartridge shotguns are increasingly used when cash is available for shells. Hunting dogs are used to pursue terrestrial animals such as collared peccary (Tayassu tajacu), paca (Agouti paca), acouchy (Myoprocta sp.), and armadillo (Dasypus sp.) (Sugiyama, 1998). Animals such as agouti (Dasyprocta sp.) are also killed by hand when cornered in a log or burrow. Additional terrestrial game taken by Shiwiar includes tapir (Tapirus terrestris) and deer (Mazama americana), while the mixed strategy of blowgun and muzzle-loading shotgun use also yields a variety of primates—primarily woolly (Lagothrix lagothricha), howler (Alouatta sp.), and capuchin (Cebus sp.) monkeys—birds, and small game such as squirrels (Sciurus sp.; Sugiyama, 1998). It also results in low failure rates and relatively high per-hour hunting returns (Sugiyama and Chacon, 2000)

Fishing is done with hook and line and fish poisons. In the rainy season, the bulk of protein comes from hunting, accompanied by fishing with hook and line. During the transition to the dry season, fishing gradually increases as the larger rivers become shallow and fishing with poison becomes increasingly efficient (Sugiyama, 1998, 2000). These dry-season fish poisonings can produce a large quantity of fish (Sugiyama, 2000), which are preserved by smoking them over the fire.

Cultural variability in disabling health crises

A discussion of Shiwiar values is necessary to put this report in perspective. Two concepts are particularly important here. The first is *shiir waras*, literally "good life" or "being." To live a good life is to engage in practices expected of one's age and sex. For males it includes hunting, fishing, clearing gardens, hauling large logs for firewood, protecting one's family, being good to one's wife and children, speaking strongly in favor of one's interests, avenging transgressions against one's interests and those

of one's kin group, fearlessness, and independence. For women it means maintaining productive gardens, harvesting the produce, caring well for one's husband and children, preparing and serving food, keeping a clean house and house clearing, and, as an index of one's productivity, growing manioc sufficient to prepare and serve large quantities of manioc beer (*nihamanch*) to family and visitors.

Kakaram is a complex concept referring not only to how one goes about these activities, but to one's personal, spiritual, and/or political power, a power acquired through and associated with various spiritual qualities (Mader, 1999, p. 295–403). Kakaram is used to refer to men who are killers, i.e., men called upon as something akin to mercenaries in warfare. However, the term is also applied to individuals (including women) who speak powerfully to advance or protect their interests, do not complain about hardship, and are recognized as extremely energetic workers in a society which values hard work. In behavioral terms, they do valued activities faster, more efficiently, and with greater intensity than others. In this context, disability (defined here as a situation that prevents an individual from leaving bed or home in a way that precludes foraging or horticultural work) entails a severity of injury or illness that is stringent by Western middle-class standards; an illness or injury must be severe to warrant the preclusion of activities in favor of bed rest for any significant length of time.

There is a logical connection between these values and Shiwiar subsistence economy and the traditional settlement pattern. Low day-to-day foraging risk and large productive gardens mean that food transfers between households are not usually critical for day-to-day subsistence, thus allowing a relatively high degree of household autonomy and a scattered, low-density settlement pattern of one or two nuclear-family household clusters. This in turn reinforces household autonomy in production and the values of hard work, individuality, and independence, while discouraging lapses in productivity. Nevertheless, food transfers between households do occur. Manioc beer is served in large quantities to all household visitors, at cooperative work parties, and during feasts. Game and fish are supplied to widows, old people, and one's core allies based on matrilocal postmarital residence and cross-cousin preferential marriage ties. In turn, these patterns increase the political importance of attending cooperative labor parties, as a venue for outward display of coalitional ties. Thus, social aid occurs in a number of domains including food sharing, cooperative labor, healing, and warfare. As the data presented below indicate, prolonged provisioning to temporarily disabled individuals also regularly occurs.

METHODS

Data on health insults were gathered from 40 individuals in two communities (resident populations of 67 and 87, respectively) during separate

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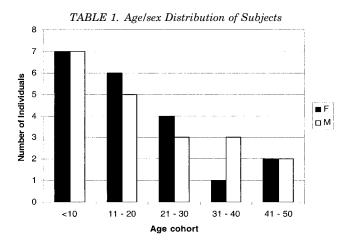
field trips by the author in 1994 and 1995. Additional information was collected from 1993-1998 in these and two additional villages. Participant observation, focal person follows, interviews, and records of injuries and illness were used to provide an ethnographic context for Shiwiar reactions to injury. Genealogical and life-history data were gathered in formal interviews in four Shiwiar and closely related villages. Age estimates for younger subjects are based on birth records, which are accurate to the month and year for approximately the last 25 years. Beyond this, accuracy varies depending on the life circumstances of different individuals, whether or not they ever attended school, or the age at which they held a job for which official documentation was necessary. For individuals roughly 30 and older, ages were cross-checked or determined by calculating birth date in relation to significant historical occurrences (e.g., 1942 border conflict with Peru, first contact with missionaries, or establishment of a mission) and the known age of other individuals. The foraging data cited above come from focal-person follows and departure/return records from two Shiwiar/Achuar villages recorded between 1993–1998.

Nineteen male and 20 female Shiwiar individuals ranging in age from 3-50 were examined to document scars, broken bones, or other observable signs of past health insults, using a standard examination technique. Beginning with the right foot, the examination proceeded up the right leg as far as was comfortable for the subject, and then down the left leg. The left and then right arm were examined, beginning with the fingers of the left hand, followed by the front and then rear of the torso, the neck, face, and head. Visible scars and evidence of broken bones were noted on standardized forms depicting front- and rear-view line drawings of the human form, with enlarged views of the hands and feet. Each health insult recorded was coded as visible, reported (by the informant), current, or some combination of these, to specify the evidence upon which each health-insult record was based. For each health insult observed, the subject was asked to provide 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 was cross-checked with other informants. Disability was defined as a condition causing informants to be confined to the bed or house and precluding foraging or horticultural activities, or a condition which caused them to stop an ongoing subsistence activity and return home. Many of the short-duration events were of the latter type. For instance, a scorpion sting during gardening caused the victim to stop work for that day and precluded work the next day. A standard set of questions about past illnesses, injuries, and treatments received (either from a shaman or Western medical practitioner) was then administered.

Potential biases in data recording

While every scar on the skin of young individuals can be recorded, and much about them recalled, older individuals appear to have been subject to so many lacerations, abrasions, and infections that only the most prominent or most recent can be accurately recorded. Therefore, recorded adult health insults reflect only the most prominent cases, i.e., the most recent and/or most severe. Further, the methods used were exceedingly time-consuming, and there may be individual differences in tolerance for the study, as well as memory effects and reporting bias. These problems could not be entirely solved, but their effect (if any) results in underreporting or missing data for some incidents recorded: independent means of cross-checking information were available, such that overestimation or false reporting were highly likely to be exposed.

Reporting bias was addressed first by using physically observable evidence as the principal source of data. Disability duration and reports of pathologies leaving no visible evidence were cross-checked with informants who were present at the time of the incident in question. Informants were often able to give considerable detail about the injuries or illnesses of close kin. Informants' discussions of health insults, which shaman caused them with what kind of iwianch (evil spirit), and a host of other details indicated frequent correspondence between informants, particularly for major injuries. Informants sometimes asked others to clarify information about which they were unclear, suggesting that they expected others to remember significant health-related incidents. Conversely, informants had little interest in most minor injuries, even though they could often report the cause of the scar in question. Finally, Shiwiar joked about preventable or foolish injuries suggesting that, at least for the incidents reported here, memory bias is not so great as to be damaging to the general picture that emerges from data on long-lasting disability. In fact, memory systems are expected to have evolved to privilege some information over others, based on the ultimate fitness effects of doing so. Particularly "foolish" causes of injury (e.g., swinging a machete around in play and cutting oneself, jumping off the house floor and sustaining a fracture) may be well-remembered specifically because they were clearly preventable. Severe health insults may be well-remembered because they can reveal prevention and healing strategies, as well as critical assessment of social support (i.e., separating true committed "friends" from "fair-weather friends"; Tooby and Cosmides, 1996). However, use of physically observable evidence as the primary data provided an independent basis for recording patterns of injury, such that potential effects of informant memory biases were reduced.



RESULTS Age/sex distribution of sample

Table 1 shows the age/sex distribution of Shiwiar individuals included in the sample. One of the males included in the 31-40-year-old cohort was not examined during the study because he was not present in the village. However, prior interviews documented the cause and duration of a case of near-lethal snakebite. Because prior documentation of all relevant variables was available for this case, 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 ($\chi^2 = 28.6$, df = 28, P = 0.42) or by 10-year age cohorts ($\chi^2 =$ 1.514, df = 4, P = 0.82). Removing the aforementioned individual from the sample does not significantly change this result. This allows direct comparison of frequency, type, and duration of pathological conditions between males and females.

