ANALYSES OF SEX-RATIOS AMONG RESIDENTS OF THE KHUMBU REGION OF NEPAL SUPPORT THE TRIVERS WILLARD HYPOTHESIS

A Thesis
Submitted to
the Temple University Graduate Board

In Partial Fulfillment
Of the Requirements for the Degree
MASTER OF ARTS

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January, 2011

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ABSTRACT

The Trivers-Willard hypothesis predicts a sex ratio bias contingent on maternal condition in species characterized by variation in male reproductive success. A male-biased sex ratio among mothers in good condition, and a female-biased sex ratio among mothers in poor condition is expected. Studies in humans have thus far provided mixed answers to the question of whether or not sex ratio is affected by maternal condition. The present study assessed whether or not the introduction of a western cash economy influenced the observed secondary sex ratio in Nepal's Khumbu region. Because acculturated villages provided better access to the cash economy and to health facilities, residence in an acculturated village was used as a proxy for "good" maternal condition. I analyzed demographic data gathered by survey in 1971 and 1982. The sample included 734 children from the 1971 survey and 1598 children from the 1982 survey. Using Poisson regression I analyzed the extent to which the sex ratios in age-stratified groups differed between the acculturated and unacculturated villages. In the 1971 dataset, the younger women in the acculturated villages displayed a significantly higher (p=.014) proportion of male offspring. It is likely that older women were subjected to minimal acculturation effects during their child-bearing years and among these data there was a lack of significant deviation between acculturated and unacculturated post-menopausal women. The rapid overall increase in acculturation between 1971 and 1982 likely made conditions in the two sets of villages much more similar by 1982. The results of this study underscore the impact that the transition to a market economy had on women in Nepal's Khumbu region.

ACKNOWLEDGEMENTS

I would first like to thank Dr. Charles Weitz for generously contributing his dataset, his time, and his insights throughout the development of this thesis project. I also wish to offer my sincere gratitude to my advisor Dr. Christie Rockwell. Her countless hours of mentoring have doubtlessly facilitated the completion of this paper. Thanks to Dr. John Gaughan at Temple University's Biostatistics Consulting Center, too, for conducting the project's statistical analyses. Finally, I would like to thank everyone else who took the time to read my thesis and comment on it: I am honored and appreciative of your interest.

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CHAPTER ONE

INTRODUCTION

The Trivers and Willard (1973) hypothesis proposes that natural selection would have favored a mechanism that enabled mothers in good condition to preferentially give birth to sons. This idea has been influential in many fields, from anthropology to epidemiology to economics (James 2006). The hypothesis spurred a plethora of researchers to test for so-called "Trivers-Willard" effects in numerous species, including modern humans (Cameron 2004; Cronk 2007; James 1996). The search for the mechanisms behind sex biasing is also an active area of research. Because Trivers and Willard (1973) hypothesized that material wealth differences would produce differential sex biasing in modern humans, economic status has historically been quite popular as a proxy for maternal condition (Lazarus 2002). The present study specifically aimed to test whether the economic disparities between two groups of Nepali villages would lead to observable Trivers-Willard effects.

The relevant demographic data was collected at two times, in 1971 and in 1982. Because of Edmund Hillary's expeditions, in the 1960's certain villages located next to the Everest Trail began to experience an influx of trekking tourism in the 1960's, and this continued through 1971 and accelerated rapidly through 1982 (Weitz et al. 1978; Furer-Haimendorf 1984). Meanwhile, another set of villages, referred to as "unacculturated villages," remained comparatively uninvolved in the cash economy until the late 1970's (Weitz et al. 1978; Furer-Haimendorf 1984). The differences between the two sets of villages, while still present, were not as dramatic by the early 1980's (Furer-Haimendorf

1984). Because acculturation brought greater amounts of resources to certain villages, the mothers residing in acculturated villages were hypothesized to be in “good” condition relative to the mothers in unacculturated villages. Based on the premise of the Trivers-Willard hypothesis, it was predicted that the mothers in acculturated villages would have a greater proportion of sons than the mothers in unacculturated villages, despite the relatively poor physical condition that the women in both sets of villages were presumably experiencing throughout their lives (Lang and Lang 1971). I also considered that the impact of acculturation could be more widespread in 1982 compared to 1971.

