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# From the womb to the tomb: The role of transfers in shaping the evolved human life history

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ABSTRACT

Humans are the longest living and slowest growing of all primates. Although most primates are social, humans are highly cooperative and social in ways that likely co-evolved with the slow human life history. In this paper we highlight the role of resource transfers and non-material assistance within and across generations in shaping low human mortality rates. The use of complex cooperative strategies to minimize risk is a necessary precursor for selecting further reductions in mortality rate in late adulthood. In conjunction with changes in the age-profile of production, the impacts of resource transfers and other forms of cooperation on reducing mortality likely played an important role in selection on post-reproductive lifespan throughout human evolution. Using medical data and ethnographic interviews, we explore several types of common risks experienced by Tsimane forager–horticulturalists, and quantify the types and targets of aid. Our results illustrate the importance of transfers in several key domains and suggest that the absence of transfers would greatly increase human mortality rates throughout the life course.



## 1. Introduction

Traditional life history theory requires that personal energy budgets cover the expenses of growth, maintenance and reproduction, such that body size and resource production are often highly significant predictors of the pace and timing of fundamental life processes (Stearns, 1992). Social animals, however, can lend and borrow critical resources in ways that inflate budgets and allow investments that otherwise would not be possible given a reliance on one's own efforts. The ability to lend and borrow resources and provide and solicit other forms of aid within and across generations (i.e. intertemporal budgets) can strongly impact selection on age-schedules of mortality and fertility, and prolong lifespan (Amdam and Page, 2005; Kaplan et al., 2000; Lee, 2003; Robson and Kaplan, 2003). Resource transfers improve the likelihood that juveniles reach adulthood and reduce adult mortality, thereby extending adult lifespan. Fitness impacts of transfers made by donors of different ages determine the value of being alive at those ages in ways that differ from the standard Hamiltonian formulation of the "force of selection" which includes direct reproduction but ignores transfers (Baudisch, 2005; Bourke, 2007). Transfers are often costly to the donor and therefore require that the donor recoups the loss by receiving fitness benefits through shared relatedness, future cooperative exchange, or direct reproduction (Hamilton, 1964; Trivers, 1971).

Several recent models have included intergenerational transfers that co-evolve with lifespan in social species (Cyrus Chu and Lee, 2006; Kaplan and Robson, 2002, 2009; Lee, 2003). These models make claims about the magnitude and direction of transfers, but assume an asexual population, and so kinship is not a part of these models. Nor are transfers specifically defined, only referring to energy flow, production and fitness in a general way. In order to further develop these models, empirical information is needed on material and non-material transfers in human populations living under similar conditions in which our ancestors evolved. Extant populations of hunter–gatherers and horticulturalists are energy-limited and physically active, experience natural fertility and lack access to public sanitation, health care and other modern services that increase welfare. Information on the kinds and frequency of risks afflicting humans in such an environment, and the extent to which transfers help overcome harmful consequences of these risks, is critical for understanding how the human life history evolved.

To date, most empirical work on transfers has focused on food exchange (Gurven, 2004; Winterhalder, 1997). Hunter–gatherer diets are often characterized by high levels of acquisition variance due to luck, resource mobility and differences in skill. For example, the

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probability that a Hadza, Hiwi and Ache hunter is successful on a hunt is about 4%, 35%, and 60%, respectively (Hill and Hurtado, 2009). Entry into this production niche therefore carries the cost of many unsuccessful foraging attempts. Such high variance is common to most foraging economies because humans subsist largely on difficult-to-acquire resources including meat, fish and extracted items like larvae, honey and roots. It often takes years for adolescents to develop foraging proficiency, resulting in another form of acquisition variance due to variation in age and ability. The human foraging niche therefore fosters a high level of dependency among juveniles for many years. In foraging and mixed foraging–horticultural economies, individuals do not produce more food than they consume until their late teens (Gurven and Kaplan, 2006; Kaplan, 1994; Lee, 1996).[1] However, the risk of food shortfalls occurs at all ages, as even adults in their peak production years cannot consistently meet the daily caloric needs of their large families.

The human foraging niche not only allows the possibility of greater risk of food shortfalls over the life course, but also includes a variety of other important risks that can impact fitness. Illness left untreated can lead to cascading morbidity and possibly death, and often impairs the ability to produce food or perform other important daily tasks. Death or divorce renders dependent children vulnerable to food shortage, disease and lack of protection, and renders adults vulnerable to labor shortage. Conflict left unresolved, especially among kin, can result in fractured social and sharing networks, migration, fighting, and homicide. Theft and breakage of important tools, possessions or other resources can potentially disrupt production and often requires substantial costs to replace. Human cooperation and sociality have evolved to reduce risk in these fitness-relevant domains. While instances of non-food transfers in social species are not rare (e.g. Carey and Gruenfelder, 1997; Galef, 2001), humans may be unique in the breadth and volume of transfers across different domains.