Overview of pathological conditions

Among the 40 individuals examined, 678 injuries and illnesses were recorded. As expected, significant differences were observed in the relative frequencies with which different types of pathologies were observed. Overall, 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 ($\chi^2 = 1,861, df = 16, P < 0.000$). Table 2 provides an overview of the relative frequency of different classes of health insult by sex of victim.

Sex differences in pathologies suffered

Males generally suffer disproportionately more illness and injury than females, a fact that has been attributed both to higher susceptibility to disease and engagement in more behavioral risk-taking among males. Among the Shiwiar, males suffered significantly more pathologies than females (n = 430 and 248, respectively; $\chi^2 = 48.855$, df = 1, P < 0.000). This was true for all pathology types with

adequate sample sizes, including lacerations (n = 226, $\chi^2 = 21.68$, df = 1, P < 0.000), infections (n = 157, $\chi^2 = 6.94$, df = 1, P = 0.008), bites/stings (n = 148, $\chi^2 = 13.08$, df = 1, P < 0.000), puncture wounds (n = 40, $\chi^2 = 6.4$, df = 1, P = 0.011), and abrasions (n = 30, $\chi^2 = 6.53$, df = 1, P = 0.011). Males also suffered more burns than females, though the difference was not quite statistically significant by conventional standards (n = 13, $\chi^2 = 3.77$, df = 1, P = 0.052). Males and females did not differ in number of broken bones (n = 17, $\chi^2 = 0.059$, df = 1, P > 0.8), contusions (n = 5, $\chi^2 = 0.2$, df = 1, P = 0.655), scars of unknown cause (n = 13, $\chi^2 = 0.077$, df = 1, P = 0.782), or incidence of severe chronic or acute pain (n = 22, $\chi^2 = 1.64$, df = 1, P = 0.2), although the sample size for each was relatively small (Table 2).

Soft-tissue wounds

As a class, soft-tissue wounds involving rupture of the epidermis and/or additional tissue not caused by animal bites or stings or resulting in significant ancillary infection (i.e., health insult coded as laceration, puncture, contusion, or abrasion) accounted for 301 (46%) of the 678 pathological conditions observed. Significantly more soft-tissue wounds were observed than infections, the next most frequently observed type of health insult (Table 2, $\chi^2 = 45.275$, df = 1, P < 0.000). Soft-tissue wounds ranged from small abrasions or cuts to serious wounds (e.g., accidental finger amputation, heel slashed to bone, or 5-inch-long gash in thigh). If serious infection was reported, the health insult was coded as infection because this was usually the more serious condition. Fourteen incidences of soft-tissue wounds resulted in serious subsequent bacterial infection, or 4.44% of the 315 primary soft-tissue rupture wounds recorded.

Lacerations were significantly more prevalent than other types of soft-tissue wounds, followed by puncture wounds, abrasions, and contusions (χ^2 = 411.31, df = 3, P = 0.000). Sampling bias may account for some of this difference: contusions can only be seen if the injury is current, and abrasions may be less likely to leave scars than lacerations. Nevertheless, the two most prevalent causes of soft-tissue wounds (machete cuts and injury from branches, sticks, and logs) are also the most frequently cited causes of soft-tissue trauma overall, and these sources of injury appear more likely to cause laceration than contusion or abrasion. The vast majority of lacerations were attributable to accidental causes: machete (46%), running into, being hit by, falling on, or stepping on branches, sticks, or logs (16%), knife (6.5%), axe (4.2%), and lance (3.7%). However, nine lacerations (4%) were sustained during interpersonal violent encounters (Table 3).

All observed puncture wounds stemmed from accidental causes. These included punctures from spines (38.9%), branches or sticks (36%), lances (8.3%), fish spines (2.78%), and harpoons (2.78%), with the remaining 8.3% coming from unidentified

TABLE 2. χ^2 tests, frequency of health insult by type and sex of victim

								Total: column, $\chi^2 = 1,861$, df = 16,			
	Fen	nale	Ma	ale	χ^2 for sex differences			p < 0.000			
Pathology	Observed	Expected	Observed	Observed Expected		df	<i>P</i> -value	Total observed	Total expected		
Laceration	77	113.0	148	113.0	21.68*	1	0.000	226^1	39.9		
Infection	62	78.5	95	78.5	6.94*	1	0.008	$157^{1,2,b1}$	39.9		
Bite/sting	52	74.0	96	74.0	13.08*	1	0.000	148^{2}	39.9		
Puncture wound	12	20.0	28	20.0	6.4**	1	0.011	40	39.9		
Abrasion	8	15.0	22	15.0	6.53**	1	0.011	30	39.9		
Pain	14	11.0	8	11.0	1.64	1	0.2	22^{b2}	39.9		
Fracture	8	8.5	9	8.5	0.059	1	0.8	17^{b1}	39.9		
Burn	3	6.5	10	6.5	3.77	1	0.052	$13^{\rm b2}$	39.9		
Scars unknown	6	13.0	7	13.0	0.077	1	0.782	13^{b2}	39.9		
Contusion	2	2.5	3	2.5	0.2	1	0.655	5	39.9		
Arthritis	1		0	0.0^{3}				1^{b2}	39.9		
Bleeding	1		0	0.0^{3}				1^{b2}	39.9		
Blisters	0		1	0.0^{3}				1^{b2}	39.9		
Concussion	0		1	0.0^{3}				1^{b2}	39.9		
Irritation	1		0	0.0^{3}				1^{b2}	39.9		
Sprain	0		1	0.0^{3}				1^{b2}	39.9		
Swelling	0		1	0.0^{3}				1^{b2}	39.9		
Total	248		430	339.0	48.455*	1	0.000	678	678.0		

 $^{^{1}\}chi^{2} = 50.568$, df = 1, P < 0.000.

causes. Similarly, all observed abrasions were due to accidental causes: branches, sticks, logs, spines, falls, and a fingernail. Finally, of the five contusions observed, three were due to accidents and two to interpersonal violence.

Infections

Infections (including infectious disease, parasitic infection, and bacterial infection of wounds) were the second most common general class of pathological condition observed, accounting for 157 of the 678 pathologies in the sample (23.2%). While the number of infections observed did not differ significantly from the next most frequently observed type of health insult (bites and stings; $\chi^2 = 0.859$, df = 1, P = 0.354), infections were more frequently observed than all remaining types of health insult combined (i.e., all health insults excluding soft-tissue wounds and bites/stings; $\chi^2 = 31.55$, df = 1, P = 0.000, Table 2). Nevertheless, infectious disease is certainly underreported in this sample, since few leave visible traces and only the most recent or severe instances are likely to have been recalled or recorded. For instance, no attempt was made to ask subjects about common colds or flu, because while the actual frequency was expected to be high, the reported frequency was not expected to be accurate. Conversely, informants were specifically asked if they had suffered from the following infectious diseases or parasitic infections known to occur in Shiwiar territory: measles, pertusis, tuberculosis, varicella, leishmaniasis, and malaria.

Parasites accounted for 94 of 157 infections recorded (60%). Ectoparasites were the most common

form of infectious condition, accounting for 63% of parasitic infections and 37.6% of infectious conditions overall (Table 4). Ectoparasites were coded based on their having left visible scars. Informants noted that these scars were usually the result their having scratched the skin off the affected area, causing minor secondary bacterial infection or delaying the healing process. None of these infections were reported as serious; nor was there visible evidence that they were. Common ectoparasites endemic to the study area include mosquitoes, no-see-ums, chiggers, ticks, and bot flies. Although some types of ectoparasites can cause disabling bacterial infection if left untreated (e.g., major infestation of sand flea larvae reportedly caused death among some Yanomamo orphans; Chagnon, 1992; Hagen et al., 2001), none of those reported here caused significant infection. Endoparasitic infection accounted for the remaining 37% of parasitic conditions, and 22.3% of infectious conditions overall. While gastrointestinal amoebas, giardia, and worms are endemic in this population, these were not recorded because it was impossible to get accurate or verifiable reports of periodic bouts of symptomatic diarrhea. The exception to this was a current case of amoebic dysentery observed at the time of the study.

