

AN ASSESSMENT OF THE IMPACT OF POPULATION HISTORY  
AND RISK ON WEANING BEHAVIOUR

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Bachelor of Arts, University of Victoria, 2006

THESIS IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF  
MASTER OF ARTS

In the Department of Archaeology

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# APPROVAL

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**Degree:** MA

**Title of Thesis:** An Assessment of the Impact of Population History and Risk on Weaning Behaviour

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**Date Defended/Approved:**

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## **ABSTRACT**

The weaning process varies considerably among human populations, but it is not yet understood why this is the case. With this in mind, I used data from natural fertility societies to test two evolutionary theory-based hypotheses concerning variation in the timing of key events in the weaning process. First, I evaluated the null hypothesis that this variation simply reflects population history. I then tested the hypothesis that risk of resource failure affects weaning variation. Among-population variation in weaning behaviour is not correlated with the proxy I employed for population history and is only weakly correlated with some of the proxies for risk of resource failure. Thus, my analyses refute the population history hypothesis and provide only limited support for the risk hypothesis. Together, these results suggest that among-population variation in weaning behaviour is shaped by selection but, contrary to expectations, risk of resource failure is not the primary selector.

**Keywords:** infant feeding; weaning; cross-cultural; human evolution; life history

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## TABLE OF CONTENTS

APPROVAL.....	ii
ABSTRACT .....	iii
ACKNOWLEDGEMENTS.....	iv
LIST OF TABLES.....	viii
CHAPTER 1, INTRODUCTION .....	1
1.1. Aims and Objectives .....	1
1.2. Background .....	4
1.2.1. <i>Life history theory</i> .....	4
1.2.2. <i>Human life history</i> .....	5
1.2.3. <i>Complementary feeding and the weaning process</i> .....	7
1.3. Phylogeny, ecology, complementary feeding, and the weaning process .....	10
1.4. Predictions .....	13
1.5. Thesis structure .....	17
CHAPTER 2, MATERIALS AND METHODS.....	18
2.1. Data collection .....	18
2.2. Analyses .....	22
2.2.1. <i>How is among-population variation in weaning milestones patterned?</i> .....	22
2.2.2. <i>Do weaning milestones reflect population history?</i> .....	22
2.2.3. <i>Are weaning milestones adapted to risk of resource failure?</i> .....	24
CHAPTER 3, RESULTS .....	29
3.1. Exploratory analyses .....	29
3.2. Population history hypothesis .....	34
3.2.1. <i>Genetic distance/ all populations/ log transformed data mantel matrix tests</i> .....	34
3.2.2. <i>Genetic distance/ sample subdivided mantel matrix tests</i> .....	35

3.3. Risk of resource failure hypothesis.....	37
3.3.1. Latitude.....	37
3.3.1.1. Latitude/all populations regression analyses .....	37
3.3.1.2. Latitude/ all populations/ partial mantel matrix tests .....	38
3.3.1.3. Latitude/ sample subdivided regression analyses .....	39
3.3.1.4 Latitude/ sample subdivided/ partial mantel matrix tests .....	42
3.3.2. Elevation .....	44
3.3.2.1. Elevation/ all populations/ regression analyses .....	44
3.3.2.2. Elevation/ all populations/partial mantel matrix tests.....	45
3.3.2.3. Elevation/ sample subdivided/ regression analyses .....	46
3.3.2.4. Elevation/ sample subdivided/ partial mantel matrix tests.....	48
3.3.3. Intra-Annual Variability in Precipitation .....	51
3.3.3.1. Variability in precipitation/ all populations/ regression analyses .....	51
3.3.3.2. Variability in precipitation/ all populations/ partial mantel matrix tests.....	52
3.3.3.3. Variability in precipitation/ sample subdivided/ regression analyses .....	53
3.3.3.4. Variability in precipitation/ sample subdivided/ partial mantel matrix tests.....	56
3.3.4. Effective Temperature .....	58
3.3.4.1. Effective temperature/ all populations/ regression analyses .....	58
3.3.4.2. Effective temperature/ all populations/ partial mantel matrix tests .....	59
3.3.4.3. Effective temperature/ sample subdivided/ regression analyses .....	60
3.3.4.4. Effective temperature/ sample subdivided/ partial mantel matrix tests .....	63
4.1. Main Findings.....	67
4.2. Reliability of the Study.....	69
4.2.1. Measuring risk of resource failure .....	69
4.2.2. Collection of Weaning and Eco-Geographic Data.....	74



4.2.3. <i>Measurement of Eco-Geographic and Phylogenetic Variables</i> .....	75
4.2.4. <i>Size and Structure of the Sample and of the Subsamples</i> .....	79
4.2.5. <i>Multiple Comparisons</i> .....	81
4.3. <i>Implications of the Results</i> .....	83
4.3.1. <i>Eco-Geographic, Demographic, Physiological, and Sociocultural Factors</i> .....	84
4.3.2. <i>Complementary Feeding, Weaning, and the Evolution of Human Life History</i> .....	89
CHAPTER 5, CONCLUSIONS.....	91
APPENDIX 1, SOURCES FOR WEANING MILESTONE DATA .....	93
APPENDIX 2, SOURCES FOR ALLELE FREQUENCIES PROXY POPULATIONS.....	104
APPENDIX 3, SOURCES FOR ECO-GEOGRAPHIC DATA.....	105
REFERENCES.....	114

## LIST OF TABLES

TABLE 1, DESCRIPTIVE STATISTICS FOR WEANING MILESTONES FOR ALL POPULATIONS.....	30
TABLE 2, DESCRIPTIVE STATISTICS FOR WEANING MILESTONES FOR FORAGER POPULATIONS .....	31
TABLE 3, DESCRIPTIVE STATISTICS FOR WEANING MILESTONES FOR PASTORALIST POPULATIONS.....	32
TABLE 4, DESCRIPTIVE STATISTICS FOR WEANING MILESTONES FOR FARMING POPULATIONS .....	32
TABLE 5, MEANS OF WEANING MILESTONES BY MODE OF SUBSISTENCE.....	33
TABLE 6, RELATIONSHIPS BETWEEN GENETIC DISTANCE AND WEANING MILESTONES/ ALL POPULATIONS .....	34
TABLE 7, RELATIONSHIPS BETWEEN GENETIC DISTANCE AND WEANING MILESTONES/ FORAGERS .....	35
TABLE 8, RELATIONSHIPS BETWEEN GENETIC DISTANCE AND WEANING MILESTONES/ PASTORALISTS .....	36
TABLE 9, RELATIONSHIPS BETWEEN GENETIC DISTANCE AND WEANING MILESTONES/ FARMERS.....	37
TABLE 10, RELATIONSHIPS BETWEEN LATITUDE AND WEANING MILESTONES/ ALL POPULATIONS .....	38
TABLE 11, RELATIONSHIPS BETWEEN LATITUDE AND WEANING MILESTONES/ ALL POPULATIONS/ GENETIC DISTANCES CONTROLLED .....	39
TABLE 12, RELATIONSHIPS BETWEEN LATITUDE AND WEANING MILESTONES/ FORAGERS .....	40
TABLE 13, RELATIONSHIPS BETWEEN LATITUDE AND WEANING MILESTONES/ PASTORALISTS.....	40
TABLE 14, RELATIONSHIPS BETWEEN LATITUDE AND WEANING MILESTONES/ FARMERS.....	41
TABLE 15, RELATIONSHIPS BETWEEN LATITUDE AND WEANING MILESTONES/ FORAGERS/ GENETIC DISTANCES CONTROLLED....	42
TABLE 16, RELATIONSHIPS BETWEEN LATITUDE AND WEANING MILESTONES/ PASTORALISTS/ GENETIC DISTANCES CONTROLLED .....	43
TABLE 17, RELATIONSHIPS BETWEEN LATITUDE AND WEANING MILESTONES/ FARMERS/ GENETIC DISTANCES CONTROLLED .....	44
TABLE 18, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS .....	45
TABLE 19, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS/ GENETIC DISTANCES CONTROLLED .....	46
TABLE 20, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ FORAGERS .....	47
TABLE 21, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ PASTORALISTS .....	47

TABLE 22, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONES/ FARMERS .....	48
TABLE 23, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ FORAGERS/ GENETIC DISTANCES	
CONTROLLED .....	49
TABLE 24, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ PASTORALISTS/ GENETIC DISTANCES	
CONTROLLED .....	50
TABLE 25, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ FARMERS/ GENETIC DISTANCES	
CONTROLLED .....	50
TABLE 26, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS	52
TABLE 27, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS/	
GENETIC DISTANCES CONTROLLED .....	53
TABLE 28, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ FORAGERS .....	54
TABLE 29, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ PASTORALISTS .....	54
TABLE 30, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ FARMERS .....	55
TABLE 31, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ FORAGERS/ GENETIC	
DISTANCES CONTROLLED .....	56
TABLE 32, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND PASTORALISTS/ GENETIC DISTANCES CONTROLLED ....	57
TABLE 33, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ FARMERS	
POPULATIONS/ GENETIC DISTANCES CONTROLLED.....	58
TABLE 34, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS .....	59
TABLE 35, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS/	
GENETIC DISTANCES CONTROLLED .....	60
TABLE 36, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ FORAGERS .....	61
TABLE 37, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ PASTORALISTS .....	62
TABLE 38, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ FARMERS.....	62
TABLE 39, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ FORAGERS/ GENETIC	
DISTANCES CONTROLLED .....	64

TABLE 22, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONES/ FARMERS .....	48
TABLE 23, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ FORAGERS/ GENETIC DISTANCES	
CONTROLLED .....	49
TABLE 24, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ PASTORALISTS/ GENETIC DISTANCES	
CONTROLLED .....	50
TABLE 25, RELATIONSHIPS BETWEEN ELEVATION AND WEANING MILESTONE VARIABLES/ FARMERS/ GENETIC DISTANCES	
CONTROLLED .....	50
TABLE 26, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS	52
TABLE 27, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS/	
GENETIC DISTANCES CONTROLLED .....	53
TABLE 28, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ FORAGERS .....	54
TABLE 29, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ PASTORALISTS .....	54
TABLE 30, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ FARMERS .....	55
TABLE 31, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ FORAGERS/ GENETIC	
DISTANCES CONTROLLED .....	56
TABLE 32, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND PASTORALISTS/ GENETIC DISTANCES CONTROLLED ....	57
TABLE 33, RELATIONSHIPS BETWEEN VARIABILITY IN PRECIPITATION AND WEANING MILESTONE VARIABLES/ FARMERS	
POPULATIONS/ GENETIC DISTANCES CONTROLLED.....	58
TABLE 34, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS .....	59
TABLE 35, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS/	
GENETIC DISTANCES CONTROLLED .....	60
TABLE 36, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ FORAGERS .....	61
TABLE 37, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ PASTORALISTS .....	62
TABLE 38, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ FARMERS.....	62
TABLE 39, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ FORAGERS/ GENETIC	
DISTANCES CONTROLLED .....	64

TABLE 40, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ PASTORALISTS/ GENETIC	
DISTANCES CONTROLLED .....	65
TABLE 41, RELATIONSHIPS BETWEEN EFFECTIVE TEMPERATURE AND WEANING MILESTONE VARIABLES/ FARMERS GENETIC	
DISTANCES CONTROLLED .....	66
TABLE 42, RELATIONSHIPS BETWEEN PRINCIPAL COMPONENT SCORE AND WEANING MILESTONE VARIABLES/ ALL POPULATIONS	
.....	71
TABLE 43, RELATIONSHIPS BETWEEN PRINCIPAL COMPONENT SCORE AND WEANING MILESTONE VARIABLES/ FORAGERS.....	72
TABLE 44, RELATIONSHIPS BETWEEN PRINCIPAL COMPONENT SCORE AND WEANING MILESTONE VARIABLES/ PASTORALISTS....	72
TABLE 45, RELATIONSHIPS BETWEEN PRINCIPAL COMPONENT SCORE AND WEANING MILESTONE VARIABLES/ FARMERS .....	73

### **1.1. Aims and Objectives**

Humans share a number of life history traits with their closest living relatives, the apes, including slow growth, a lengthy period of juvenile dependence, late age at first birth and a long life span (van Schaik et al. 2005). However, there are several features of human life history that deviate from the ape pattern. These include an extended post-reproductive lifespan in females; the ability to support multiple, dependent, offspring simultaneously; the capacity to begin weaning relatively early; and prolonged maturation (Hawkes 2006; Hawkes and Paine 2006; Robson and Wood 2008).

Although all of these unique human life history traits require explanation, the last three are of particular interest. One reason for this is that the ability to support multiple, dependent offspring and the ability to wean early are both facets of human life history that facilitate major increases in total lifetime fertility relative to chimpanzees, bonobos, gorillas and orangutans. As such, these traits likely affect demography, which in turn has the potential to influence other aspects of human evolution, such as brain size, body size, pathogenesis, and technological innovation (Barrickman et al. 2008; Henrich 2004; Kaplan et al. 2002; Kennedy 2005; Shennan, 2001; Walker and Hamilton, 2008). The other reason that the simultaneous support of multiple, dependent, offspring, relatively early weaning, and prolonged maturation are traits of particular interest is that life history theory suggests they are unlikely to co-occur in a single species. Life History Theory suggests that slow growth and development generally requires prolonged breastfeeding (later weaning) such that altricial infants receive energy from their mothers until

they are developed enough to acquire adequate and appropriate nutrition for themselves (Kennedy 2005). Furthermore, by extending juvenility and delaying age at first reproduction, an organism dedicates more time and energy to growth and development than to reproduction. This in turn can be expected to reduce total lifetime fertility (Roff 2002; Stearns 1992). In humans, neither of these expectations is borne out.

One factor that has been hypothesized to explain this unexpected aspect of human life history is the use of complementary foods in human infant feeding (Kennedy 2005; Sellen 2001, 2006, 2007; Wells 2006). According to this hypothesis, the use of nutrient-dense, soft, relatively sterile foods to feed human infants enables human mothers to wean their infants well before these infants are capable of sustaining themselves. Since lactation affects maternal energy balance and appears to inhibit fertility, the relatively early cessation of breast-feeding in humans that is facilitated by the use of complementary foods, allows for shorter birth spacing and increased total lifetime fertility in comparison with the other great apes (Sellen 2007). However, while the small amount of available evidence supports the notion that complementary feeding affects life history trade-offs, researchers are only beginning to explore this hypothesis empirically (Kennedy 2005; Sellen 2006, 2007). Although there is some culture-specific evidence available to support the proposition that ecology significantly impacts infant feeding decisions (e.g. Chen 2002; Martines et al. 1994; Sellen 2001; Sellen and Smay 2001), only one study has explored a possible relationship between an ecological variable proposed to affect human infant feeding decisions and weaning behaviour patterns cross-culturally (Sellen and Smay, 2001).

Sellen and Smay (2001) hypothesized that cross-cultural variation in complementary feeding and weaning behaviour is driven by differences in subsistence economy. Specifically, they predicted

that the higher weaning food availability associated with food production, both agricultural and pastoral, would allow for earlier complementary feeding and weaning in food-producing societies than in foraging societies. Foragers were assumed not to use weaning foods. The study suggested that food-producers do indeed cease breastfeeding earlier than foragers. However, Sellen and Smay also found that there is no significant difference between the mean times at which agriculturists and foragers introduce complementary foods. Furthermore, they found that, contrary to what they had assumed, most foragers do use weaning foods. Overall, their results suggest not only that the relationship between complementary feeding and mode of subsistence is more complex than expected but also that mode of subsistence only accounts for a small portion of the variation observed in infant feeding strategies among contemporary human populations (Sellen and Smay 2001). As such, the authors hypothesized that ecological factors may drive among-population variation in complementary feeding behaviour.

With the latter point in mind, in the study reported here, I tested two hypotheses formulated to explain variation in the time at which various complementary foods are introduced and the times at which other related events in the weaning process occur. Specifically, I tested the predictions of a null hypothesis that weaning variation reflects population history. I then tested a set of predictions derived from an adaptive hypothesis. According to the latter hypothesis, human infant feeding decisions are shaped primarily by risk of resource of failure.



## 1.2. Background

### 1.2.1. *Life history theory*

The life history of an organism – the amount of time and energy it dedicates to each of the phases that constitute its life cycle – is a key element in determining its ability to cope with its environment (Stearns 1992). For all organisms, including humans, life history strategy has major fitness consequences at the individual level and major demographic consequences at the population level. As such, understanding contemporary human fitness as well as the evolution of the human lineage requires an understanding of human life history traits (Hawkes and Paine 2006).

Life History Theory is founded on the idea that the amount of time and energy an organism can access over the course of its life is finite. Energy used for one purpose cannot be used for another (Stearns 1992; Thornhill and Palmer 2004). For example, energy dedicated to the feeding of offspring cannot be used towards the conception of additional offspring. As such, an organism must make decisions regarding how to spend its limited time and energy resources, and each of these decisions involves a trade-off. Essentially, spending energy and time on one phase of the life cycle or on one particular offspring or cohort of offspring requires a reduction in the spending of energy and time on another phase of the life cycle or on additional offspring (Stearns 1992).