CHAPTER 2
BACKGROUND

Trivers-Willard Hypothesis

In 1973, Trivers and Willard published their eponymous hypothesis in “Natural selection of parental ability to vary the sex ratio of offspring.” The paper states that in polygynous organisms, assuming that maternal condition predicts offspring condition, natural selection would favor a situation where mothers in poor condition would be predisposed towards biasing the birth sex ratio towards females, and mothers in good condition would be predisposed towards biasing the birth sex ratio towards males (Trivers & Willard 1973). This hypothesis is predicated on the notion that in polygynous species males in poor condition would be competitively disadvantaged and produce relatively fewer offspring than males in good condition, and females in poor condition would not suffer as high a reproductive cost as males in poor condition (Trivers-Willard 1973). Although the degree to which humans are polygynous varies, the physiological and molecular mechanisms by which maternal condition might influence conception and embryonic or fetal survival to result in sex ratio bias were likely selected-for early on in our species’ mammalian ancestry (Cronk 2007).

Biological Plausibility

Because the Trivers-Willard hypothesis (1973) was formulated on theoretical grounds, the original paper did not provide any biological mechanism by which a mother would be able to bias offspring sex to obtain the greatest fitness advantage. Although in the last paragraph of the paper Trivers and Willard speculated that human sex ratios would skew along economic lines, they did not go into specifics about how this would happen. Spontaneous abortion, blastocyst formation and blastocyst implantation are not under conscious maternal control, and a biochemically-based physiological mechanism is necessary to explain observed biases away from the 1:1 sex ratio predicted by random chance. There have been several attempts to identify a biological mechanism(s) that may contribute to skewed prenatal sex ratios. For example, Larson et al. (2001) posited a biological mechanism for in-utero sex-ratio biasing. Larson et al. (2001) observed that when 5.5 mM d- glucose was added to culture medium, a significantly larger number of male blastocysts were able to progress to advanced stages of development in-vitro. The glucose caused damage to female blastocycts. Larson et al. (2001) concluded that glucose interferes with x-chromosome deactivation at the blastocyst stage, resulting in deleterious effects. If high glucose serum levels during early pregnancy are a chemical signal of mother's "good condition," then maternal bodily condition could bias the birth sex ratio towards sons (Larson et al. 2001). Anderson and Bergstrom (1998) found that mothers with good nutritional status around the time of conception were more likely to have sons. Relatively high glucose levels could be associated with good nutritional status.

Although it is difficult to tease apart the cause and effect relationships between diet, exercise, and circulating hormones, James (1996) argues that most sex ratio biases can ultimately be explained by variation in the sex hormones. Specifically, he proposes that the sex ratio can be biased towards males by high levels of testosterone and estrogen in parents of *both sexes*, and it can be decreased by high levels of LH, gonadotrophin and progesterone. Stress, which would likely leave a mother in poor condition in general, is associated with secretion of adrenocorticotrophic hormone (Kemper 1990). Adrenocorticotrophic hormone is associated with excess testosterone in women *and* an excess of male births; this can be a confounding factor in studies that look for female biased birth sex ratios in stressed mothers (James 1996).

There are plausible biological mechanisms that may impact the relative proportion of male and female births. It is unknown at present if sex-biasing is mostly controlled by cyclical hormonal fluctuations or if the hormonal fluctuations are in fact highly influenced by external factors that can impact maternal condition, such as poverty, nutritional deprivation, and energetic demands. The sensitivity of reproductive hormone synthesis to ecological conditions makes a link between these factors likely. Because economic factors, which tend to correlate with a suite of quality of life factors, do seem to impact sex ratio in some capacity (Cronk 2007; Chaucon et al. 1997) it is reasonable to presume that there has been selection in favor of Trivers-Willard mechanisms in humans.

Studies in Human Populations

The Trivers-Willard hypothesis can be tested at many points along the life cycle. In humans, it is difficult to test whether good maternal condition results in a higher number of male zygotes, i.e. a bias in the likihood of an X-beaing versus a Y-bearing sperm successfully fertilizing the egg (Bean 1990; Fiala 1980; Martin R. 1990). However, it is possible to test whether maternal condition predicts sex disparities in spontaneous abortion (Chaucon 1996; Wells 2000) and to test whether one or more measures of maternal condition result in a different birth sex ratio or in different prenatal "investment" patterns depending on the sex of the fetus. The aforementioned tests attempt to associate differences in maternal biology with differences in sex ratio and/or infant weight at birth and gestation length (Braza 2004; Bereczkei et al. 1997, 2000; Almond and Edlund 2007; Gaulin and Roberts 1991; Gibson and Mace 2003). In the final paragraph of the seminal Trivers-Willard paper (1973), the authors suggest that socioeconomic status should coincide with sex ratio biasing in humans. This has inspired several researchers to examine whether parental condition is associated with sex biased investment patterns. These studies attempt to predict post-partum differences in parental investment behavior, such as sex-biased abortion and breastfeeding (See Cronk 1991; Edlund 1999; Almond and Edlund 2007).