Malaria (*Plasmodium vivax*) occurs in periodic outbreaks in the study area. Bouts of malaria, including when they occurred and whether they resulted in disability, were commonly recalled and corroborated by other informants. Eighteen of the 39 individuals surveyed (46%) had suffered from malaria, often in recurring bouts. In addition, 11 individuals showed evidence of and/or reported leish-

 $^{^{\}text{b1}}_{\text{vs. b2}} \chi^2 = 50.568, \text{ df} = 1, P < 0.000.$

 $^{^{2}\}chi^{2} = 0.859$, df = 1, P = 0.354.

³ Expected frequency less than 5, no χ^2 test performed.

^{*} Significant at P < 0.01 level.

^{**} Significant at P < 0.05 level.

TABLE 3. Frequency of soft-tissue wounds by type and cause

Pathology	Type	Cause	Female	Male	Total
Laceration	Accident	Machete Branch/stick/log	35 11	$64\\24$	99 35
		Na	15	16	31
		Knife	7	7	14
		Axe	2	7	9
		Fall		8	8
		Lance		8	8
		Collision Hit		$rac{2}{2}$	2
		Kicked		$\frac{2}{2}$	8 2 2 2
		Spine		$\frac{2}{2}$	$\overset{2}{2}$
		Blowgun		$\overline{1}$	1
		Nail		$\bar{1}$	$\bar{1}$
		Howler monkey		1	1
	Accident total		70	145	215
	Unknown	Unknown	1		1
	Violence	Assault (unarmed) Light (unarmed)	$rac{2}{2}$	1	$\frac{2}{3}$
		Machete	$\overset{\scriptscriptstyle\mathcal{L}}{2}$	$\frac{1}{2}$	3 4
	Violence Total	Wachete	$\overset{2}{6}$	$\frac{2}{3}$	9
Laceration total			77	148	225
Puncture	Accident	Spine	3	11	14
		Branch/stick/log	6	7	13
		Fall		1	1
		Lance		3	3
		Unknown Fish spine		3 1	3 1
		Harpoon		1	1
	Accident total	Trai poon	9	27	36
	Unknown	Unknown	3	1	4
	Unknown Total		3	1	4
Puncture total			12	28	40
Abrasion	Accident	Spine	2	10	10
		Branch/stick/log Unknown	$\frac{2}{4}$	5 3	$\frac{7}{7}$
		Fall	1	3 3	4
		Fingernail	1	1	$\overset{\mathtt{r}}{2}$
	Accident total	1 mgerman	8	$2\overline{2}$	30
Abrasion total			8	22	30
Contusion	Accident	Branch/stick/log		1	1
		Fall		1	1
	A: tt-1	Hit		1	1
	Accident total			3	3
	Violence	Assault	1		1
	Violence total	Fight	$rac{1}{2}$		$rac{1}{2}$
Contusion total	violence total		2	3	$\frac{2}{5}$
Grand total			99	201	301
Granu total			99	201	301

maniasis (28%); 8 of these individuals were eventually treated with a course of medication, although some did not complete the course of injections necessary for a full cure. Evidence of onchersoriasis (river blindness) was seen in three individuals. Finally, one individual had an infestation of a large unidentified "worm" in the chest area, which ultimately required surgical removal at a mission hospital.

Infectious disease was the second largest class of infectious condition, accounting for 24% of instances recorded. Of the 39 individuals for whom data on disease was recorded, 49% had suffered varicella (chickenpox), 28% sarampion (measles), 5% pertusis, and 2% clear symptoms of later-stage tubercu-

losis; 23% were vaccinated against measles. In addition, 13% reported cases of severe febrile or other illnesses whose specific medical cause could not be identified based on informants' descriptions (informants referred to these, along with most other serious conditions, as the product of shamanistic attacks).

Twenty-five cases of bacterial infection significant enough to result in either drainage of puss or other clear evidence of infection (e.g., tissue inflammation or stench) were recorded in the sample: 14 were subsequent to accidental laceration (6% of lacerations observed), and 11 were from nonaccidental causes. One of the latter, an abscessed tooth severe enough to be draining pus and causing extreme pain

TABLE 4. Frequency of infections by type and cause

Pathology	Type	Cause	Female	Male	Total
Infection	Accident (bacterial)	Machete	2	2	4
		Spine		4	4
		Branch/stick/log	1	1	2
		Unknown	1	3	$\begin{smallmatrix}2\\4\end{smallmatrix}$
	Accident total		4	10	14
	Bacteria (nonaccidental)	Injection	6	3	9
		Ear piercing	1		1
		Abscessed tooth	1		1
	Bacteria total		9	3	11
	Disease				
		Varicella	12	7	19
		Measles	5	6	11
		Unknown	2	3	$^{5}_{2}$
		Pertusis	2		2
		Tuberculosis	1		1
	Disease total		22	16	38
	Parasites				
	Ectoparasite	Insect (various)	10	48	58
	_	Bot fly		1	1
	Ectoparasite total		10	49	59
	Endoparasite	Malaria	8	10	18
		Leishmaniasis	5	6	11
		Onchersoriasis	3		3_2
		Ameoba	1	1	2
		Worm	1		1
	Endoparasite total		18	17	35
	Parasite total		28	66	94
Grand total			62	95	157

for months until it could be treated by a dentist, was current at the time of the study (for a systematic comparative study of dental health including this population, see Walker et al., 1998).

Bites and stings

Bites and stings are ubiquitous features of life in the field area. Most of these come from ectoparasitic insects (see above). People also suffer numerous stings from bees and wasps present in vast swarms during the dry season. One can hardly sit down or lean against something in the house during the height of the dry season without being stung by a wasp. These stings are too prevalent to accurately record and do no significant damage other than minor pain and localized swelling. However, the sting of one species of ground-living wasp, the conga, causes severe pain lasting several hours. By 1998, Africanized bees were reported to have entered the study area and to have inflicted serious injury on a few individuals; to date, no deaths have been reported.

The vast majority of animal bites come from vampire bats, and the majority of victims were young children (predominantly boys) who, according to informants, slept either without mosquito nets or fitfully, thus exposing their bodies to the bats (Table 5). At the time of the study, rabies was not reported to be widespread in the study area; however, in 1997, rabies transmission by vampire bats to cattle was reported just north of the study area.

Although I have seen scorpion stings and caterpillar toxin cause extreme pain and disability lasting

TABLE 5. Frequency of bites and stings by type and cause

Pathology	Type	Female	Male	Grand total	
Bite/sting	Bite	Ant	1		1
J		Bat	27	75	102
		Dog	1	1	2
		Fish		2	2
		Insect	5	5	10
		Lizard		1	1
		Person		1	1
		Pig	1		1
		Piranha		1	1
		Snake	11	7	18
		Squirrel		2	2
	Bite total	•	46	95	141
	Sting	Bee	1		1
	Ü	Scorpion	5	1	6
	Sting total		6	1	7
Grand total			52	96	148

up to 2 days, by far the most significant risk of bites/sting in the study area comes from venomous snakes. Snakebite continues to be a significant cause of death worldwide, and specific adaptations designed to reduce its occurrence are posited for humans and other primate species (e.g., Cook and Mineka, 1991; Mineka and Cook, 1988). The Ecuadorian Amazon is home to numerous widely distributed, deadly species. Fourteen of the individuals sampled suffered 18 cases of snakebite (Table 5): 4 were treated with antivenin, 2 do not appear to have resulted in significant amounts of envenomation, and 12 were untreated at the time of the bite or were

TABLE 6. Frequency of pain, fracture, burn, and other conditions by type and cause

Pathology	Type	Cause	Female	Male	Grand total
Pain	Accident	Unknown		1	1
	Bite	Snake		4	4
	Disease	Unknown	3	1	4
	Unknown	Unknown	2	2	4
	Pregnancy	Birth complications	9		9
Pain total			14	8	22
Fracture	Accident	Branch/stick/log	2	1	3
		Unknown	2	1	3
		Fall	3	4	7
		Collision		2	2
	Violence	Fight	1	1	2
Fracture total			8	9	17
Burn	Accident	Fall		1	1
		Fire	3	8	11
		Shotgun		1	1
Burn total			3	10	13
Scars unknown	Accident	Unknown		1	1
	Unknown	Unknown	6	6	12
Scars unknown total			6	7	13
Arthritis	Disease	Arthritis	1		1
Bleeding	Pregnancy	Birth complications	1		1
Blisters	Unknown	Blisters		1	1
Concussion	Accident	Collision		1	1
Skin irritation	Unknown	Unknown	1		1
Sprain	Accident	Unknown		1	1
Swelling	Bite	Snake		1	1
Grand total			34	38	72

treated by shamans. While shamans are clearly effective in treating certain conditions (e.g., controlling bleeding, setting broken bones, or preventing infection of lacerations), and medicinal plants appear to be effective in treating malaria and dysentery among adults (albeit with harsh side effects), there is no evidence of effective shamanic curing of snakebites among the Shiwiar.