For the most part, these decisions are probably not conscious but are phenotypic responses to genetic instructions for building an organism in a given environment (Stearns and Kobella 1986).

Some of these phenotypic responses are fitter than others and are likely to become increasingly common within populations. Moreover, these successful life history strategies are heritable characters on which natural selection operates and, ultimately, are as important as other morphological and behavioural traits in driving the evolution of a lineage (Bogin 1999, 2006; Hawkes and Paine 2006; Roff 2002; Stearns 1992).

### *1.2.2. Human life history*

Describing and comparing life history strategies among humans and their closest extant relatives, chimpanzees, bonobos, gorillas, orangutans, and, to a lesser extent, gibbons, can shed light on the evolution of human life history (Skinner and Wood 2006; Robson and Wood 2008). These comparisons reveal that a number of derived traits characterize all of these primates. Compared to other primates, humans and great apes are characterized by slow growth, lengthy periods of juvenile dependence and learning, delayed age at first reproduction, and longevity (Blurton Jones 2006; van Schaik et al. 2006). The most parsimonious explanation for why humans, chimpanzees, bonobos, gorillas, and orangutans possess these traits is that they inherited them from the common ancestor that they share to the exclusion of all other taxa.

Comparative life history studies have also revealed that there are several life history traits that are unique to humans among the extant hominoids. Although a relatively slow progression through the life cycle is common to all of the great apes, humans are even slower in their growth and development than are their closest living relatives. Specifically, in the great apes the onset of menarche typically occurs between 6 and 10 years of age, and the first birth occurs between 9 and 13 years of age (Tutin and McGinnis 1981; Galdikas 1981; Harcourt et al. 1981).

Humans can expect these events to occur at 13 and 15 years of age, respectively (Bogin 2006). Despite this slow growth trajectory and despite evidence suggesting that humans generally live longer than other apes (Hawkes and Paine 2006), human females cease reproduction at around the same age as do other great ape females (O'Connell et al. 1999). However, female total lifetime fertility in non-contracepting human populations is typically much higher than the total lifetime fertility of female chimpanzees, bonobos, gorillas, and orangutans (Hawkes and Paine 2006). In other words, despite having similar reproductive life spans to other great apes, humans are capable of reproducing at a higher rate. This has implications for various demographic processes including population expansion, group fission, and migration or radiation.

It has been suggested that the capacity for relatively high total lifetime fertility in humans vis-à-vis the other apes is enabled to a large extent by the flexibility that characterizes human infant feeding (Harvey et al. 1987; Kennedy 2005; Sellen 2006, 2007). There is some evidence to suggest that the range of variation in the timing of weaning events is much smaller in orangutans, gorillas, chimpanzees, and bonobos than it is in humans. For example, it appears that, in the wild, chimpanzee infants that are deprived of breast milk before the age of about three years generally do not survive (Goodall 1972, 1986). Human infants, in contrast, despite increased morbidity and mortality risks, can and do survive even if the weaning process begins immediately after parturition or if breastmilk is never given (Masmas et al. 2004). Evidence for the human ability to survive and even thrive without breastmilk comes not only from individual, anecdotal cases but also from populations. Some natural fertility human populations such as the Bhil and the Maasai usually introduce complementary foods at birth (Merker 1910; Naik 1956). At the other extreme, some natural fertility populations do not complete the weaning

process until the infant reaches perhaps four or five years of age (Brant 1954). As such, humans are relatively flexible in the time at which they initiate and in the duration for which they extend the weaning process (Sellen 2007). This flexibility, particularly the ability to reduce the costs of lactation by ending exclusive breastfeeding within the first few months of life, may allow human mothers to support multiple, dependent offspring and, ultimately, leave more descendants than their great ape counterparts.

Although there is anecdotal evidence that non-human ape mothers and alloparents provision offspring during the weaning process (Galdikas and Wood 1990; Gooddall 1972, 1986; Kuroda 1984), it is likely that regular complementary feeding is unique to humans (Sellen 2007). When juvenile provisioning is mentioned in passing in descriptions of ape field studies, it appears not to be a major component of the weaning process. Furthermore, humans generally select and prepare softened, easily digestible, relatively sterile foods for weaning. This is not the case among chimpanzees, bonobos, gorillas, or orangutans, largely because the other great apes do not have access to controlled use of fire for the preparation of softened and sterile foods. As such, on the rare occasions it occurs, transitional feeding is of a different nature in the other apes than it is in humans.

### *1.2.3. Complementary feeding and the weaning process*

Complementary feeding is the introduction of liquid or solid foods into an infant's diet prior to the cessation of breastfeeding. Such foods are generally nutrient-dense and easily digestible, and have a low pathogen risk (Sellen 2007).

As mentioned above, there is reason to think that human complementary feeding is a unique form of transitional feeding that is linked with life history variables. As such, one approach to understanding the evolution of the set of unique, derived life history traits that characterize humans and possibly earlier members of the hominin lineage is to study evolutionary causes of variation in complementary feeding and weaning patterns in extant or recent human cultures. This approach, however, is in its infancy (Sellen 2007).

The research on complementary feeding that has been conducted to date generally employs one of two approaches (van Esterik 2002). In the first, researchers investigate social factors such as maternal education, sources of maternal support, and maternal breastfeeding confidence that influence infant feeding decisions within a single culture (e.g. Abel et al. 2001; Chen 2002; Dennis 2006; Hotz and Gibson 2005; Quandt 1998). Some recent ethnographies in this vein present culture-specific evidence that suggests that infant care-givers make decisions regarding infant feeding carefully, actively soliciting advice from a variety of sources and then weighing and often synthesizing the options to best manage time and energy resources for both themselves and their infants (e.g. Abel et al. 2001; Chen 2002; Greta et al. 2002). For example, new mothers of Chinese ancestry living in Vancouver, Canada, seek advice not only from medical professionals but also from female relatives and friends. This advice is often conflicting and, as a result, infant feeding behaviour within this population is constrained not only by mothers' desires to minimize direct nutritional costs to infants but also to minimize emotional stress (that may also affect infant and maternal health) among family members (Chen 2002). This suggests that infant care-givers try to choose feeding strategies that reduce their total costs in their particular environments. Moreover, the evidence that is emerging from these ethnographic studies on infant feeding decisions and cost management is generally consistent

with the notion that complementary feeding behaviours, as predicted by Life History Theory, are constrained by energy budgets. However, since studies concerning the learning processes that drive infant-feeding decisions are few and those that have been conducted are culture-specific, a need remains for generalizable, cross-cultural research in this area.

The second and more common approach to complementary feeding and weaning research is rooted in the health sciences. This approach is embodied in a large corpus of literature regarding the effects of different complementary feeding strategies on health and growth. Typically, these studies are not comparative or cross-cultural and do not frame the complementary feeding and weaning process in light of life history theory in particular or evolutionary theory in general (Kennedy 2005). That said, collectively they provide evidence consistent with the proposition that complementary feeding strategy has major effects on rates of growth and development, on morbidity and mortality, and on life history in general. For example, multiple studies indicate that, regardless of environment, introducing complementary liquids and solids before an infant is approximately four months of age predisposes that infant to increased risk of sickness and death during juvenility (e.g. Bhandari et al. 2004; Espo et al. 2002; Hadley 2005; Rowland 1986). Similarly, the times at which complementary foods are introduced and the times at which other events in the weaning process occur have been linked with variation in morbidity and mortality risk in adulthood in some settings (e.g. Adair & Dahly 2005; Cole 2006). In essence, studies of this type provide evidence that the time at which complementary foods are introduced and the times at which related events in the weaning process occur are subject to natural selection, since failure to make optimal weaning decisions can result in increased risk of illness or death.

However, as mentioned earlier, the literature contains only one cross-cultural study that examines a possible relationship between ecology and complementary feeding (Sellen and Smay 2001). That study reports the results of a test of the hypothesis that subsistence economy affects complementary feeding patterns. The authors found that complementary feeding and subsistence economy are related but not in the ways that they had initially hypothesized. While these results suggest that there is merit in the idea that infant and young child feeding behaviours likely reflect ecological patterns, the single variable considered explains only a small portion of the variation in complementary feeding. Furthermore, this particular study contains a shortcoming in its design that needs to be addressed before its results can be accepted. The authors did not control for the descent or 'phylogenetic' relationships among the cultures they include in their sample. Failure to control for such relationships can magnify or diminish effects that might otherwise appear through the kinds of tests used in the research (Dow et al. 1984; Galton 1889; Mace et al. 2003; Mace and Pagel 1994; Murdock and White 1969).

### **1.3. Phylogeny, ecology, complementary feeding, and the weaning process**

There is reason to suspect that both ecology and phylogenetic relationships influence human infant feeding behaviours. Since differences in weaning strategy have been linked with differences in morbidity and mortality risks (Bhandari et al. 2004; Espo et al. 2002; Hadley 2005; Rowland 1986), behavioural variations in weaning strategy are likely to be influenced by natural selection. As such, it is reasonable to expect environmental selective pressures such as risk of resource failure to affect weaning decisions. Simultaneously, population history constrains the variations in behavioural strategy on which selection may act. Furthermore, although there is reason to think that weaning behaviour is subject to natural selection, in the absence of strong,

directional selective forces, among-population behavioural patterning might be expected to reflect population history (Bentley et al. 2004).

With regard to ecology, risk is a core driver of behaviour in most animal species (Stephens 1990). Although there is no consensus on what is meant by the term 'risk' (Cashdan 1990), in evolutionary anthropology risk generally refers to the unpredictability of an ecological variable that can affect fitness outcomes (Cashdan 1990; Stephens 1990; but see Winterhalder et al. 1999). Greater variance in an ecological variable equates to greater risk (Caraco et al. 1980; Cashdan 1990; Stephens 1990). Under non-extreme circumstances, individuals can be expected to utilize behavioural strategies that minimize risk (Stephens 1990). For example, low-ranking individuals of the bird species known as yellow-eyed juncos select and exploit unguarded seed patches that provide consistent caloric returns rather than fighting higher-ranking birds for access to guarded seed patches that would provide much larger returns (Caraco et al. 1980). Essentially, the probability of survival for a low-ranking junco is higher when a bird selects a resource-gathering strategy with a relatively predictable outcome. The tendency to use strategies that minimize or avoid risk is the norm for many animal taxa (Stephens 1990).

In driving the distribution of absolute terrestrial biomass around the planet, solar radiation and precipitation are critical variables in defining the riskiness of a given ecological niche (Binford 2001; Rosenzweig 1968, 1995). The amount of solar radiation in a given eco-geographic region, generally represented by proxy variables such as latitude and temperature, determines the absolute amount of energy resources available to be exploited directly by plants and indirectly through the consumption of plants by all other organisms within that region. Furthermore, the temporal distribution of solar radiation throughout an annual cycle (seasonality) determines the



predictability of available energy resources (Binford 2001). As such, regions that experience relatively low, variable levels of solar radiation generally support smaller, less dense, less predictable botanical biomasses than regions that experience higher levels. In turn, the size and the movements of animal biomass are largely contingent on the size, density, and spatial and temporal distributions of botanical communities. At the same time, the absolute volume as well as the periodicity of precipitation contributes to the distribution of plant life in terrestrial ecological zones (Binford 2001; Divale 1999; Grove 2009; Snarney 1996).

The size and distribution of terrestrial biomass constrain human decision-making by affecting risks related to food resources. Smaller biomass, typically associated with high latitudes, high altitudes, low temperatures, and low rainfall, decreases the availability and predictability of food resources (Binford 2001; Rosenzweig 1968). The available evidence suggests that human behavioural strategies have been and continue to be selected to minimize this key risk (Binford 1978, 1980, 1990, 2001; Cashdan 1990; Kelly 1999; Winterhalder et al. 1999).

Humans occupy a broad range of eco-geographic regions characterized by immense variability in risk of resource failure. Since human behavioural strategies generally seek to manage risk, among-population variation in eco-geographic risk factors necessitates among-population variation in behavioural and life history strategy (Binford 1980, 2001; Bogin 1999; Grove 2009; Kelly 1983, 1999; Walker & Hamilton 2008). Among-population variation in subsistence economy is a particularly important facet of behavioural adaptation for risk management (Binford 2001; Grove 2009; Winterhalder et al. 1999). Since infant feeding and weaning are not only aspects of subsistence but also linked to the timing of some human life history events,

there is reason to think that variation in infant feeding behaviours is at least partly driven by the environmental variables that drive variation in subsistence and life history in general.

Although ecological factors may constrain human weaning strategies, historical factors also likely play a constraining role. A growing body of literature is showing that phylogeny contributes substantially to the patterning of among-population human variation, both morphological and behavioural (e.g. Kirch and Green, 1987; Durham, 1991; Collard and Shennan, 2000; Tehrani and Collard, 2002, 2009; Bentley et al. 2004; Roseman 2004; Holden and Shennan 2005; Hewlett et al. 2002; Lipo et al. 2005; Mace 2005; Moylan et al. 2005; Collard et al., 2006; von Cramon-Taubadel and Lycett 2008). As such, in cases in which there are multiple weaning strategies that approach biological optimality or in cases in which there are no strong directional selection pressures on weaning, a population's weaning strategy can be predicted to follow the weaning strategy of its ancestor. These historical effects are likely to obscure, magnify, or diminish the effects of eco-geographic variables on human weaning.

#### **1.4. Predictions**

The objectives of this project were two-fold. The first was to test the null, phylogenetic hypothesis regarding the patterning of among-population variation in complementary feeding and weaning behaviour. If the null hypothesis could be rejected as a candidate for explaining this variation, the second objective was to test the alternative hypothesis that risk of resource failure affects variation in complementary feeding behaviours cross-culturally, while statistically controlling for potentially confounding phylogenetic effects.

To test the hypotheses, I used data on infant feeding in nonindustrial, natural fertility human societies from a cross-cultural sample from the ethnographic and ethnohistoric records. I also used data regarding genetic distances, a measure of relatedness, among the populations in the sample in order to derive a phylogenetic model as well as to control for phylogenetic effects while testing the resource risk hypothesis. Furthermore, I used data from geographic records associated with the cultures included in the sample to estimate risk of resource failure. Specifically, I reasoned that latitude, elevation, patterns of precipitation, and effective temperature, as key drivers of resource availability and predictability, affect the times at which key events in the weaning process occur. Further, I hypothesized that a population's type of subsistence economy influences the strength of the relationships between resource risk and the timing of weaning events. Each of these eco-geographic, predictive variables (latitude, elevation, precipitation, temperature, and subsistence economy) has been shown or has been predicted to have at least moderate effects on weaning in previous zoological or anthropological studies (e.g. Angerbjorn et al. 1991; Bitetti and Janson 2000; Bocquet-Appel and Naji 2006; Godoy et al. 2008; King et al. 2008; Nowell and Fletcher 2008; Sellen and Smay 2001). I outline the predictions of the null and alternative hypotheses in turn below.

**Phylogeny:** As genetic/ linguistic distance among populations increase, variability in the timing of events in the complementary feeding and weaning process should also increase. I expected this to be the case because recent evidence suggests that, in the absence of selective forces, human variation should be expected to reflect population history.

**Risk of Resource Failure:** As risk of resource failure increases (i.e. as latitude, elevation, and variability in precipitation increase and as effective temperature decreases),

complementary foods should be introduced later and cessation of breastfeeding should occur later. I expected this to be the case because caregivers, in an effort to protect vulnerable, growing infants from starvation in unpredictable, food-stressed conditions, should provide their infants with milk for as long as possible because it is a source of nutritionally adequate food that remains constant and predictable in the face of food stress. Furthermore, I expected that caregivers in food-stressed environments should be motivated to repress ovulation through extended breastfeeding so as to avoid having to divide limited resources between multiple offspring.

As mentioned above, there is reason to think that a population's primary subsistence strategy influences the degree to which resource failure impacts that population. However, there is some disagreement as to which strategy – foraging, herding, or farming – is best equipped to minimize the effects of an unpredicted resource failure (Winterhalder et al. 1999). One way of framing this is to assume that farmers, in producing food surpluses, are able to store food for seasons in which resources fail. Foragers and pastoralists, in contrast, are constrained in their capacity to store in large quantities by their relatively high levels of mobility. In this view, farming and the storage that it allows function largely to reduce risk of resource failure: farmers are less vulnerable to this risk than are foragers and pastoralists. Although there are a number of researchers that frame the problem in this light (e.g. Cohen 2009; Hayden 2009), there is in fact little empirical evidence that farming is a preferred strategy in environments in which the climate is highly unpredictable (Kelly 1992).

Another way of approaching this problem is to begin with the observation that farmers generally live in relatively large, sedentary populations and that they are often dependent on one or, at most, a handful of crops. This means that, if those few crops fail, a large population is left to subsist on a small supply of stores in a circumscribed territory. In contrast, foragers and pastoralists are generally more mobile and more flexible in their abilities to respond to unpredictable climatic events (Kelly 1992; Low 1990a). There is some evidence to suggest that foraging and pastoralism are indeed preferred economic strategies in highly unpredictable environments (e.g. Low 1990a).