Finally, a large body of literature purports to test a generalized version of the Trivers-Willard hypothesis. Many of these studies, such as the array of papers published by Kanazawa (2005, 2006, 2007), speculate beyond the purview of what Trivers and Willard intended with their original assertions regarding the connection between natural selection and maternal condition. For example, Kanazawa hypothesizes that sex ratio can also be skewed because of maternal beauty, paternal tendency for violence, paternal robusticity, and parental sociosexual freedom. Kanazawa fails to demonstrate how the aforementioned factors impact maternal physiological condition; they in fact all rely on selection based on factors other than the physiological condition of the mother. Consequently, none of Kanazawa's papers report tests of the Trivers-Willard hypothesis in the strict sense since Trivers-Willard narrowly focused on maternal physical condition as the independent variable (Cronk 2007).

Kanazawa is one of the more prolific examples of an academic who purports to test Trivers-Willard, but this generalized treatment of sex-biasing is not limited to Kanazawa's work. In Gaulin and Roberts (1991), the authors use longer interbirth intervals *prior* to the birth of a daughter as a proxy for maternal investment. This pattern clearly could not have resulted from natural selection as the theoretically unknown sex of a future child could not influence a mother's investment in extant children (Cronk 2007). On the other hand, the authors also use infant birth weight as a measure of maternal investment, which is a valid measurement of prenatal investment. Because the empirical tests that focus on the relationship between economic measures of maternal condition and birth sex ratios are most relevant to the present research, they will be the subject of further review.

Literature Review: Trivers-Willard Based Birth Sex Studies in Human Populations

Socioeconomic factors are the most common proxies for maternal condition in Trivers-Willard studies that examine modern human populations (Lazarus 2002; Cronk 2007). Several studies on human birth-sex ratios using economic proxies for maternal condition have found evidence in support of the Trivers-Willard hypothesis (Lazarus 2002). Bereczkei and Dunbar(1997)'s retrospective study found evidence for increased female births ($p=.026$) among Gypsies, presumed to be poorer and thus in worse condition, in a population of Hungarians (n=244) stratified by ethnicity and city-dwelling status. Chacon-Puignal and Jaffee (1996) found similar results with a much larger sample size (n=577,976) of Venezualans: when using poverty as a proxy for poor condition, mothers in poor condition were more likely to have daughters. Likewise, Almond and Edlund (2007) examined US birth records among white women from 1983-2001 (n=48,000,000) and found an increase in sex ratio among younger, married, and educated women, all of whom the authors had hypothesized a priori to be in good condition.

The Khumbu: Demographics and History

Due to the current evidence that economic status has been repeatedly associated with Trivers-Willard effects (Lazarus 2002; Cronk 2007), analyses testing for Trivers-Willard effects were conducted on two databases of wealth-stratified Nepali residents. At the time of data collection (1971, 1982), the Khumbu Sherpas numbered approximately 2,205- 4,000 and resided in 6 main villages: Namche Bazaar, Kunde, Kumjung, Pangboche, Phortse, and Thamichok (Ibertson et al. 1971; Lang and Lang 1971; Furer-Haimendorf 1964; Weitz et al. 1991; Furer-Haimendrof 1984). These villages differ in degree of acculturation and consequently also differ in the ease of access to schools, hospitals, and marketplace goods (Ibertson et al. 1971; Hirai et al. 1975; Weitz et al. 1978). According to Lang and Lang (1971), approximately one half of the population was younger than 25 years of age in 1970/1971. Additionally, women slightly outnumbered men in the segment of the population that is older than 19 years.

At the time of data collection, there were two main ethnic groups residing in the Nepali Khumbu: the Sherpas and Tibetans. The Tibetans were recent (mid-20th century) immigrants that co-resided with the Sherpas. According to their oral history, the Sherpas are a Nepali tribe that migrated at some point in the distant past to Nepal from Tibet; they however are removed enough in time from the immigration to represent a separate ethnic group from the more recent Tibetan immigrants (Furer-Heimandorf 1964). The social structure is relatively egalitarian; there are no village elders or chieftains and there is no elaborated caste system (Furer-Haimendorf 1964). Economically, the more recent Tibetan immigrants maintained income parity with the established Sherpa families (Furer-Haimendorf 1984). Most Sherpas and Tibetans identify as Buddhists, but their adherence to the religion varies. (Furer-Haimendorff 1964) Because there was no social institution of caste stratification, most of the existing wealth stratification occurred because of differential participation in the cash economy. The acculturated villages participated in a significantly greater extent, and thus those villages as a group were presumed to be places conducive to “better” maternal condition than the unacculturated villages.