Other health insults

Chronic or prolonged pain (22 cases), bone fractures (17 cases), burns (13 cases), and a variety of other conditions round out the pathological conditions observed in this sample (Table 6). Because pain was often subsequent to or associated with other conditions, reports of pain are here limited to conditions extending longer than, or aside from, the primary condition. For instance, the case of pain caused by snakebite recorded here (Table 6) is not primary pain engendered by the bite, but chronic pain suffered as a consequence of walking upon a limb deformed by snakebite.

Of 17 broken bones recorded, 15 (88%) were sustained in accidents, and 2 (12%) were sustained during fights. Reports of broken bones were verified by cross-checking with other informants, and by feeling for evidence of a healed fracture. Broken bones are sometimes set by a shaman, some of whom are reportedly skilled at this procedure.

Frequency, cause, and duration of disability

Informants from one sample village were asked the duration of disability, if any, associated with

TABLE 7. Duration of disability by frequency of occurrence

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	0.9	68.4	31.6
4	1	0.5	68.8	31.2
4 6	1	0.5	69.3	30.7
7	12	5.6	74.9	25.1
10	1	0.5	75.3	24.7
11	1	0.5	75.8	24.2
12	1	0.5	76.3	23.7
14	7	3.3	79.5	20.5
15	4	1.9	81.4	18.6
17	1	0.5	81.9	18.1
20	1	0.5	82.3	17.7
21	5	2.3	84.7	15.3
23	1	0.5	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	0.5	97.2	2.8
180	1	0.5	97.7	2.3
365	1	0.5	98.1	1.9
Chronic	4	1.9	100.0	0.0
Total	215	100.0		

each health insult reported, and this information was then cross-checked with other informants. The Kruskal-Wallis test indicates that the sex composition of this subsample, including 8 males and 9 females, does not differ significantly from the rest of the larger sample ($\chi^2=0.100$, df = 1, P=0.725), although it does contain an older age cohort (comprised mostly of individuals over age 15 years; $\chi^2=14.31$, df = 1, P=0.000). Estimates of disability

TABLE 8. Frequency of disability duration by pathology

Pathology	Duration in days	Number of cases
Bite/sting	1	5
	3	1
	7	3
	21	2
	30	2
	45	1
	60	2
	90	1
	180	1 1
Dlanding	$\begin{array}{c} 365 \\ 30 \end{array}$	1
Bleeding Fractures	30 7	1
rractures	14	3
	15	1
	20	1
	$\frac{20}{21}$	1
	30	3
	45	1
Burn	7	1
Concussion	3	ī
Contusion	30	ī
Infection	1	$\overline{3}$
	2	1
	6	1
	7	4
	10	1
	12	1
	14	2
	15	$\frac{-}{3}$
	21	$\frac{2}{7}$
	30	
	45	2
	60	1
Laceration	$\frac{4}{2}$	1
	7	3
	11	1
	14	1
	23	1
	30 60	2 1
Pain		$\frac{1}{7}$
raiii	$\begin{array}{c} 2\\17\end{array}$	1
	30	1
	Chronic	4
Puncture	14	1
Total	14	86
10001		00

duration were most often reported by informants in even units of days, weeks, or months. These were converted to number of days for presentation. Table 7 shows the frequency with which disabilities of various durations were reported. Most incidents recorded were minor and resulted in no disability. Of the 215 health insults recorded in this subsample, 86 (40%) resulted in disability lasting a day or longer that could be confidently established, 66 (30.7%) resulted in disability lasting a week or longer, 51 (23.7%) lasted 14 days or longer, and 32 (14.9%) lasted a month or longer (Table 7). In addition, four pathological conditions were chronic and resulted in a reported periodic disability of varying unspecified durations.

Table 8 indicates the types of health insult resulting in disability in this subsample. Included are 28 infections (13.02% of total cases in the subsample), 15 bites (6.97%), 13 cases of debilitating pain (6.05%), 11 broken bones (5.12%), 10 lacerations (4.65%), 4 stings (1.86%), and one burn, one punc-

ture wound, one case of postpartum bleeding, and one case of multiple simultaneous contusions of unknown origin (attributed to shamanistic attack). Those that caused prolonged disability of 2 weeks or longer include 10 of the 11 broken bones, 9 bites (8 of 11 of which were snakebites), 6 lacerations, 6 cases of malaria, 5 bacterial infections stemming from lacerations or puncture wounds, 3 infectious diseases of unknown type, 2 cases of postpartum complications (one near-lethal blood loss, and one severe pain), one multiple contusion, one abscessed tooth, one acute pain from disease of unknown type, one amoebic infestation, and one puncture wound. Additionally, knee injury, tooth abscess, snakebite, stroke, malaria, whooping cough, postpartum infection, respiratory ailment, and severe foot fungus resulting in periods of disability ranging from 5 days to a year were observed during four study periods between 1994–1998, but victims were not part of the sample included here. In contrast, broken fingers, severe beating resulting in black eyes and facial contusions, bites from vampire bats, a laceration in which the tip of a machete was imbedded in the chin, severe laceration of the hand, and a puncture wound from a thorn passing through the thumbnail into the thumb, observed over the same period, did not result in observable disability. Victims of these incidents continued working, with only minor pause to treat the wound.

When they occur, some types of injury/illness are significantly more likely to cause disability than expected if all pathologies are equally likely to cause disability (for pathologies resulting in disability, $\chi^2 = 20.06$, df = 9, P = 0.018). Table 9 indicates both the observed and expected frequency of disability by type of health insult for the subsample, as well as results of relevant chi-square tests for disabling conditions that could contribute to the overall effect. As one would expect, when they occur, fractures are significantly more likely to result in disability than expected by relative prevalence in the subsample $(\chi^2 = 11.438, df = 1, \dot{P} = 0.001)$. Conversely, lacerations appear to be less likely to cause disability than expected ($\chi^2 = 5.675$, df = 1, P = 0.017). This is likely due in part to the high prevalence of minor lacerations which nevertheless leave scars, and local skill at stopping bleeding and infection from lacerations. Neither infections nor pain result in significantly more or less disability than expected by their prevalence in the subsample ($\chi^2 = 1.986$, df = 1, P = 0.159; $\chi^2 = 0.693$, df = 1, P = 0.405, respectively).

Snakebite is highly likely to cause long-term disability. Ten cases for which duration of disability was estimated and cross-checked were recorded. In four of these instances, antivenin was administered. Eight of the 10 cases accounted for 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 6 months, respectively. The foot disfigurement resulted in a life-

TABLE 9. Chi-square tests for frequency of disability by health insult¹

	Observed N	Expected N	Residual	Chi-square	df	P value
Bite/sting	19	18.0	1.0			
Bleeding	1	0.4	0.6			
Fracture	12	4.9	7.1	10.858*	1	0.001
Burn	1	0.4	0.6			
Concussion	1	0.4	0.6			
Contusion	1	0.8	0.2			
Infection	27	30.7	-3.7	0.693	1	0.405
Laceration	10	19.2	-9.2	5.675*	1	0.017
Pain	13	9.0	4.0	1.986	1	0.159
Puncture	1	2.0	-1.0			
Total	86			20.060*	9	0.018

^{*} Statistically significant at P < 0.05.

TABLE 10. Frequency and duration of disability by individual and reproductive success

			Disability duration (days) RS (descending generations)						Descendants % population			
			Disability duration (days)			ys)	R	S (desce	nding gene	erations)		% Total
ID no.	Age	Sex	Total	7–13	14–29	30 +	1st	2nd	Total	In village	% village	population
8	16	\mathbf{f}	2	1	1	0	0	0	0	0	0.0	0.0
5^3	18	\mathbf{f}	8	2	3	2	0	0	0	0	0.0	0.0
$10^{1,3}$	18	f	3	0	1	1	2	0	2	2	1.94	0.40
6^3	25	\mathbf{f}	1	0	0	1	0	0	0	0	0.0	0.0
16^{1-3}	27	\mathbf{f}	6	0	1	3	2	0	2	2	1.94	0.40
12^{1-3}	29	f	14	1	1	4	8^5	0	8	8^5	7.78	1.61
$11^{1,2}$	37	f	4	1	0	3	9^4	5^1	14	7^4	6.80	2.82
2^{1-3}	43	f	10	$ar{2}$	3	5	10	8	18	15	14.56	3.6
17	7	m	2	0	2	0	0	0	0	0	0.0	0.0
15^{3}	15	m	5	0	3	2	0	0	0	0	0.0	0.0
$1^{1,3}$	22	m	4	2	0	2	2	0	2	2	1.94	0.40
7^1	24	m	7	1	5	0	3	0	3	3	2.91	6.0
14^3	34	m	1	0	0	0	9^5	0	9	9^5	8.74	1.81
$3^{1,2}$	36	m	1	na	na	1	3	0	3	3	2.91	0.60
4^1	37	m	3	2	1	0	5	1	6	6	5.83	1.20
9^1	43	m	3	2	0	0	9^4	5^6	14	7^4	6.80	2.82
$13^{1,3}$	50	m	8	$\bar{1}$	ĺ	3	11	14	$\overline{25}$	24	23.30	5.03
Total			82	15	$\overline{22}$	27	54*	28*	82*	73*	70.87*	16.49*

¹ Individuals who had begun reproduction by time of study.

long 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 walk long distances at normal speed without pain.