Although both approaches to framing the issue of whether risk of resource failure is of greater consequence to foragers, herders, or farmers are logically sound, I favour the second approach in which farmers are thought to be more vulnerable to unpredicted resource failure; I favour this view largely because it seems to be better supported by empirical evidence (Kelly 1992). As such, in this study, I expected the predicted positive correlation between resource failure riskiness and the timing of weaning milestones to be stronger among farming populations than among foraging or herding populations. I reasoned that the effects of resource failure risk are exacerbated both by sedentism and by dependence on a small number of cultivated plant foods. Therefore, caregivers in farming societies living in relatively resource risky environments should be particularly motivated to buffer their infants through extended, exclusive breastfeeding. Foragers and pastoralists, in contrast, have recourse through either greater flexibility in subsistence behaviour pattern or through reliance on energy provided by food animals. Among foragers and pastoralists, then, I expected that selection against the relatively early introduction of complementary foods in unpredictable environments to be weaker than among farmers.

## **1.5. Thesis structure**

Having introduced the aims and objectives of this research in this chapter, in Chapter Two I will describe the data sources, data collection strategy, and analytical methods used in the study. In Chapter Three, I present the results of the tests of the two hypotheses. Chapter Four discusses both the significance and the limitations of this research. In Chapter Five, I briefly summarize the central findings of the project and their implications for future cross-cultural research concerning human complementary feeding and weaning behaviours.

## CHAPTER 2, MATERIALS AND METHODS

### *2.1. Data collection*

The dataset consists of values for 13 variables recorded on 70 populations. The first five variables pertain to weaning behaviour. These are 1) infant's age at the introduction of first nutritive and non-nutritive liquids (INTLIQ), 2) infant's age at the introduction of first solids (INTSOL), 3) infant's age at the cessation of breastfeeding (CESSBF), 4) infant's age at the introduction of earliest complementary liquids or solids (INTLIQSOL), and 5) duration of the weaning process (DURWP). The first three of these variables were used in two earlier studies concerning weaning behaviour (Sellen 2001; Sellen and Smay 2001). The other two were devised especially for this study. INTLIQSOL refers to the time at which the first of any complementary food or drink is introduced, regardless of whether it is liquid or solid and regardless of whether it is nutritive or non-nutritive. DURWP measures the length of time between age at introduction of earliest complementary liquids or solids and age at the cessation of breastfeeding.

Weaning behaviour data for 64 of the 70 populations were taken from Sellen (2001) and Sellen and Smay (2001). To collect the data in question, Sellen (2001) and Sellen and Smay (2001) screened reports in the Human Relations Area Files (HRAF) for data on 'milestones' in the weaning process. Additionally, Sellen and Smay (2001) conducted a retrospective snowball search of published ethnographic literature to identify additional ethnographies of natural fertility societies that contain data on weaning. Populations in which both infant mortality and

fertility were declining were excluded on the grounds that they could not be readily treated as natural fertility populations (Sellen and Smay 2001). I collected weaning behaviour data for the other six populations from the literature using the approach employed by Sellen (2001) and Sellen and Smay (2001).

Variables six to eight are allele frequencies. The loci were the ABO locus, the HP locus, and the TF locus. Frequencies for these loci were taken from Cavalli-Sforza et al. (1994). For populations in the infant feeding sample not represented in Cavalli-Sforza et al.'s (1994) dataset, I used closely related populations as proxies. Linguistic evidence from *Ethnologue* (Raymond 2005), a database that provides information regarding the relationships among the world's languages, was used to identify appropriate proxy populations. In some cases, there were several equally closely related groups. In these instances, I employed the mean of the allele frequencies given by Cavalli-Sforza et al. (1994).

Variables nine to 12 relate to the populations' environments. These include latitude, elevation, variability in precipitation, and effective temperature. The majority of the latitudes were taken from Murdock's (1981) *Atlas of World Cultures*. To obtain latitudinal data for populations not represented in the *Atlas of World Cultures*, I screened published ethnographies for references to nearby cities or landmarks. I then used these and *Google Earth* to obtain approximate latitudes for the populations in question.

To collect data pertaining to elevation, variability in precipitation, and effective temperature, I screened both the microfiche and electronic editions of HRAF for quantitative climatic and topographic data relevant to each population for which weaning data had been collected. I



focused on HRAF categories “location” (131), “climate” (132), and “topography and geology” (132) to collect averaged figures for elevation, total monthly precipitation for both the wettest and the driest months of the year, and monthly temperatures for both the warmest and coolest months of the year. In addition, I conducted a snowball search of published ethnographic literature regarding the populations for which climatic and topographic data were not available in HRAF. When ethnographic sources did not include quantitative data on the habitats in which the relevant populations live, I collected climatic and topographic data from ecological or geographical sources that focus on a site or sites within the territory of the relevant population. As far as possible, I utilized sources published within 20 years of the time period during which the infant feeding data were observed.

After collecting the raw climatic and topographic data, I coded the values into three variables: elevation, effective temperature, and variability of precipitation. For all three variables, I first converted each case into a single numeric value. Specifically, when a source provided an inter-annual range of variation in data, I entered an average (mean) value. Further, when multiple sources were available and when slight discrepancies occurred among the figures provided, I entered an average value. In the case of elevation, this was the only necessary modification. Summarizing effective temperature and variability in precipitation required additional calculation. Effective temperature, a measure designed by Bailey (1960) to estimate the quantity of solar energy available annually at a given location, is calculated using the following formula:

$$ET = [(18 * MWM) - (10 * MCM)] / (MWM - MCM + 8)$$

where MWM is the mean temperature in degrees Celcius (°C) for the warmest month of the year, MCM is the mean temperature in °C for the coldest month of the year, 18 is a constant

representing the minimal mean temperature that can sustain tropical plant communities (18°C), 10 is a constant representing the minimal mean temperature occurring at the boundary of polar environments (10°C), and 8 is a constant representing the minimal mean temperature at the beginning and end of the growing season (8°C) (Binford 2001). Variability in precipitation was calculated simply by subtracting the value in millimetres recorded as representing the driest month of the year from the value in millimetres recorded as representing the wettest month of the year.

The last variable is subsistence strategy. The majority of the data regarding subsistence strategy were taken from Sellen and Smay (2001), who in turn took their data from Gray's (1999) revision of the second edition of Murdock's (1981) *Ethnographic Atlas*. I collected the subsistence strategy data for the populations not included in Sellen and Smay's study directly from the *Ethnographic Atlas*. The *Ethnographic Atlas* provides coded range estimates of the relative contributions of gathering, hunting, animal husbandry, and agriculture to the diet of a given population. In the *Ethnographic Atlas*, gathering refers to not only the gathering of plant foods but also the capture of small terrestrial game and avifauna. Hunting includes the procurement of not only medium and large terrestrial game but also fish and other aquatic resources. Animal husbandry and agriculture refer, respectively, to the use of domesticated animals and plants. Sellen and Smay (2001) re-coded the range estimates given in the *Ethnographic Atlas* into continuous variables, using the midpoints of the coded ranges to provide the values of interest. For the purposes of the present study, only the subsistence strategy that contributed the largest portion of the diet was considered. Populations for which gathering or hunting or both were recorded as being the most important subsistence strategy were coded as foragers. Populations for which animal husbandry was recorded as being the most important subsistence strategy

were coded as pastoralists. Populations for which the use of cultivated plants was recorded as the most important subsistence strategy were coded as farmers.

## **2.2. Analyses**

### *2.2.1. How is among-population variation in weaning milestones patterned?*

I began by assessing the general patterns of cross-cultural variation in complementary feeding and weaning behaviour. To accomplish this, I used SPSS 17.0 to carry out sets of exploratory analyses for each of the five weaning milestone variables. I recorded mean, minimum, and maximum values for all weaning variables. I also recorded skewness scores for all weaning variable distributions. In line with Moore's (2007) rule of thumb concerning skew, a distribution was deemed to violate normalcy if its skewness score exceeded one. Exploratory analyses were conducted first for all 70 populations in the sample and then after subdividing the sample by subsistence strategy.

### *2.2.2. Do weaning milestones reflect population history?*

After assessing the patterns of variation characterizing the sample, I sought to cast light on the processes driving that variation. As mentioned earlier, I began by testing the hypothesis that cross-cultural variation in the timing of weaning milestones reflects population history. This hypothesis predicts that the timing of milestones in the weaning process should be positively correlated with genetic distance. To test this prediction, I used the Mantel test. This test generates estimates of linear relatedness between two distance matrices, one representing a

dependent variable, the other an independent variable (Mantel 1967; Fortin et al. 2002). This is a pair-wise process in which the distance between each pair of populations for the independent variable is compared to the distance between the same pair of populations for the dependent variable. Since distance measures are contingent on the ordering of the objects within a matrix, distances cannot be assumed to be independent of one another. To circumvent this problem, the order of the cases is randomly permuted a large number of times. In each permutation, correlations between distances are recalculated. All correlations are then averaged to produce a final correlation coefficient (Fortin et al. 2002). A relationship is considered significant when the number of permutations producing correlation coefficients exceeding the original coefficient remains below a pre-established threshold.

I carried out two sets of analyses using the Mantel test. In the first, I converted allele frequency data from all 70 populations in the sample into a genetic distance matrix using PHYLIP's 'gdist' package. I then converted each of the five weaning variables into distance matrices using R's 'vegan' package. Subsequently, I used 'vegan' to carry out five 1000-permutation mantel tests in which I generated Pearson's correlations between the genetic distance and each of the weaning milestone distances. In the second set of analyses, I repeated the foregoing steps after subdividing the sample by subsistence strategy. For both sets of Mantel test analyses, I log transformed weaning milestone variables that were skewed in their distributions before carrying them out.

### *2.2.3. Are weaning milestones adapted to risk of resource failure?*

To test the hypothesis that the milestones in the weaning process are adapted to risk of resource failure, I examined the relationships between four variables that influence this type of risk – latitude, elevation, variability in precipitation, and effective temperature – and the timing of weaning milestones.

I began by examining the relationships between latitude and the timing of weaning milestones. The test predictions in these analyses were that infant's age at the introduction of complementary liquids (INTLIQ), infant's age at the introduction of complementary solids (INTSOL), infant's age at the introduction of earliest complementary liquids or solids (INTLIQSOL), and cessation of breastfeeding (CESSBF) should be positively correlated with latitude, while duration of the weaning process (DURWP) should be negatively correlated with latitude. This pattern was expected because higher latitudes are characterized by greater risk of resource failure than lower latitudes. As such, infant care-givers should buffer infants against resource instability by extending the duration of intensive breastfeeding. These correlations were expected to be stronger among farmers than among foragers or pastoralists because dependence on cultivated plant foods, particularly when sedentary, can exacerbate the effects of resource insecurity.

To test these predictions, I carried out four sets of analyses. In all the analyses, latitude was treated as the independent variable and the weaning variables as the dependent variables. For analyses in which the sample was subdivided, subsistence strategy code was treated as the selection variable.

In the first set of analyses, I carried out bivariate regression analyses on the sample. Before carrying out these analyses,

Populations living at equatorial and tropical

at temperate, subarctic, and arctic

INTLIQSOL, and DURWP values outnumbers

vii

DURWP values. As such, these distributions are

distributions, I logarithmically transformed the variables.

In the second set of analyses, I attempted to reduce the population

population history. Since autocorrelation resulting from common

diminish relationships between local ecological conditions and what

responses to those conditions, the accurate detection of adaptation requires

effects be taken into account (Galton 1889; Mace and Pagel 1994). To do so, I used

genetic distance while generating Pearson's correlations between latitude and each

feeding variables. This was accomplished through the use of partial Mantel tests. The partial

Mantel test is similar to the Mantel test except that it allows the analyst to control for the

effects of a third variable (Smouse et al. 1986). I used 'vegan' to generate a latitudinal distance

matrix for all 70 populations in the sample. Then, using this new matrix along with the five

weaning milestone matrices and the genetic distance matrix generated earlier, I conducted five

partial Mantel tests in which I assessed the relationships between latitudinal distance and

weaning milestone distance while controlling for genetic distance. I continued to use log

transformed values for skewed variables during this set of analyses.

Subsequently, I investigated the effect of subsistence strategy variation on the relationships

between latitude and weaning milestones. I subdivided the sample according to subsistence

In the first set of analyses, I carried out bivariate regression analyses using all 70 populations in the sample. Before carrying out these analyses, I corrected for several sample biases.

Populations living at equatorial and tropical latitudes substantially outnumber populations living at temperate, subarctic, and arctic latitudes. In addition, populations with low INTLIQ, INTLIQSOL, and DURWP values outnumber populations with high INTLIQ, INTLIQSOL, and DURWP values. As such, these distributions are positively skewed. To normalize these distributions, I logarithmically transformed the variables in question.

In the second set of analyses, I attempted to reduce the potentially confounding effects of population history. Since autocorrelation resulting from common ancestry can magnify or diminish relationships between local ecological conditions and what appear to be adaptive responses to those conditions, the accurate detection of adaptation requires that phylogenetic effects be taken into account (Galton 1889; Mace and Pagel 1994). To do so, I controlled for genetic distance while generating Pearson's correlations between latitude and each of the infant feeding variables. This was accomplished through the use of partial Mantel tests. The partial Mantel test is similar to the Mantel test except that it allows the analyst to control for the effects of a third variable (Smouse et al. 1986). I used 'vegan' to generate a latitudinal distance matrix for all 70 populations in the sample. Then, using this new matrix along with the five weaning milestone matrices and the genetic distance matrix generated earlier, I conducted five partial Mantel tests in which I assessed the relationships between latitudinal distance and weaning milestone distance while controlling for genetic distance. I continued to use log transformed values for skewed variables during this set of analyses.

Subsequently, I investigated the effect of subsistence strategy variation on the relationships between latitude and weaning milestones. I subdivided the sample according to subsistence

strategy (into foragers, pastoralists, and farmers) and then conducted another set of bivariate regression analyses (the third set of analyses for latitude) and another set of partial Mantel tests (the fourth and final set of analyses for latitude).

I then focused on the impact of elevation on the timing of the weaning milestones. The test predictions were that infant's age at the introduction of complementary liquids (INTLIQ), infant's age at the introduction of complementary solids (INTSOL), infant's age at the introduction of earliest complementary liquids or solids (INTLIQSOL), and cessation of breastfeeding (CESSBF) should be positively correlated with elevation; and duration of the weaning process (DURWP) should be negatively correlated with elevation. As with latitude, the relationships between weaning milestones and elevation were expected to be stronger among farmers than among foragers or pastoralists. The reasoning for these predictions was the same as for latitude: resource insecurity increases with elevation and increased risk of resource failure should drive mothers to buffer their infants, via frequent and extended breastfeeding, against the effects of unexpected resource stress. This pattern was expected to be stronger among farmers than among foragers or pastoralists because the reduction in mobility and increased population size associated with plant food production reduces a population's ability to respond to resource stress by simply moving farther afield to hunt, gather, or herd. To test these predictions, I employed the same analytical methods as with latitude, beginning with all populations/ log transformed data (elevation is, like latitude, positively skewed), then all populations/ log transformed data/ genetic distance controlled, then sample subdivided/ log transformed data, and ending with sample subdivided/ log transformed data/ genetic distance controlled.

The third proxy for risk of resource failure was intra-annual variability in precipitation. As such, the next four sets of analyses focused on the relationships between variability in precipitation



and the timing of weaning milestones. The test predictions were that infant's age at the introduction of complementary liquids (INTLIQ), infant's age at the introduction of complementary solids (INTSOL), infant's age at the introduction of earliest complementary liquids or solids (INTLIQSOL), and cessation of breastfeeding (CESSBF) should be positively correlated with variability in precipitation; duration of the weaning process (DURWP) should be negatively correlated with variability in precipitation. I expected the increased risk of resource failure associated with unpredictable rainfall to drive mothers to protect their infants from nutritional stress by extending exclusive breastfeeding and by extending the weaning process. I expected these relationships to be stronger among foragers and farmers than among pastoralists because, unlike pastoralists who have access to herd animal milk, foragers and farmers do not have access to large quantities of alternative sources of nutritive, relatively sterile liquids to use as complementary foods. The greater reliance on water and on other non-milk liquids by foragers and by farmers should increase water-related selection pressures on these populations. I tested these predictions using the same methods as those used for latitude and elevation.

The last set of analyses focused on the relationships between effective temperature and the timing of the weaning milestones. The test predictions were that infant's age at the introduction of complementary liquids (INTLIQ), infant's age at the introduction of complementary solids (INTSOL), infant's age at the introduction of earliest complementary liquids or solids (INTLIQSOL), and cessation of breastfeeding (CESSBF) should be negatively correlated with effective temperature, while duration of the weaning process (DURWP) should be positively correlated with effective temperature. Relatively low effective temperatures were expected to be associated with shorter seasons, harsher conditions, and thus greater risk of resource failure.