Diet and Health Status

Diet and nutrition exert a significant influence on maternal condition (Larson, 2001). The diet of the residents of the Khumbu overwhelmingly consisted of potatoes. At the time of data collection, the tuber contributed one half of the average resident’s daily caloric intake. (Hirai et al. 1975; Ibertson et al. 1971) Cereals such as deccan grass, millet, rice, and buckwheat also contributed substantially to their caloric intake, and to a lesser extent so did yak's milk, butter, yogurt and cheese (Hrai et al. 1975). The diet was generally insufficient (by Japanese standards) in protein (70%), iron (70%), calcium (53%), vitamin A (56%) and vitamin B2 (74%). Vitamin B1 (142%) and vitamin C (263%) consumption was more than adequate. Iodine deficiency was also endemic in the population (Ibertson et al. 1971). Due to the aforementioned dietary deficiencies, the skeletal ages of Khumbu children were consequently significantly stunted, with the effect being magnified in females (Ibertson et al. 1971). This chronic malnutrition in both acculturated and unacculturated villages likely had a negative impact in both sets of villages.

After 1966, the Khumbu had one "Western" style hospital located in Kunde, one of the more acculturated villages (Lang and Lang 1971). Additionally, in 1969 the Nepali government built a clinic staffed by a Nepali doctor in Namche Bazaar (Weitz, C. personal communication, December 1, 2010). Consequently, most of the population in the 1971 dataset had no access to a hospital for most of their lives. However, by 1982 people had an extra decade of hospital access over their entire lifespan. The nature of the terrain between villages made the Kunde hospital fairly inaccessible to those who resided in the unacculturated villages, and it is expected that they would have utilized the hospital more infrequently. The average completed fertility (4.77 live births) in 1971 was low compared to low-altitude agrarian women, and the infant death rate was high (15.8% of live births) compared to these same women (Weitz et al. 1978). Goiter in 1971 was also endemic, with approximately 92% of the population suffering from it (Ibertson et al. 1971). According to Lang and Lang (1971), tuberculosis was also common at this time.

Economic Activity

Because this analysis is testing whether access to cash economy impacts sex ratio, the differences between economic activities in acculturated and unacculturated villages are of primary importance. Overall, in 1971 the most common occupations for Khumbu men were potato or buckwheat farming and yak husbandry, followed by expedition and tourism services (Lang and Lang 1971). It must be noted, however, that in 1971 Khumbu men generally derived their livelihoods from several sources; for instance, wealthy trekkers would likely also own yaks due to the symbolic value of yak ownership. Tourism and expedition services almost exclusively impacted the acculturated villages economically; the unacculturated villages remained more "traditional" by comparison (Furer-Haimendorf 1984). For Khumbu dwellers, traditional economic activities involved yak husbandry and subsistence crop farming (Furer-Haimendorf 1964). In 1971, the majority of Khumbu women were homemakers with few farming responsibilities. In 1971, a significant number of residents (130 in Lang and Lang's survey), both male and female also were supported by monastery service.

By 1982, acculturation had changed the economic landscape radically. Participation in the expedition and tourism services overtook agrarian activities as the preferred male occupation throughout the Khumbu. The majority of men spent most of the year away from home (Furer-Haimendorf 1984) and women were increasingly relied upon as caretakers of the family's subsistence crops.

Marriage Habits

In his 1964 book *The Sherpas of Nepal,* Christoff von Furer-Haimendorf spilled plenty of ink about the “liberal” sexual habits of young Sherpas. While it was true that an unmarried Khumbu woman had sexual freedom, so to speak, the average number of sexual partners that the women reported was only one (Furer-Haimendorf 1964). As there was no formal legal apparatus to govern marriage in the Khumbu, informal “marriage” occurred frequently (as did divorce) and tended to be endogamous regarding village and exogamous regarding patrilineal clan identification. Polygyny and polyandry both occurred in the Khumbu; traditionally, polyandry was more frequent (Furer-Haimendorf 1964). Although monogamy is predicted to reduce variance between male and female reproductive success (Lazarus 2002), the relative flexibility of Khumbu marriage arrangements provides plenty of opportunities for polygynous mating.

Biogeography

There are also altitude differences between the village sets that influence access to farmed foods and the tourism economy. The Khumbu, situated in the Nepali Himalayas, ranges in altitude from 3,500 to 5,000 meters. The region experiences a monsoon season from June to September; during this time the monthly precipitation ranges from 99 to 295 mm. During the dry season from October to May the monthly precipitation ranges from 0 to 25 mm. Precipitation is variable from year to year and the three villages located at a lower altitude, Namche Bazaar, Kunde, Kumjung, experience significantly more rainfall than the higher-altitude settlements of Pangboche, Phortse, and Thamichok (Joshi, 1973). Because the acculturated villages are also the lower altitude villages, they experience more rainfall and are thus able to harvest greater varieties and amounts of crops (Furer-Haimendorf 1964).