Demographic and fitness effects of provisioning during healthcare crises

As of 1998, the resident population of the Shiwiar core study area in Ecuador was 410 persons living in six villages (one outside officially designated Shiwiar territory), with an additional 87 siblings or offspring of core Shiwiar individuals living in surrounding villages. While 166 persons make their

home in the two villages from which illness and injury data were collected (63 and 103, respectively), the number of people resident in the villages at any given time varies, as people go visiting or on extended foraging trips. The sample of 40 individuals thus represents 24% of the total population in these villages, and 10.25% of the population of the core study area. The 17-person disability sample represents 16.5% of the population of village two.

Both short- and long-term disability were widely distributed across individuals in the subsample: 16 of 17 individuals reported disability lasting 7 days or longer (94%), 15 reported disability of 14 days or longer (88%), and 11 reported disability of 30 days or longer (64.7%) (Table 10). A specific age of occurrence was reported for 131 of 215 pathological conditions recorded; 51 of these were cases in which disability was observed. There is no significant cor-

² Individuals who suffered pathology likely to be lethal without provisioning after age of first reproduction (during socially recognized adulthood).

³ Individuals who suffered pathology likely to be lethal without provisioning before age of first reproduction.

⁴ Represents identical individuals: offspring of a married couple, both included in sample.

⁵ Eight of these 9 are identical individuals: offspring of a married couple, both included in sample.

⁶ Represents identical individuals.

^{*} Totals calculated based on descendants of a couple, both of whom are included in subsample only once.

f, female; m, male.

	Age															
Duration (days)	Juvenile	21	22	23	24	25	26	27	28	30	35	37	39	41	43	Total
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. Duration of disability by age of occurrence in reproductive lifespan

relation between age at which a health insult occurred and duration of disability ($r^2 = -0.105$, P = 0.465)

In addition to the 51 cases of disability for which an age of occurrence estimate was available, seven cases of disability were identified as occurring during "childhood" or before the birth of the victim's firstborn child. Because complete genealogical data are available for all individuals in the subsample, it was possible to calculate whether or not an individual had entered the reproductive stage of the life cycle, and if so, the number of offspring who survived prior to the injury or illness for 59 cases of disabling event occurring in the subsample (Table 11).

At present, small population size and limited genealogical knowledge for ascending generations (largely the result of scattered settlement and locally endogamous marriage) mean that the data are insufficient to calculate age-specific Shiwiar mortality rates at this time. However, comparing the age of disability occurrence with genealogical data allows a calculation of the probable effects of disability on reproduction and mortality. Thirty-three of 59 (55.9%) cases of disability affected individuals prior to first reproduction, and 26 of 59 (44%) affected individuals after first reproduction. The former include one unmarried woman with no children who, at 26, was well past the usual age of marriage. Duration of these cases ranged from 1-365 days, with 13 of the 33 prereproduction (22%) and 14 of the 26 post-first-reproduction cases (53.85%) causing disability of 1 month or longer. The 13 prereproduction incidents were distributed among 9 of 17 individuals (52.94%) for whom data was available. The 14 post-first-reproduction incidents were distributed among 5 of 12 individuals in the subsample who had begun reproduction at the time of the study (42%). Of these 5 individuals, none were each other's mate. Two of these 5 people do have offspring with a person in the sample who did not suffer life-threatening health crises during their lifetime (Table 10).

If provisioning is required for individuals to survive disability of 30 days or longer, then 11 of 17 individuals in the subsample (64.7%) would have died prior to the study period (5 of whom had begun reproduction by the time of the study). Without provisioning, even if 1) all other living individuals in the village suffered no significant health insults and therefore no higher rate of mortality, and 2) there was no increase in juvenile mortality or decrease in births associated with increase in adult mortality, then 6.6% of the village population would not be alive due to mortality stemming from lack of provisioning. This estimate is extremely conservative.

Using age of disability occurrence in combination with genealogical data makes it possible to calculate the number of surviving offspring and grand-offspring who would not have been born without healthcare provisioning. Fifty-four offspring and 28 grandchildren were born to individuals in the sample (children/grandchildren born to parents/grandparents who are both in the sample were counted only once). However, only two members of the sample had completed or were approaching probable completed fertility. Further, several reproductiveage individuals in the sample were descendants of others in the sample. The demographic, settlement, and marriage structure of the Shiwiar population (matrilocal residence, long period of bride-service, and preferential cross-cousin marriage) means that a significant proportion of the local population is descended from only a few individuals. Thus, strategic healthcare altruism will have large effects on subsequent generations and the population structure as a whole. Forty-six of the 54 (82%) members of the first descending generation of sample individuals were born to individuals after the person survived an incident likely to be fatal without healthcare provisioning. Twenty-seven of 28 (96.4%)

members of the second descending generation were born after a direct ancestor in the sample survived such an incident. In fact, three sample individuals (i.d. numbers 2, 11, and 13, one of whose mate is also included in the sample) who survived health crises expected to be lethal without healthcare provisioning are either the mother or grandparent of the 27 second-generation descendants. Overall, these three individuals are either the parent or grandparent of 46 of the subsample village residents (45%), and 11.5% of the Shiwiar population in the study area. One (i.d. no. 13), is the parent or grandparent of 23% of the subsample village and 5% of the Shiwiar population block. Another (i.d. no. 2) is the direct ancestor of 14.5% of the village and 3.6% of the population (Table 10).

Strategic healthcare allocated to two of these people had enormous demographic and political influence. The first individual (no. 13) suffered a year of disability due to snakebite as a young man. Tissue necrosis and nerve damage left him with a deformed foot. During times of intense warfare in which his father, a noted shaman and warrior, was specifically targeted and eventually killed, this man was shuttled by allies from house to house across Shiwiar territory during the time he was disabled. Not all individuals are provided with this extreme level of care. Even though disabled, the man later distinguished himself as a warrior, and as a young man was called to live with his mother-in-law as headman of the village in which he now resides. He is now one of the two *juunt* (big men or elders) of this village. The second individual (no. 2) is his sister-inlaw: their kin group forms the basis for one of the two dominant coalitions in the Shiwiar study area.

DISCUSSION

Decreased extrinsic mortality is a key feature distinguishing human life history from that of other hominoids, yet how this is achieved has received little attention. The data presented herein indicate that provisioning to sick or injured individuals has large fitness benefits for the recipients, and that incidents resulting in potentially fatal disability occur with sufficient frequency that health aid effectively reduces extrinsic mortality in this population. To the extent that the evolution of long human lifespan, delayed maturity, and the distinctive set of subsistence, social, reproductive, and mental traits hypothesized to have coevolved with them are predicated on the evolution of decreased mortality, then the evolution of provisioning during health crises likely played a significant role in their evolution.

The data presented here were gathered via methods designed to provide evidence of incidence, duration, and fitness effects of healthcare provisioning among a living forager-horticulturalist population that can later be compared with prehistoric osteological remains. Clearly, the Shiwiar do not constitute a perfect model of other populations: no single extant or prehistoric group could provide a compre-

hensive snapshot of the pathogenic, foraging, social, and demographic conditions that form the parameters of our evolutionary history. Nevertheless, the data presented here provide information regarding the incidence of soft-tissue injury, disability duration, and fitness effects of surviving long-term health insults (data that are difficult to obtain from osteological remains alone) in a small-scale culture dependent on foraging for a significant portion of its diet and with little everyday access to Western medical care.