Mothers should, in such conditions, buffer their infants against risk by extending exclusive breastfeeding and by extending the weaning process. This pattern should be stronger among farmers than among foragers or pastoralists because effective temperature is largely a measure of growing season: the livelihoods of farmers are tied particularly closely to growing season and, as such, the selection pressures related to growing season should be particularly strong among these populations. These predictions were tested using the same methods as those used for latitude, elevation, and variability in precipitation with the exception that effective temperature was not log transformed as the relevant distribution was not skewed.

## CHAPTER 3, RESULTS

### 3.1. Exploratory analyses

The descriptive statistics pertaining to the full sample are summarized in Table 1. When all populations are included in analyses, the central tendency is to begin introducing complementary foods when infants reach approximately four or five months of age (liquids generally slightly earlier than solids), to extend the weaning process for approximately 24 months, and to cease breastfeeding when infants reach approximately 29 months of age. However, all weaning milestone variables are characterized by large ranges of variation, with the differences between minimum and maximum values ranging from 18 months (for INTSOL) to 71 months (for DURWP). All weaning milestone distributions for the full sample contain relatively few high values and, as such, are at least moderately positively skewed. INTSOL and CESSBF are characterized by relatively low levels of skewness and can therefore be treated as approximately normal. In contrast, INTLIQ, INLIQSOL, and DURWP are characterized by levels of positive skew that violate assumptions of normalcy.

**Table 1, Descriptive Statistics for weaning milestones for all populations**

<b>Weaning milestone variable</b>	<b>N</b>	<b>Minimum</b>	<b>Mean</b>	<b>Maximum</b>	<b>Skewness</b>
INTLIQ	20	0	4	24	1.810
INTSOL	52	0	5	18	0.788
INTLIQSOL	47	0	5	24	2.299
CESSBF	63	11	29	72	0.988
DURWP	45	0	24	71	1.105

The descriptive statistics pertaining to foraging populations are summarized in Table 2. Among foraging populations, INTLIQ, with a mean value of one month, appears to occur earlier than it does when all populations are included in analyses although this is likely an artefact of very small sample size. The central tendencies among foragers of four months for both INTSOL and INTLIQSOL, of 24 months for DURWP, and of 31 months for CESSBF are similar to those of the full sample although the ranges of variation for all milestones (between 0 months for INTLIQ and 36 months for CESSBF) are much smaller than those of the full sample. Although all of the weaning milestone distributions for foraging populations are negatively skewed, none is skewed to the extent that normalcy assumptions are violated.

**Table 2, Descriptive Statistics for weaning milestones for forager populations**

Weaning milestone variable	N	Minimum	Mean	Maximum	Skewness
INTLIQ	2	1	1	1	-
INTSOL	8	1	4	7	-0.399
INTLIQSOL	8	1	4	7	-0.399
CESSBF	13	12	31	48	-0.151
DURWP	8	6	24	36	-0.667

The descriptive statistics concerning pastoralist populations are summarized in Table 3.

Measures of central tendency for the introduction of complementary foods are generally slightly earlier among pastoralists than among all populations. As with all populations, INTLIQ among pastoralists has a mean value of four months, INTSOL and INTLIQSOL have mean values of four months and three months respectively (both of these values are one month lower than among all populations). Mean values for CESSBF and DURWP are the same among the subsample of pastoral populations as they are among the full sample. The ranges of variation for all weaning milestones are smaller among pastoralists than they are among the full sample. All milestone variables are positively skewed in their distribution. INTSOL is only mildly skewed but INTLIQ, INTLIQSOL, CESSBF, and DURWP are so skewed that they violate assumptions of normalcy.

**Table 3, Descriptive statistics for weaning milestones for pastoralist populations**

Weaning milestone variable	N	Minimum	Mean	Maximum	Skewness
INTLIQ	7	0	4	12	1.217
INTSOL	9	0	4	12	0.847
INTLIQSOL	13	0	3	12	1.352
CESSBF	15	12	29	72	1.108
DURWP	11	5	24	71	1.772

Descriptive statistics concerning weaning variation in farmers are summarized in Table 4.

Among farmers, both liquid and solid complementary foods are generally introduced slightly later, the cessation of breastfeeding occurs slightly earlier, and the duration of the weaning process is slightly shorter than among all populations. All weaning milestone distributions for farmers are at least moderately positively skewed although INTSOL and DURWP are not skewed to the extent that normalcy assumptions are violated. However, INTLIQ, INTLIQSOL, and CESSBF violate normalcy assumptions.

**Table 4, Descriptive statistics for weaning milestones for farming populations**

Weaning milestone variable	N	Minimum	Mean	Maximum	Skewness
INTLIQ	11	0	5	24	2.276
INTSOL	30	0	6	18	0.820
INTLIQSOL	31	0	6	11	1.889
CESSBF	35	11	28	66	1.120
DURWP	26	0	23	60	0.827

A comparison among subsistence groups of the means for all milestones is presented in Table 5. Essentially, the dataset is characterized by a considerable amount of variation regarding all infant feeding variables considered, both when all populations are included and when the sample is subdivided by subsistence strategy. As described above, both center and spread values vary among primary subsistence strategy groups. Although (with one exception) mean values for the ages at which both liquid and solid complementary foods are introduced are between three and six months regardless of primary subsistence strategy, mean values for foraging and for pastoralist populations are at the lower end of this range and mean values for farmers are at the higher end. Similarly, CESSBF occurs earlier and DURWP is shorter among farmers than among the other subsistence groups or among all populations. Furthermore, the differences between minimum and maximum values of all milestone variables are greater among farmers than among other subsistence groups.

**Table 5, Means of weaning milestones by mode of subsistence**

<b>Weaning milestone variable</b>	<b>All Populations</b>	<b>Foragers</b>	<b>Pastoralists</b>	<b>Farmers</b>
INTLIQ	4	1-	4	5
INTSOL	5	4	4	6
INTLIQSOL	5	4	3	6
CESSBF	29	31	29	28
DURWP	24	24	24	23

### 3.2. Population history hypothesis

#### 3.2.1. Genetic distance/ all populations/ log transformed data mantel matrix tests

Table 6 presents the results of the tests of the population history hypothesis in which all populations are included, skewed variables are log transformed, and genetic distance is controlled. In these analyses, INTLIQ is weakly negatively correlated with genetic distance and this relationship is not significant. INTSOL is weakly positively correlated with genetic distance but this relationship is not significant. INTLIQSOL is weakly positively correlated with genetic distance but again this relationship is not significant. CESSBF is also weakly positively correlated with genetic distance but, once again, the relationship is not significant. DURWP is weakly negatively correlated with genetic distance and this relationship is not significant. Accordingly, the results of these analyses do not support the hypothesis that variation in the timing of events in the weaning process is primarily a consequence of population history.

**Table 6, Relationships between genetic distance and weaning milestones/ all populations**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	16	-0.1472	0.861
INTSOL	47	0.04456	0.238
Log 10 INTLIQSOL	46	-0.05237	0.732
CESSBF	62	-0.005096	0.504
Log 10 DURWP	43	0.001532	0.498



### 3.2.2. Genetic distance/ sample subdivided mantel matrix tests

The results of the analyses in which genetic distance is used to predict weaning variation, the sample is subdivided by subsistence type, and the data are log transformed are summarized in Tables 7-9. When only foragers are included in analyses, I could not assess the effect of genetic distance on INTLIQ because the sample size is too small. INTSOL is weakly negatively correlated with genetic distance but the relationship is not significant. INTLIQSOL is negatively correlated with genetic distance but the relationship, again, is not significant. CESSBF is weakly positively correlated with genetic distance but, once again, the relationship is not significant. DURWP is weakly negatively correlated with genetic distance; this relationship is not significant.

**Table 7, Relationships between genetic distance and weaning milestones/ foragers**

Weaning milestone variable	N	R	P
INTLIQ	2	1	-
INTSOL	8	-0.04343	0.520
INTLIQSOL	8	-0.1035	0.631
CESSBF	13	0.003024	0.368
DURWP	8	-0.0343	0.414

When only pastoralists are included in analyses, INTLIQ is positively correlated with genetic distance although this relationship does not reach statistical significance. INTSOL is weakly negatively correlated with genetic distance but this relationship is not significant. INTLIQSOL is negatively correlated with genetic distance but, again, this relationship is not significant. CESSBF is negatively correlated with genetic distance but, once again, the relationship is not of

statistical significance. DURWP is weakly negatively correlated with genetic distance; the relationship is not significant.

**Table 8, Relationships between genetic distance and weaning milestones/ pastoralists**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	5	0.550	0.107
INTSOL	9	-0.2745	0.978
Log 10 INTLIQSOL	9	-0.3378	0.978
Log 10 CESSBF	15	-0.1034	0.772
Log 10 DURWP	11	-0.07341	0.638

Among farmers, INTLIQ is weakly negatively correlated with genetic distance but this relationship is not significant. INTSOL is weakly positively correlated with genetic distance; this relationship is not significant. INTLIQSOL is weakly negatively correlated with genetic distance and, again, the relationship is not significant. CESSBF is weakly positively correlated with genetic distance but the relationship is not of significance. DURWP is negatively correlated with genetic distance but, once again, the result is not significant.

**Table 9, Relationships between genetic distance and weaning milestones/ farmers**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	9	-0.06472	0.616
INTSOL	30	0.05488	0.247
Log 10 INTLIQSOL	29	-0.004089	0.457
Log 10 CESSBF	34	0.02993	0.347
DURWP	24	-0.07179	0.794

Thus, the results of the sample subdivided/ genetic distance analyses do not support the null hypothesis that population history drives the times at which any of the key milestones in the weaning process occur.

### **3.3. Risk of resource failure hypothesis**

#### *3.3.1. Latitude*

##### *3.3.1.1. Latitude/all populations regression analyses*

The results of the latitude/ all populations regression analyses are summarized in Table 10. When all populations are included in analyses, INTLIQ is positively correlated with latitude but this relationship is not significant. INTSOL is negatively correlated with latitude but again this relationship is not significant. INTLIQSOL is negatively correlated with latitude and again this relationship is not significant. CESSBF is positively correlated with latitude but, once again, this relationship is not significant. DURWP is negatively correlated with latitude but this relationship

does not achieve statistical significance. Essentially, the all populations/log transformed data analyses do not support the expectations of the resource failure risk hypothesis that latitude affects the timing of events in the weaning process.

**Table 10, Relationships between latitude and weaning milestones/ all populations**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	16	0.033	0.980
INTSOL	47	-0.093	0.532
Log 10 INTLIQSOL	46	-0.069	0.648
CESSBF	52	0.067	0.636
Log 10 DURWP	43	-0.200	0.197

*3.3.1.2. Latitude/ all populations/ partial mantel matrix tests*

The results of the latitude/ all populations/ partial mantel tests are summarized in Table 11. When all populations are included in analyses and genetic distance is controlled, INTLIQ is negatively correlated with latitude but this relationship is not significant. INTSOL is negatively correlated with latitude but this relationship is not significant. INTLIQSOL is negatively correlated with latitude but this relationship is not significant. CESSBF is positively correlated with latitude but this relationship is not significant. DURWP is negatively correlated with latitude but, again, this relationship is not significant. Thus, the results of the all populations/ log transformed data/ genetic distance controlled analyses do not support the prediction that latitude affects the timing of events in the weaning process.

**Table 11, Relationships between latitude and weaning milestones/ all populations/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	16	-0.1686	0.925
INTSOL	47	-0.08127	0.926
Log 10 INTLIQSOL	46	-0.07882	0.880
CESSBF	62	0.007808	0.390
Log 10 DURWP	43	-0.02362	0.581

*3.3.1.3. Latitude/ sample subdivided regression analyses*

The results of the latitude/ sample subdivided regression analyses are summarized in Tables 12-14. I was unable to assess the effects of latitude on INTLIQ in the forager sample because the sample size is too small. INTSOL is negatively correlated with latitude but this relationship is not significant. INTLIQSOL is negatively correlated with latitude but, again, this relationship is not significant. CESSBF is negatively correlated with latitude but, once again, this relationship is not significant. DURWP is negatively correlated with latitude but this relationship is not significant.

**Table 12, Relationships between latitude and weaning milestones/ foragers**

Weaning milestone variable	N	R	P
INTLIQ	2	1	-
INTSOL	7	-0.191	0.681
INTLIQSOL	7	-0.155	0.740
CESSBF	12	-0.232	0.468
DURWP	7	-0.174	0.709

Among pastoralists, INTLIQ is negatively correlated with latitude but this relationship is not significant. INTSOL is negatively correlated with log 10 latitude but, again, this relationship is not significant. INTLIQSOL is negatively correlated with latitude but again this relationship is not significant. CESSBF is positively correlated with latitude although this relationship is not significant. DURWP is negatively correlated with latitude but this relationship, once again, is not significant.

**Table 13, Relationships between latitude and weaning milestones/ pastoralists**

Weaning milestone variable	N	R	P
Log 10 INTLIQ	5	-0.263	0.669
INTSOL	9	-0.224	0.563
Log 10 INTLIQSOL	9	-0.046	0.906
Log 10 CESSBF	15	0.144	0.607
Log 10 DURWP	11	-0.077	0.822

Among farmers, INTLIQ is positively correlated with latitude but this relationship is not significant. INTSOL is positively correlated with latitude although this relationship is not significant. INTLIQSOL is positively correlated with latitude but this relationship is not significant. CESSBF is negatively correlated with latitude at a level that reaches significance. DURWP is negatively correlated with latitude among farmers but not at a statistically significant level.

**Table 14, Relationships between latitude and weaning milestones/ farmers**

Weaning milestone variable	N	R	P
Log 10 INTLIQ	9	0.324	0.395
INTSOL	30	0.132	0.487
Log 10 INTLIQSOL	29	0.077	0.693
Log 10 CESSBF	34	-0.371	0.031
DURWP	24	-0.277	0.189

Thus, among populations that rely chiefly on foraging or animal husbandry for subsistence, the expectation that latitude affects the timing of events in the weaning process does not receive support from the sample divided by subsistence strategy/ log transformed data analyses.

Among populations that rely chiefly on the production of plant food, however, the expectation that latitude affects the timing of events in the weaning process receives a small amount of support from the sample subdivided/ log transformed data analyses.

### 3.3.1.4 Latitude/ sample subdivided/ partial mantel matrix tests

The results of the latitude/ sample subdivided/ genetic distance controlled analyses are summarized in Tables 15-17. In these analyses, among foraging populations, it is not possible to assess the impact of latitude on INTLIQ due to small sample size. INTSOL is negatively correlated with latitude but this relationship is not significant. INTLIQSOL is also negatively correlated with latitude but again this relationship is not significant. CESSBF is negatively correlated with latitude but this relationship is also not significant. DURWP is negatively correlated with latitude but, once again, the relationship is not significant.

**Table 15, Relationships between latitude and weaning milestones/ foragers/ genetic distances controlled**

Weaning milestone variable	N	R	P
INTLIQ	2	-	-
INTSOL	8	-0.2612	0.995
INTLIQSOL	8	-0.2774	0.996
CESSBF	13	-0.1715	0.775
DURWP	8	-0.1139	0.587

Among pastoralists, INTLIQ is negatively correlated with log 10 latitude but this relationship is not statistically significant. INTSOL is positively correlated with INTSOL; this relationship approaches but does not reach significance. INTLIQSOL is negatively correlated with latitude but this relationship is not significant. CESSBF is also negatively correlated with latitude but, once



more, this relationship is not significant. DURWP is negatively correlated with latitude among pastoralists although this relationship is not significant.

**Table 16, Relationships between latitude and weaning milestones/ pastoralists/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	5	-0.3401	0.828
INTSOL	9	0.302	0.077
Log 10 INTLIQSOL	9	0.02099	0.388
Log 10 CESSBF	15	-0.1537	0.850
Log 10 DURWP	11	-0.2453	0.934

Among populations that rely primarily on farming for subsistence, INTLIQ is negatively correlated with latitude although this relationship is not statistically significant. INTSOL is positively correlated with latitude; however, while this relationship reaches statistical significance, it is very weak. INTLIQSOL is negatively correlated with latitude but this relationship is not statistically significant. CESSBF is positively correlated with latitude but this relationship is not significant. DURWP is positively correlated with latitude but this relationship is not significant.

**Table 17, Relationships between latitude and weaning milestones/ farmers/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	9	-0.1194	0.590
INTSOL	30	0.1681	0.028
Log 10 INTLIQSOL	29	-0.1078	0.895
CESSBF	34	0.08088	0.199
Log 10 DURWP	24	0.05848	0.235

Thus, among foragers and pastoralists, the results of the sample subdivided/ log transformed data/ genetic distance controlled analyses do not support the prediction that latitude impacts the timing of events in the weaning process. Among plant food producers, the results of the sample subdivided/ log transformed data/ genetic distance controlled analyses may provide a small amount of support for the prediction that latitude, albeit weakly, affects the timing of events in the weaning process.