CHAPTER 3

MATERIALS AND METHODS

Figure 3.1 Map of the Khumbu Region of Nepal; region is highlighted

Collection of Demographic Data

The present study used demographic data collected via household survey by Weitz and colleagues in 1971 and in 1982 in the Khumbu (see Figure 3.1) region of Nepal to test the prediction that the women from acculturated villages would express male-biased sex ratios of their offsrping relative to unacculturated villages. The survey methods are described in detail in Weitz et al. (1978, 1991). A brief description follows. Women were questioned about their age, occupation, village of residency, ethnic group, marital status, years wed, husband's occupation, number of children, number of dead children, and the sex of their living children. Information regarding past births was obtained retrospectively and is therefore subject to the recall of individual women (Weitz et al. 1991). In the 1982 round of data collection, the sex of every child that a woman carried was recorded. For the vast majority of cases, this included both living and deceased children. However, there were 14 deceased children out of the 1612 total children in the 1982 dataset for whom sex was not assessed. In the 1971 dataset there is no available data on the sex of deceased children. For older individuals in both datasets, ages were estimated using recall for important events in the area or by relating those events to the presumably more-accurate ages of younger individuals (Weitz et al. 1978). The latter technique was used because individuals aged 30 and below typically had more formal education than their older counterparts and the age estimations for these individuals were thus presumed to be more accurate (Weitz et al. 1978).

Study subjects in the 1971 dataset resided in five villages: Kumjung, Kunde, Namche Bazaar, Pangboche, and Thamichok. The five villages were separated into "acculturated" and "unacculturated" groups based on the extent of market penetration. Participation in the market economy was primarily through trekking expeditions for men and to a lesser extent through inn keeping, shop keeping, and restaurant businesses for both men and women (Weitz et al. 1978; Furer-Haimendorf 1964, 1984). Kumjung, Kunde, and Namche Bazaar were coded as acculturated villages, and Pangboche and Thamichok were coded as unacculturated villages. The 1982 dataset represented a broader range of villages: Kumjung, Kunde, Phortse, Namche Bazar, Tzarok, Tzorkum, Syangboche, Thami, Orsho, Thamote, Yulajung, Kerok, Chanapa, Thamo, Upper Pangboche, and Lower Pangboche. Kumjung, Kunde, Namche Bazar, Tzarok, Tzorkum, Sygangboch, and Thami were coded as acculturated villages, and the remaining eight villages were coded as unacculturated villages.

Inference of Maternal Condition

In this study acculturation status was used as a surrogate for maternal condition. Residence in an acculturated village was treated as a proxy for “good” condition and residence in an unacculturated village was treated as a proxy for “poor” condition. Acculturated villiages were identified as such because of their proximity to the Everest Trail; this proximity facilitated their integration into the Nepalese cash economy via tourism, trekking, and mountaineering (Weitz et al. 1991).

Analyses testing the Trivers-Willard hypothesis typically report population-level secondary sex ratios presumably because maternal condition is assessed relative to other mothers in her population (Mace 2000). This analysis similarly compared population-wide sex ratios; the acculturated group was presumed to be in “better” condition and thus more likely to display a male-biased sex ratio than the unacculturated group.

Calculation of Sex Ratio

The primary sex ratio is the ratio of males conceived divided by the number of females conceived, and this information was not available for analysis. Only sex ratio data from living children was used in the analysis of the data collected in 1971. This analysis most closely approximates a comparison of secondary sex ratios, or the ratios of male to female births. To assess the effect of maternal condition on the children's sex ratios, Khumbu mothers were grouped into various analytical cohorts depending on their age and acculturation status. The women were separated into acculturated and unacculturated villages to test the village level acculturation effect on maternal condition. The women were also separated into age cohorts to separate women under 50 years of age who had been exposed to acculturation during their child bearing years from women over 50 years of age, who had not been exposed to acculturation during their child bearing years. Finally, the women were separated into 10-year age cohorts to see if there was a particular time period during which the acculturation process heavily impacted maternal condition. The sex ratios under comparison were calculated at the larger village and age-cohort level: individual womens' sex ratios were not calculated. The process of calculating the sex ratios for the women in the 1982 datasets were very similar to the previously described calculations of sex ratio for the 1971 dataset. The 1982 dataset, however, is a more accurate measure of the Khumbu women's secondary sex ratio because it included data from both living and deceased children.