Results reported here would lose comparative relevance for understanding the evolution of mortality reduction via healthcare provisioning if Shiwiar disabling conditions were primarily the result of industrial technology, diseases, or a nonforaging lifestyle. This is not the case: disabling health insults reported are not overwhelmingly due to factors directly associated with Western industrial technology. While machete wounds (and concomitant infections) are common, they are more likely to leave visible evidence than many other types of health insult (e.g., infectious disease, insect bites, endoparasitic infection, or influenza), and are therefore likely to be overrepresented in this sample. On the other hand, because machete cuts leave clear physical evidence on the skin, all machete lacerations causing prolonged disability among sample individuals were almost certainly recorded. Because Shiwiar use machetes as general-purpose cutting, scraping, chopping, and digging tools (and occasionally in hand-to-hand combat), frequency of exposure to cutting tools may be expected to be about equal between machetes and the wood, stone, and bone tools used before they had access to Western implements. Specific comparison is needed to determine whether or not machetes pose a greater or lesser risk of injury/disability than precontact cutting implements. On the one hand, stone tool manufacture and use are expected to result in minor lacerations from flakes and flake fragments not associated with machete use, and some of these are expected to result in infection. On the other hand, efficient use of the machete for chopping or cutting branches involves using it with high speed (achieved by a whiplike use of the blade) to generate high force. Thus, the most severe machete wounds I have observed, both in this sample and over the course of ethnographic fieldwork in general, involve the machete hitting a branch at an odd angle and ricocheting with high force into an appendage of the person wielding it. Because machetes are kept razor-sharp, the result is a severe laceration cutting deep into the soft tissue, usually to the bone of the leg or foot. However, because the sharper the cutting tool, the more "bite" it obtains and the more precisely it can be wielded, severe chopping/cutting accidents might be less likely with a machete than with a stone axe. Indeed, conventional wisdom in our own culture cautions that dull tools cause more injury than sharp ones. In sum, while stone or palmwood axes

might be more likely than machetes to cause injury, they might be less likely than machetes to cause deep lacerations (causing contusions or fractures instead).

When they do occur, fractures among the Shiwiar are more likely to result in long-lasting disability than are lacerations; the Shiwiar may therefore experience less long-term disability from tool use than our hominid ancestors did. Future comparison of the incidence of fracture between Shiwiar and preindustrial foragers can help resolve this issue, since nonlethal fractures leave clear osteological signatures. Among the Shiwiar, the primary cause of fractures is collision with logs and branches. Taken together, naturally occurring causes of laceration (e.g., branches, logs, or spines) produced as many cases of disability lasting a month or longer as Western tools, even though the former represent a smaller proportion of total cases observed (13.7% vs. 19.4%, respectively). Overall, the number of disabilities lasting a month or longer directly attributable to industrial technology (two machete lacerations, and two machete cuts leading to subsequent infection; 14.28%) is less than that from all naturally occurring sources (85.72%). Furthermore, industrial technology is less likely to cause disability of a month or more than expected from its prevalence in this sample (20.6% vs. 79.4%, respectively). Snakebites, fractures, and infections not associated with steel tool technology or Western causes are all more prevalent causes of prolonged disability than machetes, even in this society where machetes are ubiquitous allpurpose tools. Snakes arguably present the greatest threat: snakebite is highly likely to result in disability and resulted in the longest lasting disabilities.

Results of this study indicate that health risk and temporary, potentially lethal disability are recurrent features of Shiwiar life. Disabling conditions were observed in individuals at all stages of the lifespan. Almost all individuals suffer a disability lasting 7 days or longer, almost 90% suffer a disability of 14 days or longer, and over 60% suffer a disability of 30 days or longer. Without provisioning, over 60% of the subsample are unlikely to have survived, or at the very least, the mortality rate of the subsample would be much higher. These findings point to two critical questions: when did healthcare provisioning arise in hominid prehistory, and did specific adaptations evolve which function to elicit and confer provisioning to temporarily disabled individuals?

With regard to the first question, results of this study indicate that chronic conditions are not primary causes of disability for which individuals require provisioning from others. Rather, intense acute conditions are more likely causes of disability severe enough to require aid. This suggests that, in seeking evidence for the evolution of mortality reduction via healthcare provisioning in the hominid record, investigation should focus on evidence for acute major trauma or infection which took interme-

diate time frames to heal (e.g., Dettwyler, 1991). It is fairly clear that provisioning during health crises evolved at least by the time of *Homo sapiens nean-derthalensis* (Berger and Trinkaus, 1995; Dettwyler, 1991; Trinkaus, 1983). A concerted effort should therefore be made to compile available data to test this issue using *Homo erectus* remains, i.e., the time frame at issue in the debates about the evolution of distinctively human life history (e.g., Hawkes et al., 1998; Kaplan et al., 2000).

The second question has begun to be addressed elsewhere, but the results reported herein suggest that further work on the issue is needed. Here I summarize one set of hypotheses about adaptations for healthcare provisioning, as a stimulus to additional research. Once the ability to provide effective provisioning to sick or injured individuals arose, then evolutionarily stable strategies for increasing the likelihood, level, and duration of such care are expected to have evolved (Kaplan et al., 2000; Sugiyama, 1996; Sugiyama and Chacon, 2000). One proposal is that the provisioning of fitness benefits to other individuals makes the provider an important social resource to the recipients, such that recipients are motivated to provide long-term provisioning to the provider when he or she is sick, injured, or otherwise disadvantaged (Dettwyler, 1991; Kaplan and Hill, 1985; Sugiyama, 1996; Sugiyama and Chacon, 2000; Tooby and Cosmides, 1996). Gurven et al. (2000) expand upon these and related ideas, arguing that the relative proportion of an individual's kills transferred to a recipient provides a clear signal of the provider's "generosity," which can be seen as an indicator of the provider's commitment to the recipient's interests (see also Sugiyama, 1996; Sugiyama and Chacon, 2000; Sugiyama and Scalise Sugiyama, 2003). Zahavi and Zahavi (1997) argue that, the more costly a signal, the more confidence can be placed in its "honesty" because the very cost of the signal makes it unprofitable to fake. Recipients of the signal benefit because they receive reliable information about the quality being signaled. Benefit transfers can provide a costly signal of both intent and value as a coalitional ally (e.g., Hawkes and Bird, 2002; Zahavi and Zahavi, 1997).

Most relevant work on benefit transfers among foragers focuses on food transfers. The most widely cited explanations for asymmetric food transfers (kin selection, reciprocal altruism, foraging risk reduction, and "showing off") leave unexplained variance in food transfer behavior (e.g., Bird et al., 2002; Bird and Smith, 2001; Hawkes, 1991; Hawkes et al., 1997, 2001; Kaplan and Hill, 1985; Sugiyama, 1996; Wiessner, 2002; Winterhalder, 1996). Gurven et al. (2000) showed that slightly over half the food given to temporarily disabled Ache foragers is predicted by the generosity of food sharing exhibited by the disabled individual when he/she is healthy. Other important benefits can be given to others besides food, and generous provisioning of these is also expected to result in increased solicitude to those who provide

them (e.g., Dettwyler, 1991; Gurven et al., 2000; Sugiyama, 1996; Sugiyama and Chacon, 2000; Tooby and Cosmides, 1996).

While some researchers have discounted "risk reduction hypotheses" for explaining some of the unexplained variance in food transfers, these researchers focus on whether food sharing functions to reduce day-to-day foraging risk, expecting balanced reciprocity over time (e.g., Bird et al., 2002; Hawkes and Bird, 2002). Health insurance models also suffer because individuals are expected to discount future healthcare benefits against the current cost of maintaining alliances with potential healthcare providers, and the probability that healthcare aid will be needed. It is fairly clear, however, that balanced reciprocity is unlikely to solve the health risk problem (Sugiyama, 1996; Sugiyama and Chacon, 2000), and from this perspective, the generous consistent conferral of benefits to others does not reap enhanced healthcare provisioning based on the logic of reciprocal altruism. Rather, those who honestly signal positive coalitional intent through costly benefit transfers to others are for that very reason important individuals for those to whom they signal: reliable allies or "true friends" are a real benefit (e.g., Gurven et al., 2000; Sugiyama, 1996; Tooby and Cosmides, 1996). The cost is an expected feature of signal quality regarding coalitional intent (e.g., Gintis et al., 2000; Hawkes and Bird, 2002; Zahavi and Zahavi, 1997). Additionally, those who receive signals of generosity gain not only a coalitional signal, but the benefits conferred as a signal of coalitional intent, and should therefore be even more highly motivated to retain access to those benefits if they are threatened. A major threat to future access to those benefits occurs when their provider is grievously injured. Healthcare to an individual who has been consistently generous to you is one way to buffer this threat. The recipient of costly signals of intent thus receives generously confered benefits in a manner closer to byproduct mutualism than to reciprocal altruism per se. This is because the value of benefits conferred loses signal value if they are "repaid." Finally, results from this study indicate that the future probability that one will need lifesaving healthcare aid is high, as are the fitness benefits of receiving extended care. To date, only Gurven et al. (2000) have attempted a direct test of the health-risk buffering or signaling-generosity hypothesis. As noted, results from that study lend support to the health-risk buffering hypothesis. Given the importance of mortality reduction to the evolution of human life history, it seems that further testing of health-risk buffering aspects of cooperative signaling is warranted.