### **3.3.2. Elevation**

#### *3.3.2.1. Elevation/ all populations/ regression analyses*

The results of the elevation/ all populations/regression analyses are summarized in Table 18. In these analyses, INTLIQ is positively correlated with elevation but this relationship is not significant. INTSOL is also positively correlated with elevation but, again, this relationship is not significant. INTLIQSOL is positively correlated with elevation but this relationship is not

significant. CESSBF is positively correlated with elevation but, once again, this relationship is not significant. DURWP is negatively correlated with elevation but this relationship is not significant. Thus, the results of the all populations analyses are counter to the expectation that elevation affects the timing of events in the weaning process.

**Table 18, Relationships between elevation and weaning milestone variables/ all populations**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	16	0.190	0.481
INTSOL	46	0.146	0.334
Log 10 INTLIQSOL	41	0.175	0.273
CESSBF	60	0.018	0.890
Log 10 DURWP	43	-0.033	0.837

*3.3.2.2. Elevation/ all populations/partial mantel matrix tests*

The results of the all populations/ log transformed data/ genetic distance controlled analyses are summarized in Table 19. When all populations are included in analyses and when genetic distance is controlled, INTLIQ is negatively correlated with elevation but this relationship is not significant. INTSOL is negatively correlated with elevation but this relationship is not significant. INTLIQSOL is negatively correlated with elevation but this relationship is not significant. CESSBF is positively correlated with elevation but this relationship is not significant. DURWP is negatively correlated with elevation but, once again, this relationship is not significant. In essence, the results of the all populations/ genetic distance controlled analyses are not in line

with the predictions of the resource failure risk hypothesis regarding the relationships between elevation and the timing of events in the weaning process.

**Table 19, Relationships between elevation and weaning milestone variables/ all populations/ genetic distances controlled**

Weaning milestone variable	N	R	P
Log 10 INTLIQ	16	-0.04273	0.544
INTSOL	46	0.0711	0.156
Log 10 INTLIQSOL	45	-0.06568	0.752
CESSBF	60	-0.09334	0.960
Log 10 DURWP	42	-0.04783	0.720

### 3.3.2.3. Elevation/ sample subdivided/ regression analyses

The elevation/ sample subdivided results are summarized in Tables 20-22. In these analyses, I was not able to assess the effect of elevation on INTLIQ among populations that rely chiefly on foraging for subsistence due to small sample size. INTSOL is positively correlated with elevation but this relationship is not significant. INTLIQSOL is also positively correlated with elevation but, again, this relationship is not significant. CESSBF is also positively correlated with elevation but, once again, this relationship is not significant. DURWP is positively correlated with elevation among foragers but this relationship is not significant.

**Table 20, Relationships between elevation and weaning milestone variables/ foragers**

Weaning milestone variable	N	R	P
INTLIQ	2	1	-
INTSOL	6	0.503	0.309
INTLIQSOL	6	0.535	0.274
CESSBF	10	0.360	0.307
DURWP	6	0.452	0.369

Among pastoralists, INTLIQ is strongly negatively correlated with elevation at a highly significant level. INTSOL is negatively correlated with elevation but this relationship is not significant. INTLIQSOL is also negatively correlated with elevation but again this relationship is not significant. CESSBF is positively correlated with elevation but this relationship is not significant. DURWP is negatively correlated with elevation but this relationship is, once again, not significant.

**Table 21, Relationships between elevation and weaning milestone variables/ pastoralists**

Weaning milestone variable	N	R	P
Log 10 INTLIQ	5	-0.992	0.001
INTSOL	9	-0.471	0.201
Log 10 INTLIQSOL	9	-0.502	0.169
Log 10 CESSBF	15	0.031	0.912
Log 10 DURWP	11	-0.222	0.511

In populations that rely primarily on farming for subsistence, INTLIQ is positively correlated with elevation but this relationship is not statistically significant. INTSOL is also positively correlated with elevation although, again, this relationship is not significant. INTLIQSOL is positively correlated with elevation but, again, this relationship is not significant. CESSBF is negatively correlated with elevation but this relationship is not significant. DURWP is negatively correlated with elevation but this relationship, again, is not significant.

**Table 22, Relationships between elevation and weaning milestones/ farmers**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	9	0.351	0.355
INTSOL	30	0.260	0.165
Log 10 INTLIQSOL	29	0.246	0.199
Log 10 CESSBF	34	-0.022	0.901
DURWP	24	-0.062	0.774

As such, the resource failure risk hypothesis does not receive support from the elevation/ sample subdivided analyses among foragers or among farmers. This hypothesis receives some support among pastoralists from the elevation/ sample subdivided analyses.

*3.3.2.4. Elevation/ sample subdivided/ partial mantel matrix tests*

Tables 23-25 present the results of the elevation/ sample subdivided/ genetic distance controlled analyses. When genetic distance is controlled, I could not assess the effects elevation on INTLIQ among foraging populations as the sample size is too small. INTSOL is weakly

negatively correlated with elevation among foragers although this relationship is not significant. INTLIQSOL is also weakly negatively correlated with elevation but this relationship is also not significant. CESSBF is negatively correlated with elevation but this relationship is not significant. DURWP is weakly positively correlated with elevation although this relationship, again, is not significant.

**Table 23, Relationships between elevation and weaning milestone variables/ foragers/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
INTLIQ	2	-	-
INTSOL	7	-0.0459	0.543
INTLIQSOL	7	-0.01064	0.440
CESSBF	11	-0.1023	0.707
DURWP	7	0.06096	0.336

Among pastoralists, INTLIQ is strongly positively correlated with elevation at a statistically significant level. INTSOL is positively correlated with elevation although this relationship is not significant. INTLIQSOL is positively correlated with elevation but this relationship failed to achieve statistical significance. CESSBF is negatively correlated with elevation although this relationship is not significant. DURWP is negatively correlated with elevation among pastoralists, albeit this relationship is not significant.

**Table 24, Relationships between elevation and weaning milestone variables/ pastoralists/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	5	0.9573	0.010
INTSOL	9	0.0834	0.252
Log 10 INTLIQSOL	9	0.2116	0.129
CESSBF	15	-0.1018	0.849
Log 10 DURWP	11	-0.09534	0.694

Among farmers, INTLIQ is negatively correlated with elevation although this relationship is not significant. INTSOL is negatively correlated with elevation but this relationship is not significant. INTLIQSOL is also negatively correlated with elevation but this relationship, again, is not significant. CESSBF is negatively correlated with elevation but this relationship is not significant. DURWP is negatively correlated with elevation among farmers but this relationship is not significant.

**Table 25, Relationships between elevation and weaning milestone variables/ farmers/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	9	-0.0206	0.445
INTSOL	30	-0.0404976	0.491
Log 10 INTLIQSOL	29	-0.0878	0.733
Log 10 CESSBF	34	-0.1324	0.977
DURWP	24	-0.09311	0.929



As such, the results from the elevation/ sample subdivided/ genetic distance controlled analyses do not support the hypothesis that risk of resource failure affects the timing of events in the weaning process among foragers, or among farmers. The results of this set of analyses do offer some support to the hypothesis among pastoralists, however.

### **3.3.3. Intra-Annual Variability in Precipitation**

#### *3.3.3.1. Variability in precipitation/ all populations/ regression analyses*

Table 26 presents the results of the variability in precipitation/ all populations/ log transformed data regression analyses. INTLIQ is negatively correlated with variability in precipitation but this relationship is not significant. INTSOL is weakly positively correlated with variability in precipitation but this relationship is not significant. INTLIQSOL is negatively correlated with variability in precipitation but this relationship is not significant. CESSBF is weakly positively correlated with variability in precipitation but this relationship is not significant. DURWP is weakly negatively correlated with variability in precipitation. Thus, the results from the variability in precipitation/ all populations/ log transformed data do not support the resource failure risk hypothesis.

**Table 26, Relationships between variability in precipitation and weaning milestone variables/ all populations**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
INTLIQ	14	-0.376	0.185
INTSOL	41	0.038	0.814
INTLIQSOL	40	-0.108	0.509
CESSBF	54	0.047	0.735
DURWP	36	-0.007	0.968

*3.3.3.2. Variability in precipitation/ all populations/ partial mantel matrix tests*

A summary of the variability in precipitation/ all populations/ genetic distance controlled analyses is provided in Table 27. INTLIQ is positively correlated with variability in precipitation but this relationship is not significant. INTSOL is negatively correlated with variability in precipitation but, again, this relationship is not significant. INTLIQSOL is positively correlated with variability in precipitation but this relationship is not significant. CESSBF is negatively correlated with variability in precipitation but this relationship, again, is not significant. DURWP is weakly negatively correlated with variability in precipitation at a level that approaches but does not achieve statistical significance. Thus, the results from the variability in precipitation/ all populations/ genetic distance controlled analyses do not provide strong support for the hypothesis that risk of resource failure affects the timing of events in the weaning process.

**Table 27, Relationships between variability in precipitation and weaning milestone variables/ all populations/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	14	0.1211	0.242
INTSOL	41	-0.1079	0.958
Log 10 INTLIQSOL	40	0.0451	0.276
CESSBF	54	-0.09334	0.960
Log 10 DURWP	36	0.1356	0.053

*3.3.3.3. Variability in precipitation/ sample subdivided/ regression analyses*

Tables 28-30 present the results of the variability in precipitation/ sample subdivided/ log transformed data regression analyses. Among foragers, I was unable to assess the affect of variability in precipitation on INTLIQ as the sample size is too small. INTSOL is positively correlated with variability in precipitation but this relationship is not significant. INTLIQSOL is positively correlated with variability in precipitation but, again, this relationship is not significant. CESSBF is negatively correlated with variability in precipitation but this relationship is not a significant one. DURWP is negatively correlated with variability in precipitation among foraging populations; however, this relationship does not reach or even approach significance.

**Table 28, Relationships between variability in precipitation and weaning milestone variables/ foragers**

Weaning milestone variable	N	R	P
INTLIQ	2	-1	-
INTSOL	6	0.281	0.589
INTLIQSOL	6	0.209	0.690
CESSBF	10	-0.493	0.204
DURWP	6	-0.599	0.209

Among pastoralists, while INTLIQ is strongly, positively correlated with variability in precipitation, this relationship does not reach or even approach statistical significance. INTSOL is positively correlated with variability in precipitation but this relationship is not significant. INTLIQSOL is positively correlated with variability precipitation but, again, the relationship is not significant. CESSBF is negatively correlated with variability in precipitation but this weak relationship is not a significant one. DURWP is negatively correlated with variability in precipitation but, again, this relationship is not statistically significant.

**Table 29, Relationships between variability in precipitation and weaning milestone variables/ pastoralists**

Weaning milestone variable	N	R	P
Log 10 INTLIQ	4	0.673	0.327
INTSOL	8	0.235	0.575
Log 10 INTLIQSOL	8	0.205	0.816
Log 10 CESSBF	13	-0.015	0.962
Log 10 DURWP	9	-0.197	0.612

Among populations that subsist primarily on cultivated plant foods, INTLIQ is negatively correlated with variability in precipitation although this relationship does not achieve significance. INTSOL is also negatively correlated with variability in precipitation but, again, the relationship is not significant. INTLIQSOL is negatively correlated with variability in precipitation although this relationship approaches but did not reach statistical significance. CESSBF is positively correlated with variability in precipitation although again this relationship approaches without reaching significance. Among farmers, DURWP is positively correlated with variability in precipitation although this relationship approaches but does not reach statistical significance.

**Table 30, Relationships between variability in precipitation and weaning milestone variables/ farmers**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	8	-0.567	0.143
INTSOL	27	-0.186	0.353
Log 10 INTLIQSOL	26	-0.338	0.091
Log 10 CESSBF	31	0.332	0.077
DURWP	29	0.409	0.066

Thus, the results from the variability in precipitation/ sample subdivided/ log transformed data analyses do not support the hypothesis that risk of resource failure affects the timing of milestones in the weaning process among foraging or pastoral populations. The results from these sets of analyses may weakly support this hypothesis among farmers.

3.3.3.4. *Variability in precipitation/ sample subdivided/ partial mantel matrix tests*

The variability in precipitation/ sample subdivided/ log transformed data/ genetic distances controlled results are summarized in Tables 31-33. In foraging populations, when log transformed data are used and when genetic distance is controlled, I was unable to assess the effect of variability in precipitation on INTLIQ because the sample size is too small. INTSOL is negatively correlated with variability in precipitation but this relationship is not statistically significant. INTLIQSOL is also negatively correlated with variability in precipitation but, again, the relationship is not significant. CESSBF is also negatively correlated with variability in precipitation but, once again, the relationship is not of statistical significance. DURWP is weakly positively correlated with variability in precipitation among foraging populations at a statistically significant level.

**Table 31, Relationships between variability in precipitation and weaning milestone variables/ foragers/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
INTLIQ	2	-	-
INTSOL	6	-0.1947	0.662
INTLIQSOL	6	-0.219	0.670
CESSBF	10	-0.1461	0.155
DURWP	6	0.1853	0.013

Among pastoralists, INTLIQ is negatively correlated with variability in precipitation although the relationship is not significant. INTSOL is also negatively correlated with variability in

precipitation but, again, the relationship is not significant. INTLIQSOL is negatively correlated with variability in precipitation although this relationship is not significant. CESSBF is also negatively correlated with variability in precipitation although the relationship is not significant. Among pastoralists, DURWP is positively correlated with variability in precipitation but this relationship is not significant.

**Table 32, Relationships between variability in precipitation and pastoralists/ genetic distances controlled**

Weaning milestone variable	N	R	P
Log 10 INTLIQ	4	-0.1503	0.553
INTSOL	8	-0.08949	0.602
Log 10 INTLIQSOL	8	-0.04805	0.523
Log 10 CESSBF	13	-0.2373	0.991
Log 10 DURWP	9	0.221	0.846

Among farmers, INTLIQ is positively correlated with variability in precipitation although the relationship is not of statistical significance. INTSOL is negatively correlated with variability in precipitation but, again, the relationship is not significant. INTLIQSOL is positively correlated with variability in precipitation but the relationship does not achieve significance. CESSBF is negatively correlated with variability in precipitation but this relationship is not significant. DURWP is positively correlated with variability in precipitation but this relationship is non-significant.

**Table 33, Relationships between variability in precipitation and weaning milestone variables/ farmers populations/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	8	0.2442	0.175
INTSOL	27	-0.1183	0.893
Log 10 INTLIQSOL	26	0.1043	0.175
Log 10 CESSBF	31	-0.0257	0.356
DURWP	21	0.0362	0.304

Thus, the results of the variability in precipitation/ sample subdivided/ genetic distance controlled analyses provide some support for the hypothesis that resource failure risk drives a small portion of among-population variation in DURWP among foraging populations. The results of these sets of analyses do not strongly support the risk of resource failure hypothesis among pastoral or plant food producing populations.

### **3.3.4. Effective Temperature**

#### *3.3.4.1. Effective temperature/ all populations/ regression analyses*

The results of the effective temperature/ all populations/ log transformed data analyses are summarized in Table 34. When the full sample is used, INTLIQ is significantly negatively correlated with effective temperature. INTSOL is negatively correlated with effective temperature but this relationship is non-significant. Similarly, INTLIQSOL is negatively correlated with effective temperature; this relationship begins to approach but does not reach significance.



CESSBF is also negatively correlated with effective temperature although again the relationship is not significant. Finally, DURWP is positively correlated with effective temperature but this relationship is not significant. Thus, the results of the effective temperature/ all populations/ log transformed data analyses offer a small amount of support to the hypothesis that resource risk influences the timing of events in the weaning process.

**Table 34, Relationships between effective temperature and weaning milestone variables/ all populations**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	15	-0.543	0.036
INTSOL	45	-0.063	0.680
Log 10 INTLIQSOL	43	-0.276	0.073
CESSBF	59	-0.055	0.676
Log 10 DURWP	40	0.169	0.297

#### *3.3.4.2. Effective temperature/ all populations/ partial mantel matrix tests*

The results of the effective temperature/ all populations/ genetic distance controlled analyses are summarized in Table 35. When all populations are included and genetic distance is controlled, INTLIQ is weakly positively correlated with effective temperature at a level that approaches statistical significance. INTSOL is negatively correlated with effective temperature but this relationship is not significant. INTLIQSOL is also negatively correlated with effective temperature but, again, the relationship is not a significant one. CESSBF is positively correlated

with effective temperature but the relationship is not significant. DURWP is positively correlated with effective temperature but this relationship fails to achieve statistical significance. As such, the results of the effective temperature/ all populations/ phylogenetically controlled analyses do not provide strong support for the resource insecurity hypothesis.

**Table 35, Relationships between effective temperature and weaning milestone variables/ all populations/ genetic distances controlled**

Weaning milestone variable	N	R	P
Log 10 INTLIQ	15	0.2081	0.059
INTSOL	45	-0.0122	0.559
Log 10 INTLIQSOL	43	0.05536	0.139
CESSBF	59	0.02448	0.209
Log 10 DURWP	40	0.1007	0.102

*3.3.4.3. Effective temperature/ sample subdivided/ regression analyses*

The results of the effective temperature/ sample subdivided/ log transformed data analyses are summarized in Tables 36-38. I was unable to assess the impact of effective temperature on INTLIQ among populations of foragers as the sample size is too small. INTSOL is positively correlated with effective temperature but the relationship is not significant. INTLIQSOL is positively correlated with effective temperature but this relationship is not significant. CESSBF is also positively correlated with effective temperature but, again, the relationship is not

significant. DURWP is positively correlated with effective temperature but this relationship is non-significant.