Statistical Analyses

Data on the sex of offspring were stratified first by age group and then by acculturation status, and the numbers of male and female children were then totaled within each stratum. Each stratum's sex ratio was obtained by dividing the number of male children by the number of female children. Because the number of children born to each mother was not uniform, some of the mothers are more heavily represented in a population-level sample than others. This non-independence of the data in the samples required the use of an analytical method that accommodates multiple, non-independent events, and Poisson regression was chosen (Armitage and Berry 1994; Lindsey 1995; Agresti 2007). Poisson regression was then used to calculate whether the differences between the ratios of males to females in each stratified group were significant.

CHAPTER 4
RESULTS

Table 4.1 shows the secondary sex ratios for age cohorts representing older (>50) and younger (<50) women. The analysis combined the population level sex ratios from both the acculturated and unacculturated Nepali Khumbu villages. Table 4.1 shows the sex ratios as stratified by age group. In the 1971 dataset, the younger women displayed a slight female bias and the older women displayed a more marked male bias. In the 1982 dataset, both age cohorts had a slight male bias.

Table 4.1. Sex Ratio Comparison by Age Group

Age Group	n(1971)	sex ratio	n(1982)	sex ratio
< 50	575	0.97	1025	1.10
> 50	159	1.27	573	1.02

Next, both age cohorts were broken into groups depending upon village acculturation status. The results of this analysis are shown in Table 4.2. For the women represented in the 1971 dataset, the secondary sex ratios for women under 50 varied significantly from one another ($p = 0.014$). The acculturated villages displayed a slight male bias and the unacculturated villages had a marked female bias in the women who were younger than 50 years of age. Both groups of women over 50 in the 1971 dataset had male-biased ratios, and the difference between them was not statistically significant (p= 0.808). In the 1982 dataset the secondary sex ratios for women under 50 did not vary significantly from one another (p = 0.905). The acculturated women over 50 displayed a male-biased sex ratio, and the unacculturated women over 50 displayed a female-biased sex ratio. However, the difference between them was not statistically significant (p= 0.159).

Table 4.2. Sex Ratio Comparison by Age Group and Acculturation Status

Age Group	**1971 Sex Ratio, # of Individuals**			**1982 Sex Ratio, # of Individuals**		
	Acculturated	Unacculturated	PValue	Acculturated	Unacculturated	PValue
<50	1.09, n=448	0.65, n=127	**0.014**	1.10, n=631	1.10, n=394	0.905
>50	1.36, n=71	1.20, n=88	0.808	1.16, n=361	0.81, n=212	0.159

The third secondary sex ratio analysis divided the women into ten-year age cohorts and then stratified them by acculturation status. The results of this analysis are shown in Table 4.3. In the 1971 dataset, only the age 31-40 cohort was shown to display a significant difference between acculturated and unacculturated villages (*p*= .007). The acculturated village had a male-biased ratio and the unacculurated village had a female-biased sex ratio. In the 1982 dataset, none of the age cohorts displayed a significant acculturation effect.

Table 4.3. Sex Ratio Comparisons by Age Group and Acculturation Status

Age Group	**1971 Sex Ratio, # of Individuals**			**1982 Sex Ratio, # of Individuals**		
	Acculturated	Unacculturated	PValue	Acculturated	Unacculturated	PValue
21-30	1.21, n=104	0.52,n=26	0.105	1.08, n=166	1.20, n=86	0.102
31-40	1.11, n=249	0.52,n=76	**0.007**	1.00, n=288	1.09, n=159	0.153
41-50	0.96, n=90	1.50,n=25	0.449	1.35, n=242	0.89, n=178	0.133
51-60	1.24, n=38	1.50,n=46	0.676	1.03, n=179	0.85, n=120	0.790

CHAPTER 5
DISCUSSION

Significance of the Findings

The present study analyzed whether women from acculturated villages had a greater number of sons than daughters as predicted by Trivers-Willard. Some of the results support the prediction that the proportion of male births will increase as economic conditions improve. In the 1971 dataset, the women under 50 years of age in the acculturated villages gave birth to a higher proportion of males than the women under 50 years of age in the unacculturated villages. The fact that the Trivers-Willard effects were evident in the younger portions of the population and not among women over 50 probably reflects the fact that during the older womens' childbearing years the Khumbu was not yet experiencing acculturation. By 1982, the relative proportion of male births in women under 50 in unacculturated villages dramatically increased, which nullified the previous sex ratio differences between the two sets of villages. This is perhaps a result of increased male participation in the cash economy among residents in the unacculturated villages.