CONCLUSIONS

Mortality reduction is a critical factor allowing the evolution of delayed maturity, long lifespan, and a variety of distinctive human traits. As extrinsic mortality decreases, relative fitness benefits of delayed maturity and long lifespan increase due to the increased probability of living long enough to realize fitness benefits from investments in further growth, production, and/or skill and knowledge acquisition. In turn, the fitness benefits of investment in long-term foraging cooperation, and/or noncontingent, asymmetric, and/or intergenerational food transfers may also increase, due to an increased probability that the individual will live long enough to realize the payoffs of these investments. As Hill and Kaplan (1999) noted, understanding the evolution of decreased human mortality is therefore central for understanding basic features of human evolution.

Results from this study indicate that 1) sickness and injury occur with significant frequency throughout the lifespan; 2) these periods are temporally unpredictable; 3) these periods are not primarily attributable to impacts from the Western/industrial world; 4) males suffer more health insults than females; 5) most living individuals suffer health crises during their lifetimes that are likely to have been lethal without extended provisioning; 6) provisioning during health crises reduces mortality in this population; and 7) the Shiwiar population structure and lifeway are dependent on infrequent but extended provisioning to temporarily disabled individuals.

Evidence regarding the frequency, duration, and fitness effects of disabling conditions in forager and forager-horticulturalist societies with little access to Western medicine is sparse. Given this, as well as the well-developed literature in paleopathology and the hypothesized importance of health risk for the evolution of human sociality, studies such as this one would be profitably added to the basic data collected on all remaining foraging and forager-horticulturalist societies. Comparative data to estimate disability risk, actual rates of mortality reduction via healthcare provisioning, and the relative fitness benefits of healthcare altruism within specific populations are needed to estimate the probable strength of selection pressure from health risk. Compilation of hominid evidence for acute disabling health insults of more than a month's duration is needed to identify the emergence of provisioning during health crises. Finally, further testing of hypotheses about specific health-risk buffering adaptations is warranted.

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LITERATURE CITED

- Aiello L, Wheeler P. 1995. The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. Curr Anthropol 36:199–221.
- Alejandro P. 1990. Notes on populational significance of paleopathological conditions: health, illness and death in the past. Barcelona: Fundaci.
- Alvarez H. 2000. Grandmother hypothesis and primate life histories. Am J Phys Anthropol 113:435–450.
- Aufderheide AC, Rodriguez-Martin C. 1998. The Cambridge encyclopedia of human paleopathology. Cambridge: Cambridge University Press.
- Bailey RC. 1991. The behavioral ecology of Efe Pygmy men in the Ituri Forest, Zaire. Ann Arbor: Museum of Anthropology, University of Michigan.
- Baksh M, Johnson A. 1990. Insurance policies among the Machiguenga: an ethnographic analysis of risk management in a non-Western society. In: Cashdan E, editor. Risk and uncertainty in tribal and peasant economies. San Francisco: Westview Press. p 193–228.
- Berger TD, Trinkaus E. 1995. Patterns of trauma among the Neanderthals. J Archaeol Sci 22:841–852.
- Bird D, Bird RB. 2002a. Children on the reef: slow learning or strategic foraging? Hum Nat 13:269–298.
- Bird RB, Bird D. 2002b. Constraints of knowing or constraints of growing? Fishing and collecting by the children of Mer. Hum Nat 13:239–265.
- Bird RB, Smith EA. 2001. Turtle hunting and tombstone opening: public generosity as costly signaling. Evol Hum Behav 21:245– 261
- Bird RB, Bird D, Smith EA, Kushnick GC. 2002. Risk and reciprocity in Meriam food sharing. Evol Hum Behav 23:297–321.
- Blurton Jones N. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. Soc Sci Info 26:31–54.
- Blurton Jones NG, Marlowe F. 2002. Selection for delayed maturity: does it take 20 years to learn to hunt and gather? Hum Nat 13:199–238.
- Blurton Jones NG, Hawkes K, Draper P. 1994. Differences between Hadza and !Kung children's work: original affluence or practical reason? In: Burch ES, Ellanna LJ. Key issues in hunter-gatherer research. Oxford: Berg. p 189–215.
- Bock J. 2002. Learning, life history, and productivity: children's lives in the Okavango Delta, Botswana. Hum Nat 13:161–197.
- Boesch C, Boesch H. 2000. The chimpanzees of the Taï Forest: behavioral ecology and evolution. Oxford: Oxford University Press.
- Bogin B. 1999. Patterns of human growth. Cambridge: Cambridge University Press.
- Bonner JT. 1965. Size and cycle: an essay in the structure of biology. Princeton: Princeton University Press.
- Bush H, Zvelebil M. 1991. Health in past societies: biocultural interpretations of human skeletal remains in archaeological contexts. Oxford: Tempus Reparatum.
- Byrne RW. 1997. Machiavellian intelligence. Evo Anthropol 5:172–180.
- Chagnon NA. 1975. Genealogy, solidarity and relatedness: limits to local group size and patterns of fissioning in an expanding population. Yrbk Phys Anthropol 19:95–110.
- Chagnon NA. 1979. Mate competition, favoring close kin, and village fissioning among the Yanomamö Indians. In: Chagnon NA, Irons W. Evolutionary biology and human social behavior: an anthropological perspective. North Scituate, MA: Duxbury. p 86–131.
- Chagnon NA. 1992. Yanomamö. New York: Harcourt Brace.

- Charnov EL. 1993. Life history invariants: some explanations of symmetry in evolutionary ecology. Oxford: Oxford University.
- Charnov EL, Berrigan D. 1993. Why do female primates have such long lifespans and so few babies? Or life in the slow lane. Evol Anthropol 1:191–194.
- Charnov EL, Schaffer WM. 1973. Life-history consequences of natural selection: Cole's result revisited. Am Nat 107:791–793.
- Cook M, Mineka S. 1991. Selective associations in the origins of phobic fears and their implications for behavior therapy. In: Martin PR, editor. Handbook of behavior therapy and psychological science: an integrative approach. New York: Pergamon. p 413–434.
- Descola P. 1988. La Selva Culta: simbolismo y praxis en la ecologia de los Achuar, 1a ed. Quito, Ecuador: Ediciones Abya-Yala.
- Dettwyler K. 1991. Can paleopathology provide evidence for compassion? Am J Phys Anthropol 84:375–384.
- Fisher RA. 1958. The genetical theory of natural selection. New York: Dover.
- Geary D, Flinn M. 2001. Evolution of human parental behavior and the human family. Parent Sci Pract 1:5–61.
- Gintis H, Smith EA, Bowles S. 2000. Costly signaling and cooperation. J Theor Biol 213:103–119.
- Grauer AL, Stuart-Macadam P. 1998. Sex and gender in paleopathological perspective. Cambridge: Cambridge University.
- Gurven M, Allen-Arave W, Hill K, Hurtado AM. 2000. "It's a Wonderful Life": signaling generosity among the Ache of Paraguay. Evol Hum Behav 21:263–282.
- Hagen EH, Hames RB, Craig NM, Lauer MT, Price ME. 2001. Parental investment and child health in a Yanomamö village suffering short-term food stress. J Biosoc Sci 33:503–528.
- Hamilton WD. 1966. The molding of senescence by natural selection. J Theor Biol 12:12–45.
- Harvey PH, Clutton-Brock TH. 1985. Life history variation in primates. Evolution 39:559–581.
- Harvey PH, Zammuto RM. 1985. Patterns of mortality and age at first reproduction in natural populations of mammals. Nature 315:318–329.
- Hawkes K. 1991. Showing off—tests of an hypothesis about mens foraging goals. Ethol Sociobiol 12: 29–54.
- Hawkes K, Bird RB. 2002. Showing off, handicap signaling, and the evolution of men's work. Evol Anthropol 11:58–67.
- Hawkes K, O'Connell JF, Blurton Jones NG. 1997. Hardworking Hadza grandmothers. In: Standen V, Foley RA, editors. Comparative socioecology of humans and other mamals. London: Basil Blackwell. p 341–366.
- Hawkes K, O'Connell JF, Blurton Jones NG, Alvarez H, Charnov EL. 1998. Grandmothering, menopause, and the evolution of human life histories. Proc Natl Acad Sci USA 95:1336–1339.
- Hawkes K, O'Connell JF, Blurton Jones NG, Alvarez H, Charnov EL. 2000. The grandmother hypothesis and human evolution. In: Cronk L, Chagnon NA, Irons W, editors. Human behavior and adaptation: an anthropological perspective. New York: Aldine. p 371–395.
- Hawkes K, O'Connell JF, Blurton Jones NG. 2001. Hunting and nuclear families: some lessons from the Hadza about men's work. Curr Anthropol 42:631–695.
- Hewlett BS. 1992. Father-child relations: cultural and biosocial contexts. New York: Aldine.
- Hill K. 2002. Altruistic cooperation during foraging by the Ache, and the evolved human predispostion to cooperate. Hum Nat 13:105–128.
- Hill K, Hurtado AM. 1996. Ache life history: the ecology and demography of a foraging people. New York: Aldine.
- Hill K, Kaplan H. 1999. Life history traits in humans: theory and empirical studies. Annu Rev Anthropol 28:397–430.
- Hill K, Boesch C, Goodall J, Pusey A, Williams J, Wrangham R. 2001. Mortality rates among wild chimpanzees. J Hum Evol 40:437-450.
- Hoppa RD. 2002. Paleodemography: looking back and thinking ahead. In: Hoppa RD, Vaupel JW, editors. Paleodemography: age distribution from skeletal samples. Cambridge: Cambridge University. p 9–28.