**Table 36, Relationships between effective temperature and weaning milestone variables/ foragers**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
INTLIQ	2	1	-
INTSOL	7	0.104	0.825
INTLIQSOL	7	0.044	0.925
CESSBF	12	0.029	0.929
DURWP	7	0.208	0.654

Among pastoralists, INTLIQ is strongly negatively correlated with effective temperature although this relationship fails to achieve significance. Among pastoralists, INTSOL is positively correlated with effective temperature although this relationship is not a significant one. INTLIQSOL is negatively correlated with effective temperature although this relationship also failed to achieve significance. CESSBF is negatively correlated with effective temperature; again, the relationship is not significant. DURWP is negatively correlated with effective temperature although this relationship is not significant.

**Table 37, Relationships between effective temperature and weaning milestone variables/ pastoralists**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	4	-0.866	0.124
INTSOL	9	0.076	0.846
Log 10 INTLIQSOL	8	-0.518	0.189
Log 10 CESSBF	13	-0.379	0.201
Log 10 DURWP	10	-0.296	0.406

Among farmers, INTLIQ is negatively correlated with effective temperature at a statistically significant level. INTSOL is negatively correlated with effective temperature although this relationship is non-significant. INTLIQSOL is also negatively correlated with effective temperature but, again, the relationship is not a significant one. CESSBF is positively correlated with effective temperature but the relationship is not significant. DURWP is positively correlated with effective temperature at a statistically significant level.

**Table 38, Relationships between effective temperature and weaning milestone variables/ farmers**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	9	-0.631	0.068
INTSOL	28	-0.245	0.209
Log 10 INTLIQSOL	27	-0.288	0.146
Log 10 CESSBF	33	0.240	0.179
DURWP	22	0.443	0.039

Thus, the results of the effective temperature/ sample subdivided analyses do not support the hypothesis that resource failure risk is related to the times at which some of the milestones in the weaning process occur among some foraging or pastoralist populations. The results of these sets of analyses do support, however, the prediction that effective temperature affects weaning decisions among farmers.

#### *3.3.4.4. Effective temperature/ sample subdivided/ partial mantel matrix tests*

The results of the effective temperature/ sample subdivided/ genetic distance controlled analyses are presented in Tables 39-41. When genetic distance is controlled and when log transformed data were used, among foragers, I was unable to assess the effects of effective temperature on INTLIQ due to small sample size. INTSOL is weakly negatively correlated with effective temperature although the relationship is not significant. INTLISOL is negatively correlated with effective temperature but non-significantly. CESSBF is positively correlated with effective temperature but this relationship is not statistically significant. DURWP is weakly negatively correlated with effective temperature but this relationship, again, is not significant.

**Table 39, Relationships between effective temperature and weaning milestone variables/ foragers/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
INTLIQ	2	-	-
INTSOL	8	-0.08701	0.622
INTLIQSOL	8	-0.1028	0.598
CESSBF	13	-0.0104	0.415
DURWP	8	-0.1186	0.513

Among pastoralists, INTLIQ is weakly positively correlated with effective temperature but the relationship is not significant. INTSOL is also weakly positively correlated with effective temperature but this relationship, again, is not significant. INTLIQSOL is positively correlated with effective temperature at a level that begins to approach but fails to reach significance. CESSBF is weakly positively correlated with effective temperature but this relationship is not significant. DURWP is positively correlated with effective temperature among pastoralists but, again, the relationship is not statistically significant.

**Table 40, Relationships between effective temperature and weaning milestone variables/ pastoralists/ genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	4	0.09368	0.377
INTSOL	9	0.02099	0.388
Log 10 INTLIQSOL	8	0.3161	0.094
Log 10 CESSBF	13	0.03495	0.360
Log 10 DURWP	10	-0.1351	0.761

Among farmers, INTLIQ is positively correlated with effective temperature at a level that begins to approach but does not reach statistical significance. INTSOL is correlated with effective temperature but the relationship is not significant. INTLIQSOL is weakly negatively correlated with effective temperature; this relationship is non-significant. CESSBF is weakly positively correlated with effective temperature and this is again non-significant. DURWP is weakly positively correlated with effective temperature among farmers at a level that approaches statistical significance.





**Table 41, Relationships between effective temperature and weaning milestone variables/ farmers genetic distances controlled**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	9	0.3	0.087
INTSOL	28	0.0282	0.301
Log 10 INTLIQSOL	27	-0.2848	0.637
Log 10 CESSBF	33	0.008294	0.394
DURWP	22	0.1267	0.057

As such, the results of the effective temperature/ sample subdivided/ log transformed data/ genetic distance controlled analyses do not support the hypothesis that risk of resource failure affects the timing of events in the weaning process among foragers or pastoralists. The results of these sets of analyses do weakly support the risk hypothesis among plant food producers.

## CHAPTER 4, DISCUSSION

### 4.1. Main Findings

The timing of the events in the weaning process is not significantly correlated with genetic distance. This is the case both when the entire sample is included in analyses and when the sample is subdivided by subsistence prior to analyses. Thus, the hypothesis that population history drives weaning variation is not supported. These findings are significant because they indicate that weaning behaviours have not evolved neutrally. Rather, the fact that they do not correlate with genetic distance demonstrates that they have been under some form of selection.

None of the proxies for risk of resource failure is correlated with any of the weaning milestone variables at statistically significant levels when genetic distance is controlled and when all populations are included in analyses. However, when the sample is subdivided by subsistence strategy, each proxy is correlated at a level that reaches or approaches statistical significance with at least one weaning milestone variable in one or more subgroups, even when genetic distance is controlled.

Regardless of type of analytical treatment, when all populations are included in analyses, latitude does not affect the times at which milestones in the weaning process occur at statistically significant levels. When the sample is subdivided according to subsistence strategy, latitude appears to affect a small portion of among-population variation in the timing of one event in the weaning process among one subsistence group – infants' age at the introduction of

complementary solids among farmers. As such, the latitude analyses may provide a small amount of support for the adaptive, resource risk hypothesis.

Elevation is not strongly correlated with any of the markers in the weaning process at levels that reach or even approach statistical significance when all populations are included in analyses. When the sample is subdivided by subsistence code, however, regardless of type of analytical treatment, elevation is correlated with the time at which at least one milestone in the weaning process occurs among at least one subdivision of the sample at a statistically significant level. As with the latitude analyses, the elevation analyses may provide some support for the adaptive hypothesis.

When all populations are included in analyses, regardless of type of analytical treatment, variability in precipitation is not strongly correlated with infants' age at which any of the markers in the weaning process occur at levels that reach statistical significance. When the sample is subdivided by subsistence strategy, variability in precipitation is weakly correlated with at least one milestone in the weaning process in at least one subdivision in the sample at a level that approaches statistical significance, even when the most rigorous tests are applied. This may provide a small amount of support for the resource risk hypothesis.

Regardless of type of analytical treatment or whether or not the sample was subdivided by subsistence strategy code, effective temperature is consistently correlated in the expected direction with at least one marker in the weaning process at a level that approaches or reaches statistical significance. Thus, the effective temperature analyses support the adaptive hypothesis that resource insecurity impacts the timing of weaning milestones.

In sum, genetic distance is not correlated with any of the weaning milestones. As such, the null population history hypothesis is not supported by the analyses conducted here. In contrast, the four proxies for risk of resource failure, latitude, elevation, variability in precipitation, and effective temperature, are weakly correlated with the timing of some weaning milestones. Thus, the adaptive hypothesis that risk of resource failure affects the timing of events in the weaning process is partially supported by these analyses. However, while a small portion of the among-population variation in the timing of weaning milestones can possibly be attributed to risk of resource failure, the vast majority of the variation remains unexplained.

## **4.2. Reliability of the Study**

There are several potential shortcomings of the analyses reported here. These shortcomings fall into five broad categories, namely, 1) uncertainty as to whether individual proxies effectively track risk of resource failure, 2) variability in the quality of the data as gathered and reported by ethnographers or other researchers, 3) issues regarding the measurement of the variables of interest, 4) possible problems with the size and the structure of the sample, and 5) a statistical concern regarding the number of analyses conducted.

### *4.2.1 Measuring risk of resource failure*

The results of the analyses reported in the previous section of this work suggest that ecology, particularly ecological factors related to resource risk, influence patterns of among-population variation in weaning behaviour. That said, each variable used as a proxy for resource risk is

responsible for a much smaller portion of this variation than was expected. Since all of the independent variables are correlated with each other to begin with and since they all affect the timing of weaning milestones, there is reason to think that a single underlying component that represents the communalities of all of the resource risk proxies might explain a larger portion of weaning variation. As such, after completing all of the analyses that I had initially intended to carry out, I conducted an additional set of analyses to generate and evaluate a better proxy of risk of resource failure.

To this end, I subjected the four proxy variables, latitude, elevation, variability in precipitation, and effective temperature, to Principal Components Analysis (PCA). This yielded a sample of 56 populations for which a single, principle component score could be obtained. Having created a new independent variable that accounts for approximately 53% of the variance in the four proxies, I carried out a set of bivariate regression analyses in which the principle component score was used to predict the timing of weaning milestones. As with the previous sets of analyses, this was done first while including all populations and second after subdividing the sample by subsistence strategy code. Log transformed data were used for strongly skewed variables.

The results of the principal component/ all populations analyses are summarized in Table 42. When all populations are included in analyses, INTLIQ is negatively correlated with the principal component score; however this relationship is not statistically significant. INTSOL is negatively correlated with the principal component score although, again, this relationship is not significant. INTLIQSOL is negatively correlated with the principal component score; this relationship also fails to achieve statistical significance. CESSBF is very weakly positively

correlated with the principal component score but, once again, the relationship is not significant. DURWP is positively correlated with the principal component score but the relationship is not statistically significant.

**Table 42, Relationships between principal component score and weaning milestone variables/ all populations**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	14	-0.447	0.109
INTSOL	40	-0.014	0.930
Log 10 INTLIQSOL	39	-0.128	0.438
CESSBF	49	0.077	0.598
Log 10 DURWP	35	0.132	0.452

The results from the principal component/ sample subdivided analyses are summarized in Tables 43-45. When the sample is subdivided by subsistence strategy and only foraging populations are included in analyses, the effects of the principal component score on INTLIQ cannot be assessed as the sample size is too small. INTSOL is positively correlated with the principal component score. INTLIQSOL is positively correlated with the principal component score but the result is not significant. CESSBF is negatively correlated with the principal component score but this relationship is not statistically significant. DURWP is also negatively correlated with the principal component score although this relationship is not statistically significant.

**Table 43, Relationships between principal component score and weaning milestone variables/ foragers**

Weaning milestone variable	N	R	P
INTLIQ	2	1	-
INTSOL	6	0.351	0.495
INTLIQSOL	6	0.239	0.649
CESSBF	9	-0.023	0.954
DURWP	6	-0.503	0.309

When only pastoralists are included in analyses, INTLIQ is positively correlated with the principal component score but this relationship is not significant. INTSOL is positively correlated with the principal component score; this relationship is not significant. INTLIQSOL is negatively correlated with the principal component score but the relationship does not achieve statistical significance. CESSBF is negatively correlated with the principal component score but the relationship is not significant. DURWP is negatively correlated with the principal component score and, again, the relationship fails to achieve or approach statistical significance.

**Table 44, Relationships between principal component score and weaning milestone variables/ pastoralists**

Weaning milestone variable	N	R	P
Log 10 INTLIQ	4	0.289	0.711
INTSOL	8	0.241	0.566
Log 10 INTLIQSOL	8	-0.107	0.802
Log 10 CESSBF	12	-0.275	0.387
Log 10 DURWP	9	-0.147	0.706

When only farmers are included in analyses, INTLIQ is negatively correlated with the principal component score; this relationship approaches but does not reach statistical significance.

INTSOL is also negatively correlated with the principal component score although this relationship is not significant. INTLIQSOL is negatively correlated with the principal component score but the relationship is not statistically significant. CESSBF is positively correlated with the principal component score at a level that approaches but does not reach statistical significance. DURWP is positively correlated with the principal component score; this relationship begins to approach but fails to achieve significance.

**Table 45, Relationships between principal component score and weaning milestone variables/ farmers**

<b>Weaning milestone variable</b>	<b>N</b>	<b>R</b>	<b>P</b>
Log 10 INTLIQ	8	-0.672	0.068
INTSOL	26	-0.277	0.171
Log 10 INTLIQSOL	25	-0.291	0.158
Log 10 CESSBF	28	0.370	0.053
DURWP	20	0.410	0.072

Essentially, the results of the regression analyses in which the principal component derived from latitude, elevation, variability in precipitation, and effective temperature was used to predict weaning milestone variation do not provide strong support for the resource risk hypothesis.

Although several of the correlations between the principal component and the weaning milestone variables are fairly strong, only a few of these relationships approach statistical significance and none of the relationships achieve statistical significance. Thus, it does not seem



to be the case that the failure to find strong support for the risk of resource failure hypothesis in earlier analyses was because the proxy variables individually only capture a small part of risk.

#### *4.2.2. Collection of Weaning and Eco-Geographic Data*

In addition to the concern that the individual eco-geographic variables may not effectively capture risk of resource failure is the concern that the quality of the data varies among sources. The first possible shortcoming in the quality of the data pertains to the collection of weaning data. This cross-cultural study relied on ethnographic data collected and recorded by multiple, different observers. As a result, there was considerable variability in the quality of the weaning data that I was able to access. Some observers report average infants' ages at which markers in the weaning process occur with precision, providing specific figures in weeks or months. Many others, however, report average infants' ages at which markers in the weaning process occur in broad, monthly ranges. Furthermore, in a few instances, ethnographers report infants' ages at which events in the weaning process occur in qualitative phrases. For example, some authors note that complementary liquids are introduced "from birth", "very early", or "when [the infant begins] crawling" (Blackwood 1935; Dentan 1988; McIlwraith 1948). Lastly, there is a large number of natural fertility, nonindustrial populations for which no infant feeding data has been recorded and it is difficult to assess the amount of bias introduced by underreporting (Sellen 2001). As such, as with any large-scale cross-cultural study, inter-observer differences in approach to observation and reporting as well as inter-observer differences in error rate may influence the findings (Bernard 2000; Sekaran 1983; Udy 1973).

Similar variability characterizes the reporting of the eco-geographic data. Whereas some researchers report discrete figures, others report ranges of variation. Furthermore, while the majority of sources present data that represent considerable breadth in time and/ or space, some sources present data that represents as little as a single year of observation or a single measurement location (e.g. Glucken 1953; Jochelson 1908).

Although this variability in both the weaning and the eco-geographic data needs to be recognized, it probably does not fundamentally undermine the reliability of this study for two reasons. First, I attempted to reduce inconsistencies while coding and summarizing the variables of interest. This was accomplished by systematically replacing range estimates with median values and by excluding imprecise, qualitative data. Second, since the observers each have different research foci and different training, it is likely that the majority of the variability in this kind of cross-cultural study is non-systematic in its distribution through the dataset (Divale 1975; Sellen 2001). As such, inconsistencies that remain in the data after coding and summarizing are unlikely to have produced the appearance of relationships between variables where real relationships do not exist; instead, the presence of random, inter-observer error is likely to have minimized relationships, thus producing more conservative tests (Divale 1975).

#### *4.2.3. Measurement of Eco-Geographic and Phylogenetic Variables*

Along with concerns with the inter-observer variability in the collection and reporting of ethnographic and eco-geographic data, there are also concerns with the precision of measurement of eco-geographic and phylogenetic variables.

As mentioned above, for the purposes of statistical analyses, I summarized and coded the eco-geographic variables of interest into discrete, scalar values. Although coding was necessary, it is possible that these coded, median values do not reflect an accurate measure of the ecological constraints proposed here to affect complementary feeding and weaning decisions. This is the case because many of the populations in the sample are mobile and occupy a range of territory; these ranges are often characterized by variability in eco-geographic parameters. While this potential problem is worth noting, other cross-cultural studies that demonstrate relationships between eco-geographic variables and human behavioural variables use summarized values (e.g. Barber 2002; Collard et al. 2005; Grove 2009; Johnson 2002; Low 1990b; Snarney 1996). The success of previous cross-cultural studies that use summarized values of eco-geographic correlates of human behaviour suggests that these measures capture a substantial portion of important ecological constraints, despite their coarse grain. As such, while measures used here do not necessarily reflect the full range of eco-geographic risk for a given population, they nonetheless reflect a reasonable estimate of eco-geographic risk variation.