When fine grained analyses of the 1971 data were conducted to examine the data stratified by 10 year age cohorts there is a highly significant (p=.007) difference in the sex ratios between the women in acculturated and unacculturated villages aged 31-40 years, but there were no significant deviations observable in the other 10-year age cohorts despite the aforementioned differences that are observable when the entire sample of women younger than 50 years of age is considered. This could be a result of small non-significant differences in sex ratio aggregating into a larger difference when the samples are combined.

Like many tests of the Trivers-Willard hypothesis, the present study used a proxy for maternal condition that relied on economic status rather than a direct measurement of the physiological condition of women. Almond and Edlund's (2007) analysis of American birth records and Chaucon-Puignau et al.'s (1996) analysis of Venezuelan birth records provide a context for the present anaylsis of Khumbu residents. Both of these other studies found a statistically significant association between economic status and birth sex ratios in the direction of Trivers-Willard predictions, and both studies focused on groups stratified by wealth with no significant genetic differences presumed between the mothers in "good" and "poor" condition. Bereczkei and Dunbar (1997), on the other hand, compared different ethnic groups. The biased sex ratios that they found when comparing Gypsies and Hungarians occurred in the direction predicted by Trivers-Willard, but they may not be a reflection of economic disparities (Lazarus 2002). Ellis and Bonin (2002) also tested wealth's effects on sex ratio but their data did not indicate a Trivers-Willard effect. However, the latter study's measures of parental economic status were questionable because the primary data collection only consisted of college students and their siblings and only included the students' measures of parental wealth. Other recent studies that failed to find Trivers-Willard effects (e.g. Stein et al. 2004; Cypryk et al. 2007) focused on nutritional status rather than economic status.

This study is unusual among human sex ratio studies because it uses Poisson regression for statistical analysis. Wilson and Hardy (2002) advocated for use of generalized linear models (GLMs) like Poisson regression in sex ratio studies due to GLMs' aptness both for analyzing proportions and for trying to detect small differences in populations with similar means. Despite the advantages of GLMs, the vast majority of Trivers-Willard studies in humans rely on chi-square and ANOVA based analyses. These tests are not ideal because many Trivers-Willard researchers fail to normalize their datasets for Chi-Square analysis (Wilson and Hardy 2002) and ANOVAs were not developed for the analysis of proportional data. ANOVAs can compare the average number of girls and the average number of boys born in a dataset, but that is not the same as comparing the ratio of boys to girls (Wilson and Hardy 2002). The sex ratios in the acculturated and unacculturated Khumbu villages were quite close to each other in the present study population, and the ability of Poisson regression to detect the differences between the proportions of males and females in these two sectors of the populations provides further evidence that GLMs should be incorporated into future sex ratio analyses.

Issues with Testing Trivers-Willard in Humans

There are several problems that researchers have encountered when trying to evaluate Trivers-Willard effects in modern human populations. First and foremost, the idea that natural selection would result in the presence of genes that promote maternal sex biasing contingent on maternal condition rests on two assumptions. One of these assumptions is that maternal condition ultimately reflects offspring condition; although this is intuitive it is not something that Trivers-Willard tests tend to analyze directly. The second assumption is that good maternal condition is more beneficial for one sex than it is for the other sex. As stated earlier, Trivers and Willard (1973) hypothesized that the high variance in male reproductive success in polygynous species should result in evolved mechanisms wherein mothers in good condition would have more sons and mothers in poor condition would have more daughters. When researchers test for Trivers-Willard effects in modern human societies, they are working from a presumption of higher variance in male reproductive success in a given society (Lazarus 2002; Cronk 2007), and they are also presuming that good maternal condition confers a greater fitness benefit to sons than it does to daughters.

Occasionally attempts have been made to demonstrate the effectiveness of a Trivers-Willard strategy in modern human societies (Cronk 1992; Bereckzkei 1997), but thus far the results are inconclusive. Although it was not in the context of a Trivers-Willard study, Nettle and Pollett (2008) presented findings that there is wealth-based selection on male reproductive success, especially in non-industrialized agrarian societies. However, their research did not examine wealth-contingent female reproductive success or its variance. This component would be useful for researchers working with the Trivers-Willard hypothesis because higher variance in males is necessary for Trivers-Willard effects to materialize and one would have to know the variance in female reproductive success to claim that the variance in males is higher than it is in females. Additionally, it is often difficult for researchers to access the number of children that a man has outside of his “official” relationship; this detail is integral for measures of male reproductive success, especially if it is more likely to occur in men with more wealth and status (Lazarus 2002).