- Horn HS. 1978. Optimal tactics of reproduction and life history. In: Krebs JR, Davies NB, editors. Behavioral ecology: an evolutionary approach. Sunderland, MA: Sinauer. p 411–429.
- Janson CH, Von Shaik CP. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira M, Fairbanks L, editors. Juvenile primates: life history, development and behavior. New York: Oxford University Press. p 57-76.
- Kaplan H, Hill K. 1985. Food sharing among Ache foragers: tests of explanatory hypotheses. Curr Anthropol 26:223–245.
- Kaplan H, Hill K, Lancaster J, Hurtado ÅM. 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol Anthropol 9:156–185.
- Lambert P. 1993. Health in prehistoric populations of the Santa Barbara Channel Islands. Am Antiq 58:504–522.
- Lindstedt SL, Swain SD. 1988. Body size as a constraint of design and function. In: Boyce MS, editor. Evolution of life histories of mammals. New Haven: Yale University Press. p 93–105.
- Lukacs JR, Pastor RF. 1988. Activity-induced patterns of dental abrasion in prehistoric Pakistan: evidence from Mehrgarh and Harappa. Am J Phys Anthropol 76:377–398.
- MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton: Princeton University Press.
- Mader E. 1999. Poder y metamorphosis. Quito: Abya Yala.
- Marlowe F. 1999. Showoffs or providers? The parenting effort of Hadza men. Evol Hum Behav 20:391–404.
- Marlowe F. 2001. Male contribution to diet and female reproductive success among foragers. Curr Anthropol 42:755–763.
- Martin DL, Frayer DW. 1997. Troubled times: violence and warfare in the past. War and society volume 3. Amsterdam: Gordon and Breach.
- Medawar PB. 1952. An unsolved problem in biology. London: Lewis.
- Mineka S, Cook M. 1988. Social learning and the acquisition of snake fear in monkeys. In: Zentall TR, Galef BG, editors. Social learning: psychological and biological perspectives. Hillsdale, NJ: Erlbaum. p 51–73.
- Nishida T, Takasaki H, Takahata Y. 1990. Demography and reproductive profiles. In: Nishida T, editor. The chimpanzees of the Mahale Mountains. Tokyo: University of Tokyo Press. p 3–97.
- Owsley DW, Jantz RL. 1994. Skeletal biology in the Great Plains: migration, warfare, health, and subsistence. Washington, DC: Smithsonian Institution.
- Pagel MD, Harvey PH. 1993. Evolution of the juvenile period in primates. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. New York: Oxford University Press. p 28–37.
- Pereira ME. 1993. Juvenility in animals. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. New York: Oxford University Press. p 17–27.
- Pereira ME, Altman J. 1985. Development of social behavior in free-living nonhuman primates. In: Watts ES, editor. Nonhuman primate models for human growth and development. New York: Liss. p 217–309.
- Pereira ME, Fairbanks LA. 1993. Why be juvenile? In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. New York: Oxford University Press. p 13–15.
- Promislow DEL, Harvey PH. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. J Zool 220:417–437.
- Pusey A. 1990. Behavioral changes at adolescence in chimpanzees. Behavior 115:203–246.
- Rose MR. 1983. Theories of life-history evolution. Am Zool 23:15–23.
- Rothschild BM, Martin LD 1993. Paleopathology: disease in the fossil record. Boca Raton: CRC Press.

- Schaffer WM. 1974. Selection for optimal life histories: the effects of age structure. Ecology 55:291–303.
- Steckel RH, Rose JC, Larsen CS, Walker PL. 2002. Skeletal health in the Western Hemisphere from 4000 BC to the present. Evol Anthropol 11:142–155.
- Sugiyama LS. 1996. In search of the adapted mind: a study of human cognitive adaptations among the Shiwiar of Ecuador and the Yora of Peru [dissertation]. Ann Arbor, MI: UMI.
- Sugiyama LS. 1998. Evolutionary ecology of Native Amazonians. Institute for Latin American Studies, post-graduate lecture series on biological studies in Latin America. University of Vienna, Austria.
- Sugiyama LS, Chacon R. 2000. Effects of illness and injury on foraging among the Yora and Shiwiar: pathology risk as adaptive problem. In: Cronk L, Chagnon NA, Irons W, editors. Human behavior and adaptation: an anthropological perspective. New York: Aldine. p 371–395.
- Sugiyama LS, Scalise Sugiyama M. 2003. Social roles, prestige, and health risk: social niche specialization as a risk-buffering strategy. Hum Nat (in press).
- Tooby J, Cosmides L. 1996. Friendship and the banker's paradox: other pathways to the evolution of adaptations for altruism. Proc Br Acad 88:119–143.
- Tooby J, DeVore I. 1987. The reconstruction of hominid behavioral evolution through strategic modeling. In: Kinzey WG, editor. The evolution of human behavior: primate models. Albany: State University of New York. p 183–237.
- Trinkaus E. 1983. The Shanidar Neandertals. New York: Academic Press.
- Truswell AS, Hansen JDL. 1976. Medical research among the !Kung. In: Lee RB, DeVore I, editors. Kalahari hunter-gatherers: studies of the !Kung San and their neighbors. Cambridge, MA: Harvard University Press.
- Walker PL. 1989. Cranial injuries as evidence of violence in prehistoric southern California. Am J of Phys Anthropol 80: 313–323.
- Walker PL, Hewlett BS. 1990. Dental health diet and social status among Central African foragers and farmers. Am Anthropol 92:383–398.
- Walker PL, Sugiyama LS, Chacon R. 1998. Diet, dental health, and cultural change among recently contacted South American Indian hunter-horticulturalists. In: Lukacs J, Hemphill BE, editors. Human dental development, morphology and pathology: essays in honor of Albert Dahlberg. Eugene, Oregon: University of Oregon Anthropological Papers. p 356–386.
- Walker R, Hill K, Kaplan H, McMillan G. Age-dependency in hunting ability among the Ache of eastern Paraguay. J Hum Evol 42:639-657.
- Watts DP, Pusey AE. 1993. Behavior of juvenile and adolescent great apes. In: Pereira ME, Fairbanks LA, editors Juvenile primates: life history, development, and behavior. New York: Oxford University Press. p 148–171.
- Webb S. 1995. Palaeopathology of Aboriginal Australians: health and disease across a hunter-gatherer continent. Cambridge: Cambridge University.
- Wiessner P. 2002. Hunting, healing, and hxaro exchange—a longterm perspective on !Kung (Ju/hoansi) large-game hunting Evol Hum Behav 23:407–436.
- Williams GC. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:298-411.
- Williams GC. 1966. Adaptation and natural selection. Princeton, NJ: Princeton University Press.
- Winterhalder B. 1996. Social foraging and the behavioral ecology of intragroup resource transfers. Evol Anthropol 5:46–57.
- Wood JW, Milner GR, Harpending HC, Weiss KM. 1992. The osteological paradox: problems of inferring prehistoric health from skeletal samples. Curr Anthropol 33:343–371.
- Zahavi A, Zahavi A. 1997. The handicap principle: a missing piece of Darwin's puzzle. New York: Oxford.