While it may be appropriate to code and summarize eco-geographic variables, there is not always consensus on how best to do so. This is another potential shortcoming of the present study, particularly in regards to variability in precipitation. That is, most cross-cultural behavioural ecologists agree that median or bisecting points are appropriate for summarizing latitude and elevation (e.g. Barber 2002; Johnson 2002); these points were used in this study to summarize these variables. Effective temperature, while certainly only one of many ways to estimate the effects of temperature and solar radiation on human behaviour, is generally considered an acceptable measure of growing season and, by proxy, of energy resource security (e.g. Bailey 1960; Binford 2001; Collard et al. 2005; Grove 2009); since energy resource security

was proposed to be of interest here, this was the measure used in this study. There is much less agreement, however, on how to measure and code variability in precipitation (Binford 2001). Here, largely because I gave preference to ethnographic sources so as to obtain site-specific precipitation data, only mean figures for the wettest and driest months of the year were available for the majority of the populations in the sample. In coding, then, I subtracted the driest month value from the wettest month value for each population in the sample to obtain a rough measure of variability in precipitation. Unfortunately, this measure does not capture the distribution of precipitation throughout the year. Further, this measure does not take into account the role of groundwater in sustaining biomass. While other studies have shown that the method used here may be a valid one (e.g. Divale 1999; Johnson 2002), it is likely that the difference between wettest and driest months is not the most accurate measure of intra-annual variability in precipitation. Moreover, while the measurements of latitude, elevation, and effective temperature are fairly robust, the measurement of variability in precipitation is problematic. The results concerning the relationships between variability in precipitation and weaning decisions should therefore be treated with caution.

Similar caution needs to be applied to the results of the tests in which genetic distance was used to predict among-population variation in weaning and complementary feeding behaviour. The genetic distance data are based primarily on the allele frequencies from the Cavalli-Sforza et al. (1994) dataset. Unfortunately, the Cavalli-Sforza dataset was unable to accommodate all of the populations in the infant feeding and weaning sample used here. This raises two concerns regarding measurement. First, in order to perform the analyses reported here, I modified the measures of genetic distance on the basis of linguistic affinities so that all of the populations for which weaning data were available could be accommodated. These combined genetic and

linguistic measures are not completely resolved and do not take into account possible reticulations in cultural trees. As such, there are likely small discrepancies between the real relationships among populations and the estimated relationships used here (McElreath 1997). Second, even using modified trees, the Cavalli-Sforza dataset contains data for only a few genetic loci for the majority of the populations in the infant feeding sample. As such, genetic distance estimates were based on only three loci, the ABO locus, the HP locus, and the TF locus. Three loci, while likely adequate to provide control for the effects of phylogeny while testing for relationships between eco-geographic and weaning variation, may not measure phylogenetic distance accurately enough for use as an independent variable.

The first problem concerning the resolution of modified distance measures is likely not of sufficient scope to undercut the results reported in this study. Although there is some debate in the literature as to the structure of linguistic families, in recent years, many of these issues have been resolved using molecular genetic evidence (McMahon & McMahon 2008; Renfrew 2000). Other linguistic relationships remain characterized by uncertainty. In such cases, I used average genetic distance measures regarding all populations within the narrowest linguistic taxonomic level possible that included the population of interest. For example, data regarding some loci used in this study were not available for the Dogon population of Mali within the Cavalli-Sforza dataset. For this population, then, I substituted values that were the result of averaging all allele frequency data from all populations within the Cavalli-Sforza dataset that share the Dogon's branch of its linguistic family tree. This is a method similar to those applied successfully by others conducting phylogenetically controlled cross-cultural research (e.g. Cavalli-Sforza et al. 1988; Dembo 2007; Holden and Mace 1997). While it is likely that in some cases the combined genetic-linguistic phylogenies used in the present study are not entirely accurate in their

resolution, there is no reason to think that the error rate is such that the results of the phylogenetically controlled analyses cannot be readily accepted.

The small number of loci used here to estimate genetic distance likely does not undermine the results of the phylogenetically controlled analyses. However, the lack of precision in measuring among-population genetic distances based on only three loci may be obscuring real relationships between genetic distances and variation in complementary feeding when genetic distance is used as the independent variable. Although this is a possibility, it seems unlikely to be the case. Even using only three loci, it seems reasonable to expect that a real relationship would produce at least a weak trend towards correlation between genetic and weaning variation. The results of the first set of analyses in which I tested the hypothesis that population history is responsible for the majority of among-population variation in complementary feeding and weaning behaviour fail to indicate that such a trend exists.

#### *4.2.4. Size and Structure of the Sample and of the Subsamples*

The sample was biased in its structure in several ways. First, none of the three broad groups of subsistence categories are equally represented in the sample: the subsample of foragers constitute only a small portion of the overall sample; the subsample of pastoralists are marginally better represented than foragers; the subsample of farmers outnumber the subsample of foragers and the subsample of pastoralists combined. As such, when all populations are included in analyses, especially given that subsistence strategy has previously been shown to affect weaning decisions in some capacity (Sellen and Smay 2001), it is possible that the effects of subsistence strategy on weaning variables confound the effects of eco-

geographic variables on weaning variables. Second, three of the eco-geographic variables and three of the weaning variables are positively skewed in their distribution. Specifically, populations that live at high latitudes, at high altitudes, and in regions characterized by high variability in precipitation are substantially overrepresented. Similarly, populations that introduce complementary liquids early, that introduce complementary liquids or solids early, and that extend the duration of the weaning process are substantially overrepresented.

To reduce the effects of these biases in the structure of the sample, I subdivided the sample according to subsistence strategy code and log transformed the skewed variables.

Unfortunately, while both of these modifications reduced biases, they both also reduced sample sizes substantially, from 17-63 to 2-33. Although there are potentially problems associated with smaller sample sizes, the differences between results produced in analyses in which biases were not taken into account and those produced in analyses in which biases were taken into account suggest that the problems of over-representation and confounding are substantial. Specifically, many of the analyses in which all populations were included produced results that suggested that the timing of events in the weaning process were in no way related to the eco-geographic proxies for risk of resource failure. When the sample is subdivided, however, some weak trends become discernible in the data. As such, subdividing and log transforming the dataset, even at the expense of sample size, was necessary. Unfortunately, then, several of the results presented here, particularly those associated with sample sizes of less than 15, should be treated with caution as analyses using small sample sizes can produce unreliable results (Hill and Kintigh 2009).

#### 4.2.5. Multiple Comparisons

I carried out 40 sets of analyses pertaining to each eco-geographic proxy when testing the risk of resource failure hypothesis, a total of 160 analyses for this hypothesis. For all analyses, alpha was set at 0.05. Unfortunately, the probability of producing one or more significant results by chance alone when multiple analyses are carried out, each at the same significance level, is greater than that significance level (Moran 2003; Zaykin et al. 2002). As such, in regards to the analyses reported here, it is possible that as many as 20 per cent of these analyses (a total of 32 tests) may have achieved significant results by chance. As only 18 out of 160 tests of the risk of resource failure hypothesis achieved significance, it is possible that these results may reflect randomness rather than genuine relationships between proxies for risk of resource failure and weaning milestones.

There are at least three possible way of addressing this problem. The first is to reduce the number of comparisons by replacing the bivariate approach used here with a multivariate one. However, a multivariate linear approach to these data is inappropriate as each of the four proxies for risk of resource failure affect different milestones in the weaning process among different subsistence strategy groups. For example, effective temperature is a predictor of infant's age at the introduction of complementary liquids (INTLIQ) and duration of the weaning process (DURWP) among farmers but seems to have little bearing on infant's age at the introduction of complementary solids (INTSOL). Elevation appears to predict infant's age at the introduction of complementary liquids (INTLIQ) among pastoralists. That effective temperature is an important driver of weaning among farmers but not among pastoralists is line with the prediction that farmers should be particularly sensitive to effective temperature, a proxy for



growing season. That infant's age at the introduction of complementary liquids (INTLIQ) is the most sensitive dependent variable among pastoralists is logical given that pastoralists have greater access to nutrient-dense, clean complementary liquids in the form of animal milk than do foragers or farmers. A single, multivariate linear model would not capture differences in most important proxy for risk or most sensitive weaning milestone variable between subsistence groups. To maintain the integrity of these posited relationships, I chose to conduct separate bivariate analyses.

The second approach to correcting the problem of multiple comparisons is to decrease the alpha threshold. The most common method for this is the sequential Bonferroni adjustment (Moran 2003). The sequential Bonferroni adjustment requires that the tester divide alpha by the number of tests conducted; the number of tests in the calculation decreases as successively weaker null test results are rejected. While this approach is widespread in the ecological literature, it suffers from several mathematical and practical problems (Moran 2003; Nakagawa 2004). Specifically, the sequential Bonferroni method is highly conservative: researchers are likely to exclude results as non-significant even when relationships are real (Moran 2003). Furthermore, this adjustment penalizes researchers that attempt to shed light on fine-grained relationships because such relationships generally require larger numbers of tests. Since the method dictates that alpha be divided by the number of tests, Bonferonni-adjusted results of fine-grained analyses are particularly unlikely to achieve statistical significance (Moran 2003). For these reasons, I am reluctant to apply the sequential Bonferonni correction to the tests reported here.

The third approach to correcting for the problem of multiple comparisons is to consider the number of significant or near significant results per set of analyses. Essentially, while it is probable that one out of any five tests may produce a significant result by chance, it is highly improbable that more than one out of a group of five tests would produce a significant result by chance (Moran 2003). When this approach is applied to the analyses carried out in the present study, only effective temperature and possibly variability in precipitation and the principal component score remain reasonably reliable predictors of weaning milestones among farmers (and only when genetic distance is not controlled). When this criterion is used, none of the proxies for risk of resource failure affect weaning milestones among all populations, among foragers, or among pastoralists. As such, I include only the effects of effective temperature, variability in precipitation, and principal component score on the timing of events in the weaning process among farmers when interpreting the results of the risk of resource failure hypothesis.

#### **4.3. Implications of the Results**

Having reviewed issues regarding variability in the quality and the measurement of data, the structure of their distributions, and the problem of multiple comparisons, there is reason to think that the results presented here reflect a reasonable approximation of the relationships between among-population phylogenetic and eco-geographic variation and among-population weaning variation. As such, the proposed explanatory factors, population history and risk of resource failure, are likely genuinely only weakly correlated with the times at which key markers in the weaning process occur. The failure to find support for the null, population history hypothesis in this study provides evidence that variation in the timing of weaning milestones is

not selectively neutral. However, that this study did not find any support for the risk of resource failure hypothesis among all populations, foragers or pastoralists and only found weak support among farmers, particularly in light of the fact that weaning behaviours appear to be the subject of selection, raises at least two fundamental questions: First, what light do these results shed on the understanding of the evolution of human life history? And second, if the proposed variables are not the primary drivers of variation, what drives the cross-cultural patterning of variation in the weaning process? In this section, I discuss a number of other eco-geographic, physiological, and human ecological factors that may affect complementary feeding and weaning decisions. I then proceed to a discussion of what the result reported here signifies for the study of human life history evolution in general and complementary feeding and weaning evolution in particular; I do so while bearing in mind the other possible drivers of weaning variation.

#### *4.3.1. Eco-Geographic, Demographic, Physiological, and Sociocultural Factors*

The specific aim of the analyses concerning eco-geographic variation, after establishing that the patterning of behaviour was not an artefact of population history, was to assess the effects of latitude, elevation, variability in precipitation, and effective temperature on complementary feeding and weaning behaviour cross-culturally. That said, the logic underscoring these hypothesized relationships was rooted in the idea that behavioural strategies are constrained by resource insecurity risk. I found only a small amount of support for this hypothesis. Essentially, it is possible that either direct measures of this risk or a more comprehensive list of proxy ecological (including social) variables may explain a larger portion of among-population variation in weaning strategy.

I intended for the chosen eco-geographic variables to serve as proxies for the primary variable, risk of resource failure. However, while latitude, elevation, variability in precipitation, effective temperature, and the principal component underlying all of these four proxy variables appear to track resource risks, they do so only coarsely. As such, it is possible that a direct measure of energy resource availability, based on estimations of plant and non-human animal biomass and biodiversity along with human population density would be more strongly related to the timing of events in the weaning process than are the proxy variables. Furthermore, the proxy variables used here to estimate risk of resource failure are also related to pathogen risks (Low 1990b); pathogen risk may affect weaning variation in ways counter to the predictions of the resource insecurity hypothesis. If pathogen risk is confounding the affects of energy resource risk on weaning variation, a direct measure of endemic pathogen load, hypothesized to be a particularly important factor in weaning decisions (Sellen and Smay 2001), may be an important explanatory variable to consider. Although data regarding biomass, biodiversity, and pathogenesis are available (see Barone 2001; Binford 2001; Cashdan 2002; Low 1990a; Rosenzweig 1968), the collection of such complex data was beyond the scope of this study.

Since estimating energy resource availability and pathogen load is necessarily complex, another avenue through which to approach the hypothesis that ecological variation affects weaning and complementary feeding variation is to employ a more comprehensive suite of proxy variables. The ecological hypothesis tested here concerned risk of resource failure, approximated using measures of latitude, elevation, variability in precipitation, effective temperature, and a principal component of these. This neglects the possible role of at least one important eco-geographic variable along with a host of other demographic, physiologic, and socio-cultural

variables that, if incorporated into a single study, would facilitate a finer-grained tracking of habitat quality.

Available groundwater is an eco-geographic factor not considered in this study that may be critical in driving weaning and complementary feeding decisions. The presence or absence of available groundwater can exacerbate or ameliorate the effects of the energy resource insecurity that is otherwise expected to accompany unpredictable precipitation (Binford 2001; Snarney 1996). Further, both the movement and the stagnation of water can be important determinants of pathogenesis (Davies et al. 2004; Low 1990b; Thomas et al. 2006). Lastly, the intensive use marine or lacustrine resources can affect dietary decisions during pregnancy (Henrich 2009) – some aquatic foods can be harmful during development – so this may also be an important factor in infant feeding decisions. For all of these reasons, the inclusion of a measure of a population's available groundwater and/ or a measure of a population's proximity to a body of water may be essential in measuring habitat quality and therefore in assessing the effects of resource insecurity risk variation on weaning variation. The failure of the analyses carried out here to find convincing support for the resource risk hypothesis may be related to the fact that I did not include a measure of available groundwater.

In addition to eco-geographic factors such as groundwater, there are number of other ecological factors that correlate or intersect with habitat quality and risk. Many of these have been demonstrated to have affects on the cross-cultural patterning of human behavioural decision-making and, in some instances, on life history decision-making. As such, these variables may be of interest in future cross-cultural weaning and complementary feeding research.

One such factor to consider is the potential impact of among-population variation in maternal health and body size on among-population variation in weaning strategies (Harvey & Clutton-Brock 1985; Kennedy 2005). While there is reason to expect that maternal health and body size is related to habitat quality, there is also reason to expect that there are a number of factors aside from habitat quality that determine these variables. For example, population history, population density, and the status of women in the population, may influence maternal health and body size, largely independent of habitat quality (Cardillo 2002; Shen and Williamson 1999). Bearing in mind that life history decisions are contingent on a finite energy budget, it is reasonable to propose that the larger maternal energy budget that accompanies larger and/ or healthier body size might impact the allocation of energy, nutrient, and immunological resources to infants (Kennedy 2005; Lee 1996; van Noordwijk & de Jong 1986). As such, maternal health and body size may be one of the factors driving cross-cultural variation in the timing of events in the weaning process.

Another avenue that may be worthy of exploration is the potential impact of population density on complementary feeding and weaning behaviour. As with maternal physiology, while there is reason to think that population density is linked to risk of resource failure (Binford 2001; Grove 2009; Walker and Hamilton 2008), there is also reason to think that other variables aside from risk of resource failure contribute to population density. These other influences include, for example, population history and primary subsistence strategy (Winterhalder & Kennet 2006). Population density affects resource stress, pathogenesis, and maternal body size (Ember et al. 2007; Low et al. 2008; Walker and Hamilton 2008). Furthermore, population density probably affects group mobility and political complexity, each of which is an ecological variable in its own right (Binford 1978, 1980, 1990, 2001; Currie and Mace 2009; Grove 2009; Kelly 1999). For

these reasons, population density is a variable that may drive at least a small portion of among-population variation in weaning strategy.

If group mobility and political complexity are at least partially independent of risk of resource failure, then these are also variables that may contribute to cross-cultural variation in weaning behaviour. A recent cross-cultural study suggests that it is likely the case that between a quarter and half of variation in mobility is unrelated to habitat quality (Grove 2009). Another recent cross-cultural study suggests that political complexity drives a much greater portion of the distribution of human linguistic diversity than do eco-geographic risk factors (Currie and Mace 2009), lending support to the notion that political complexity is a driver of human behaviour that is largely independent of measures of habitat quality. Given that these variables can be partially disentangled from one another, it is reasonable to propose that the greater energetic costs and stresses associated with higher mobility might be linked to variation in weaning and complementary strategy. Similarly, the costs attached to low status – a status likely to characterize the majority of infant care-givers in a politically complex, stratified society – might also be linked to variation in weaning and complementary feeding strategy.