Ultimately it is not necessary to demonstrate that, among modern humans, sons will provide a greater reproductive success return than daughters will for mothers in good condition. Trivers-Willard mechanisms could have evolved further back in the hominin evolutionary lineage, perhaps at a time when polygynous mating was the norm. Without selection against such sex-biasing genes, they could remain in the human genome long after their reproductive success-influencing ability has expired. Early hominins had reduced canine dimorphism which has been interpreted as evidence for monogamy (Lovejoy 1981) but body size dimorphism remained ape-like until about 1.8 million years ago with the appearance of *Homo ergaster* suggesting some form of polygamous mating system was in place until at least that point in our evolutionary history. Although the lack of sexual dimorphism and reduced canines imply monogamy in ancient *Homo sapiens,* there is also evidence to suggest that polygyny was the mating system in humans up until quite recently (Dupanloup et al. 2003; Nelson et al. 2010). Nelson et al. (2010) cite evidence of digit ratios indicating polygyny in early modern humans and Neanderthals, and Dupanloup et al. (2003) suggest that Y-chromosome analysis indicates a recent (approximately 5,000-10,000ya) shift from polygyny to monogamy in modern humans.

The idea that an individual's economic status itself results in differences in maternal health (and by proxy "condition") is frequently presumed on the basis of observed disparities between richer and poorer populations in the areas of nutrition, stress, healthcare, and related health outcomes. This presumption is made regardless of whether or not the health disparities have actually been found in the study population in question (Cronk 2007). Additionally, although one may be able to observe these trends at a population level, the fact remains that there are going to be individual differences in the extent to which any individual woman either benefits or suffers from living in a given economic context. Consequently, poorer maternal condition due to low socioeconomic status is inferred rather than directly tested in most studies that test the effect of "economic status" on sex ratio. Without data on mothers' physiological health status, it is difficult to isolate the precise contributions that economically driven factors make to a woman's physical condition: it is a rough, broadly-sketched measure at best. A study such as this one on Nepali Khumbu residents has limited explanatory power because the acculturation status cannot differentiate between the relative contributions of nutritional quality and healthcare access. Both of those variables are subsumed under acculturation status.

Issues with this Particular Dataset

The lack of physiological measures, either hormonal, anthropometric, or otherwise, for the women in Nepal's Khumbu is one of the shortcomings in the present study. Because physiological data were not collected, there is no way of knowing the extent to which the womens' physiology differed depending on acculturation status. This information would help to elucidate more proximate indicators of "good" and "poor" maternal condition. Another constraint of the study is that for the 1971 dataset, data on deceased children are missing. The working assumption in the present analyses is that there was no sex bias in mortality suffered in acculturated compared with unacculturated villages. In the 1982 dataset, there was a bias of similar strength towards male child deaths in both acculturated (88:48) and unacculturated (32:18) villages. Presuming that infant mortality rates were similar for the mothers in the 1971 and 1982 datasets, this missing data would not serve as an explanatory factor for the significant finding in 1971.

Future Directions

The current study provides several possible points of departure for future studies that seek to test for Trivers-Willard effects. Based on the available literature that describes Trivers-Willard mechanisms, it is essential that future studies continue to isolate the physiological and biochemical mechanisms by which the female body skews sex ratio prenatally. Additionally, future studies that use economic proxies for maternal condition should make a greater effort to assess cash economy's relative influence on the biological outcomes that manifest themselves as either good or poor maternal condition. Finally, the usefulness of Poisson regression for the present study emphasizes Wilson and Hardy's (2002) call for further application of generalized linear statistical models in sex ratio studies.

CHAPTER SIX

CONCLUSION

The present study of Khumbu residents supports Trivers and Willard's hypothesis that relative economic wealth will positively influence maternal condition and consequently increase the number of male births. There has been a great amount of academic interest in testing whether or not Trivers and Willard's predictions about maternal condition and offspring sex ratio were correct. For many researchers (Cronk, 2007; James, 2006), the experimental findings of Larson (2001) were enough evidence to conclude that there is an evolved sex-biasing mechanism. Others, (Brown and Silk 2002; Krackow 2002), however, question the existence of Trivers-Willard effects in primates due to the high number of studies that do not support Trivers-Willard predictions (James 2006; Lazarus 2002).

Because this study does not provide nuanced measures of maternal condition or nuanced measures of maternal access to resources, it does not contribute to the debate about whether or not finely-tuned data is more likely to yield positive Trivers-Willard results (Cameron 2004; Cronk 2007). However, this study may owe its positive results to the usage of the ideally suited Poisson regression as opposed to the classically preferred Chi-square and ANOVA analysis techniques. Perhaps many of the previous studies that have not found evidence Trivers-Willard effects would have had different results had they used a generalized linear model (Wilson and Hardy 2002). Ultimately, despite some of the data's shortcomings, this study provides further evidence that wealth disparities can predict sex ratio, and that it is imperative that authors utilize proper statistical techniques when testing for the Trivers-Willard hypothesis.

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