This paper examines sources of risk and cooperative solutions to risk reduction among Tsimane forager–horticulturalists in lowland Bolivia. In addition to the basic problem of daily food shortfalls, we focus on the prevalent problems of longer-term food shortages, illness and disability, parental and spousal loss due to death or divorce, social conflict and tool loss. This is the first systematic survey of multiple risks and transfers in an indigenous population living under fairly traditional conditions. Study of these populations can act as an important lens for gaining insight into past conditions and selection pressures that shaped the evolved human life history. We argue that the cooperative solutions to common problems helped humans survive from birth to adulthood, and helped adults live longer lives. We expect: (1) the level of risk to be non-trivial across the domains investigated, (2) the level of support to be substantial, with (3) targeting of close kin, and (4) substantial contributions from adults over the age of 40, which increase the fitness value of being alive at late ages, including during the post-menopausal life stage.

## 2. Material and methods

The Tsimane Health and Life History Project (THLHP)[2] aims to understand the rate of actuarial and physiological senescence in ecological and cultural contexts. Tsimane are Bolivian forager–horticulturalists who subsist from horticulture (plantains, manioc, rice and corn), hunting, fishing and fruit gathering. Closely related families often reside together in residential clusters, which act as units of cooperative production and consumption. Tsimane have relatively short life expectancy, high work load, and minimal access to modern amenities such as healthcare, sanitation and electricity (Gurven et al., 2007). THLHP employs research methods commonly utilized by epidemiologists, biodemographers, and anthropologists. All methods are approved by Human Subjects Review Boards at UCSB and UNM, and approved by the Tsimane government council, village leaders and study participants.

### 2.1. Shocks interview

A detailed retrospective interview was administered to 671 individuals age 16+ by a bilingual (Spanish–Tsimane) research assistant from March 2005 to July 2006. Participants were queried about numerous aspects of recent illness, crop failure, theft, residence, divorce and conflict, including frequency over a specified time interval, impact of the loss, and type and amount of assistance received and given. Kinship among donors and recipients of assistance was recorded, and ages were assigned to named helpers or recipients based on prior demographic analysis and census records (Gurven et al., 2007).

### 2.2. Production and sharing interview

From January 2005 to December 2009, adults from 11 villages were interviewed once or twice per week about time allocation to work for each co-resident individual over age 6 during the previous two days (n = 1245 individuals). We recorded number of hours engaged in subsistence macro-categories (i.e., hunting, fishing, garden labor, foraging), specifying type of activity within each macro-category (e.g., hook and line fishing, harvesting rice, hunting with bow/arrow). For each activity per person per day we inquired about quantities produced and shared. Each family was interviewed an average of 45.5 times (SD = 20.4), yielding a mean of 92.8 sample days per individual. For details about estimation of age-specific production, consumption and distribution, see Hooper (2011).

### 2.3. Medical exam/interview

Bolivian physicians working with bilingual Tsimane research assistants diagnosed patient illnesses during annual medical exams as part of the THLHP. Diagnoses from the International Classification of Disease (ICD-10) are grouped into gastrointestinal, respiratory, and other ailments for exams conducted from 2002 to 2004.

## 3. Results

### 3.1. Incapacitating illness/injury

Infections and other ailments are common occurrences, with <10% of adults diagnosed as "healthy" in a given year (Fig. 1). Common diagnoses impacting infants and children include diarrhea, pneumonias, fevers and macro-parasites; adults often suffer from osteoarthritis, respiratory infections, skin infections, common cold, urinary tract infections, and injuries such as falls and machete wounds.[3] Despite this high level of morbidity, many of these illnesses and injuries do not necessarily incapacitate an individual. Tsimane often work and engage

[1] Agricultural tasks appear to increase the production of teenagers and lower the age of caloric independence to the mid-teens (Kramer, 2002).

[2] http://www.unm.edu/tsimane.

[3] Ancestral humans were probably exposed to a variety of viruses, bacteria, protozoans and parasites due to the consumption of meat and fish in our omnivorous diet (Finch and Stanford, 2004). For example, molecular genetics and paleoparasitological studies show that helminthic parasites have long been a central feature of hominin disease ecology (Goncalves et al., 2003; Hurtado et al., 2008). There is growing evidence that human foragers experienced high rates of infectious disease prior to the advent of agriculture. Phylogenetic evidence for several pathogens, including smallpox, malaria and tuberculosis, (previously assumed to post-date the advent of agriculture and animal domestication) now suggests an earlier evolutionary history of exposure (see review in Pearce-Duvet, 2006). Sexually transmitted diseases also likely have a long evolutionary history among humans (Donovan, 2000). Antibodies to viral infections, such as herpes, Epstein–Barr and varicella have been documented in relatively isolated Amazonian groups (Black et al., 1970; Salzano and Callegari-Jacques, 1988). Cytomegalovirus, pneumonias, intestinal geohelminths, herpes, hepatitis B and arboviruses have long co-existed among pre-contact Amazonian populations (Black, 1975). Thus, prior to and following the advent of agriculture, humans experienced a greater pathogen burden than is currently experienced in developed nations (Hurtado et al., 2008; McKeown, 1976).