Along similar lines and probably related to group mobility and political complexity, marriage and inheritance patterns may be contributing factors as well. As shown in previous studies, polygyny and population history intersect to affect parental investment (Cowlshaw & Mace 1996; Holden and Mace 2003). Furthermore, allo-parenting, kin support, and maternal work, largely driven by marriage and residence pattern, affect infant nutrition and health (Quinlan and Quinlan 2007). These and other such studies suggest that marriage and residence are potential contributing factors to among-population variation in human weaning and complementary feeding decisions.

As such, these socio-cultural ecological factors, marriage and inheritance patterns, along with group mobility and political complexity, may be of interest in future cross-cultural research concerned with among-population variation in human complementary feeding and weaning behaviour.

Moreover, there are a host of ecological variables beyond those considered in this study that may affect weaning decisions. The predictions of these ecological hypotheses need to be tested both separately and in tandem with one another before the larger hypothesis that ecological risk is a primary determinant of weaning and complementary feeding behaviour can be rejected.

#### *4.3.2. Complementary Feeding, Weaning, and the Evolution of Human Life History*

The results of the genetic distance analyses suggest that the null hypothesis in which I proposed that among-population variation in complementary feeding and weaning behaviour tracks population history can probably be rejected. The results of the tests of the resource risk hypothesis suggest that among-population variation in complementary feeding and weaning behaviour correlates with effective temperature, intra-annual variability in precipitation, and a principal component score underlying four proxies for risk of resource failure, particularly when subsistence strategy is taken account. Taken together, the genetic distance and the resource risk results support the notion that, while the eco-geographic variables considered here may not drive the majority of variation in complementary feeding and weaning decisions, ecological factors in general affect these decisions.



The notion that ecological factors constrain complementary feeding and weaning behaviour is in line with the expectations of life history theory (van Noordwijk and de Jong 1986). An infant given complementary liquids or solids is at greater risk of being exposed to food- or water-borne pathogens than is an infant exclusively breastfed, particularly in very early life prior to the development of active immune-competence. An infant expected to predominantly rely on complementary liquids or solids is likely to be at greater caloric and nutrient risk during unexpected resource stress than an infant exclusively or predominantly breastfed. In other words, young infants benefit from exclusive or nearly exclusive breastfeeding (Weaver & Michaelsen 2001). However, there is a cost to care-givers attached to exclusive or nearly exclusive breastfeeding. The large portion of maternal energy budget required to sustain exclusive breastfeeding for one offspring not only is taxing on a mother's own body but also prevents the conception of additional offspring (Ellison 2003). In essence, the decision to begin the weaning process involves a life history trade-off. There is reason to think that all such trade-offs are constrained ecologically (Ellison 1990, 2003; Roff 2002; Stearns 1976, 1992; van Noordwijk and de Jong 1986). In the case of the complementary feeding and weaning decisions, it is reasonable to think that maternal energy budget should track habitat quality as well as, perhaps, population density and mother's status in society (van Noordwijk and de Jong 1986). Essentially, while further research is needed to identify specific ecological variables that may be driving cross-cultural variation in the timing of events in the weaning process, the study reported here, in providing evidence for the rejection of a null hypothesis and in providing some evidence in support of an ecological hypothesis, supports the predictions of human life history theory.

## CHAPTER 5, CONCLUSIONS

The goal of this study was to enrich our understanding of the cross-cultural patterning of variation in human complementary feeding and weaning behaviour. I selected this topic with the view that the weaning process is an integral component of human health and life history and, as such, has the capacity to shed new light on the evolution of human life history and on anthropological demography. To address this goal, I tested the predictions of two hypotheses proposed to affect the timing of events in the weaning process. I first tested the null hypothesis that variation in the times at which milestones in the weaning process occur reflects descent relationships among populations. After refuting the null hypothesis, I tested an adaptive hypothesis that variation in the timing of events in the weaning process is adapted to minimizing the effects of risk of resource failure on infant health and mortality.

The results of the tests of those hypotheses as reported in this study suggest three things. First, genetic/ linguistic distance among populations is not correlated with variation in complementary feeding and weaning behaviour among populations. Essentially, this provides evidence that the null hypothesis – that cross-cultural variation in the weaning process evolved neutrally – can be rejected. Second, variation among populations in eco-geographic factors used to approximate risk of resource failure is weakly correlated with variation among farming populations in complementary feeding and weaning behaviour. As such, the alternative hypothesis that resource risk drives among-population weaning variation receives a small amount of support. Third, since the eco-geographic proxy variables only account for a negligible portion of the variation, other ecological and historical factors not considered here are likely important in driving this variation.

Finer-grained analyses that account for more ecological variables than those that I used here are needed to generate an effective model for the life history of earlier hominins. However, this study generated not only an important null result regarding the effects of phylogeny on weaning variation but also a weak positive result regarding the effects of ecology on weaning variation that future research in this vein can build upon.

**APPENDIX 1, SOURCES FOR WEANING MILESTONE DATA**

<b>Population</b>	<b>Variable</b>	<b>Data Point</b>	<b>Source</b>
!Kung	Complementary Liquids	-	Howell 1979; Lee 1979
	Complementary Solids	6	Howell 1979; Lee 1979
	Complementary Liquids or Solids	6	Howell 1979; Lee 1979
	Cessation of Breastfeeding	42	Howell 1979; Lee 1979
	Duration of the Weaning Process	36	Howell 1979; Lee 1979
Amele	Complementary Liquids	-	-
	Complementary Solids	7.5	Worthman 1993
	Complementary Liquids or Solids	7.5	Worthman 1993
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process	-	-
Arapho	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	48	Levine 1965
	Duration of the Weaning Process	-	-
Aymara 1	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	30	Hickman 1964
	Duration of the Weaning Process	-	-
Aymara 2	Complementary Liquids	-	-
	Complementary Solids	18	Tscopik 1951
	Complementary Liquids or Solids	18	Tscopik 1951
	Cessation of Breastfeeding	30	Tscopik 1951
	Duration of the Weaning Process	12	Tscopik 1951
Azande	Complementary Liquids	-	-
	Complementary Solids	2	Larken 1927
	Complementary Liquids or Solids	2	Larken 1927
	Cessation of Breastfeeding	42	Larken 1927
	Duration of the Weaning Process	40	Larken 1927



	Process		
Badaga	Complementary Liquids	-	-
	Complementary Solids	4	Hockings 1980
	Complementary Liquids or Solids	4	Hockings 1980
	Cessation of Breastfeeding	12	Hockings 1980
	Duration of the Weaning Process	8	Hockings 1980
Bang Chan	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	17	Hauck 1959
	Duration of the Weaning Process	-	-
Bella Coola	Complementary Liquids	1	Mcllwraith 1948
	Complementary Solids	1	Mcllwraith 1948
	Complementary Liquids or Solids	1	Mcllwraith 1948
	Cessation of Breastfeeding	30	Mcllwraith 1948
	Duration of the Weaning Process	29	Mcllwraith 1948
Bhil	Complementary Liquids	0	Naik 1956
	Complementary Solids	10.5	Naik 1956
	Complementary Liquids or Solids	10.5	Naik 1956
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process	-	-
Buka	Complementary Liquids	-	-
	Complementary Solids	0	Blackwood 1935
	Complementary Liquids or Solids	0	Blackwood 1935
	Cessation of Breastfeeding	54	Blackwood 1935
	Duration of the Weaning Process	54	Blackwood 1935
Cayapa	Complementary Liquids	2	Altschuler 1965
	Complementary Solids	4	Altschuler 1965
	Complementary Liquids or Solids	3	Altschuler 1965
	Cessation of Breastfeeding	36	Altschuler 1965
	Duration of the Weaning Process	33	Altschuler 1965
Chipewyan	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or	-	-

	Solids	42	VanStone 1963
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process		
Chuckchee	Complementary Liquids	-	-
	Complementary Solids	12	Sverdrup 1938
	Complementary Liquids or Solids	12	Sverdrup 1938
	Cessation of Breastfeeding	42	Sverdrup 1938
	Duration of the Weaning Process	30	Sverdrup 1938
Datoga	Complementary Liquids	3.6	Sellen 1998
	Complementary Solids	10.6	Sellen 1998
	Complementary Liquids or Solids	3.6	Sellen 1998
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process	-	-
Dogon	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	24	Dieterlen 1960
	Duration of the Weaning Process	-	-
Dorobo	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	12	Huntingford 1953
	Duration of the Weaning Process	-	-
Fang	Complementary Liquids	-	-
	Complementary Solids	9	Alexandre 1958
	Complementary Liquids or Solids	9	Alexandre 1958
	Cessation of Breastfeeding	21	Alexandre 1958
	Complementary Liquids	12	Alexandre 1958
	Complementary Solids	-	
	Complementary Liquids or Solids	9	
	Cessation of Breastfeeding	9	
	Duration of the Weaning Process	21	
	Duration of the Weaning Process	12	
Gainj	Complementary Liquids	-	-

	Complementary Solids	11	Wood 1985
	Complementary Liquids or Solids	11	Wood 1985
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process	-	-
Garó	Complementary Liquids	2	Burling 1963
	Complementary Solids	11	Burling 1963
	Complementary Liquids or Solids	2	Burling 1963
		24	Burling 1963
	Cessation of Breastfeeding	17.5	Burling 1963
	Duration of the Weaning Process		
Goajiro	Complementary Liquids	-	-
	Complementary Solids	7	Gutierrez de Pineda 1950
	Complementary Liquids or Solids	7	Gutierrez de Pineda 1950
		24	Gutierrez de Pineda 1950
	Cessation of Breastfeeding	17	Gutierrez de Pineda 1950
	Duration of the Weaning Process		
Hare	Complementary Liquids	-	-
	Complementary Solids	6	Hurlbert 1962
	Complementary Liquids or Solids	6	Hurlbert 1962
		30	Hurlbert 1962
	Cessation of Breastfeeding	24	Hurlbert 1962
	Duration of the Weaning Process		
Igorot	Complementary Liquids	-	-
	Complementary Solids	4	Raphael 1985
	Complementary Liquids or Solids	4	Raphael 1985
		15	Raphael 1985
	Cessation of Breastfeeding	11	Raphael 1985
	Duration of the Weaning Process		
Ila	Complementary Liquids	-	-
	Complementary Solids	1	Smith 1920
	Complementary Liquids or Solids	1	Smith 1920
		30	Smith 1920
	Cessation of Breastfeeding	29	Smith 1920
	Duration of the Weaning Process		
Javanese	Complementary Liquids	-	-
	Complementary Solids	0	Geertz 1961
	Complementary Liquids or Solids	0	Geertz 1961
		-	-
	Cessation of Breastfeeding	-	-



	Duration of the Weaning Process		
Jivaro2	Complementary Liquids	-	-
	Complementary Solids	6	Harner 1973
	Complementary Liquids or Solids	66	Harner 1973
	Cessation of Breastfeeding	60	Harner 1973
	Duration of the Weaning Process		
Kapauku	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	36	Pospisil 1958
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process		
Kogi	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	12	Reichel-Dolmatoff 1951
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process		
Koryak	Complementary Liquids	-	-
	Complementary Solids	2	Jochelson 1908
	Complementary Liquids or Solids	30	Jochelson 1908
	Cessation of Breastfeeding	28	Jochelson 1908
	Duration of the Weaning Process		
Kpelle	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	36	Westerman 1921
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process		
Kwoma	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	36	Whiting 1941
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process		
Lolo1	Complementary Liquids	-	-
	Complementary Solids	-	-

	Duration of the Weaning Process		
<i>Jivaro2</i>	Complementary Liquids	-	-
	Complementary Solids	6	Harner 1973
	Complementary Liquids or Solids	6	Harner 1973
	Cessation of Breastfeeding	66	Harner 1973
	Duration of the Weaning Process	60	Harner 1973
<i>Kapauku</i>	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	36	Pospisil 1958
	Duration of the Weaning Process	-	-
<i>KoBi</i>	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	12	Reichel-Dolmatoff 1951
	Duration of the Weaning Process	-	-
<i>Koryak</i>	Complementary Liquids	-	-
	Complementary Solids	2	Jochelson 1908
	Complementary Liquids or Solids	2	Jochelson 1908
	Cessation of Breastfeeding	30	Jochelson 1908
	Duration of the Weaning Process	28	Jochelson 1908
<i>Kpelle</i>	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	36	Westerman 1921
	Duration of the Weaning Process	-	-
<i>Kwoma</i>	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	36	Whiting 1941
	Duration of the Weaning Process	-	-
<i>2101</i>	Complementary Liquids	-	-
	Complementary Solids	-	-

	Complementary Liquids or Solids	- 54	- Lin 1947
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process		
Lolo2	Complementary Liquids	-	-
	Complementary Solids	0	Abadie 1924
	Complementary Liquids or Solids	0	Abadie 1924
	Cessation of Breastfeeding	12	Abadie 1924
	Duration of the Weaning Process	12	Abadie 1924
Maasai	Complementary Liquids	0	Merker 1910
	Complementary Solids	-	-
	Complementary Liquids or Solids	0	Merker 1910
	Cessation of Breastfeeding	24	Merker 1910
	Duration of the Weaning Process	24	Merker 1910
Marshalls	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	30	Kramer 1938
	Duration of the Weaning Process	-	-
Micmac	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	30	Wallis 1955
	Duration of the Weaning Process	-	-
Nahane	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	30	Honigman 1954
	Duration of the Weaning Process	-	-
Navaho	Complementary Liquids	6	Leighton & Kluckhohn 1947
	Complementary Solids	6	Leighton & Kluckhohn 1947
	Complementary Liquids or Solids	6	Leighton & Kluckhohn 1947
	Cessation of Breastfeeding	21	Leighton & Kluckhohn 1947
	Duration of the Weaning	15	Leighton & Kluckhohn 1947

	Process		
Okayama	Complementary Liquids	-	-
	Complementary Solids	5.5	Norbeck 1954
	Complementary Liquids or Solids	5.5 24	Norbeck 1954 Norbeck 1954
	Cessation of Breastfeeding Duration of the Weaning Process	18.5	Norbeck 1954
Okinawan	Complementary Liquids	6	Maretzki 1963
	Complementary Solids	9	Maretzki 1963
	Complementary Liquids or Solids	6 24	Maretzki 1963 Maretzki 1963
	Cessation of Breastfeeding Duration of the Weaning Process	18	Maretzki 1963
Pygmies	Complementary Liquids	-	-
	Complementary Solids	2	Cavalli-Sforza 1986
	Complementary Liquids or Solids	2 36	Cavalli-Sforza 1986 Cavalli-Sforza 1986
	Cessation of Breastfeeding Duration of the Weaning Process	34	Cavalli-Sforza 1986
Quechua1/2	Complementary Liquids	-	-
	Complementary Solids	8	Beals 1946; Parsons 1936
	Complementary Liquids or Solids	8 33	Beals 1946; Parsons 1936 Beals 1946; Parsons 1936
	Cessation of Breastfeeding Duration of the Weaning Process	25	Beals 1946; Parsons 1936
Quechua3/4	Complementary Liquids	6	Greene 1976; Forman 1973
	Complementary Solids	6	Greene 1976; Forman 1973
	Complementary Liquids or Solids	6 18	Greene 1976; Forman 1973 Greene 1976; Forman 1973
	Cessation of Breastfeeding Duration of the Weaning Process	12	Greene 1976; Forman 1973
Saami	Complementary Liquids	-	-
	Complementary Solids	3.5	Itkonen et al. 1984; Whitaker 1955
	Complementary Liquids or Solids	3.5 21	Itkonen et al. 1984; Whitaker 1955
	Cessation of Breastfeeding Duration of the Weaning Process	11.5	Itkonen et al. 1984; Whitaker 1955 Itkonen et al. 1984; Whitaker 1955
Senoi	Complementary Liquids	-	-

	Complementary Solids	6	Dentan 1988
	Complementary Liquids or Solids	6	Dentan 1988
		54	Dentan 1988
	Cessation of Breastfeeding	48	Dentan 1988
	Duration of the Weaning Process		
Siriono	Complementary Liquids	-	-
	Complementary Solids	6	Holmberg 1950
	Complementary Liquids or Solids	6	Holmberg 1950
		42	Holmberg 1950
	Cessation of Breastfeeding	36	Holmberg 1950
	Duration of the Weaning Process		
Tallensi	Complementary Liquids	-	-
	Complementary Solids	2	Fortes 1945
	Complementary Liquids or Solids	2	Fortes 1945
		36	Fortes 1945
	Cessation of Breastfeeding	34	Fortes 1945
	Duration of the Weaning Process		
Tarahumara	Complementary Liquids	-	-
	Complementary Solids	6	Fried 1951
	Complementary Liquids or Solids	6	Fried 1951
		42	Fried 1951
	Cessation of Breastfeeding	36	Fried 1951
	Duration of the Weaning Process		
Tarasco	Complementary Liquids	-	-
	Complementary Solids	3.5	Beals 1946
	Complementary Liquids or Solids	3.5	Beals 1946
		3.5	Beals 1946
	Cessation of Breastfeeding	15	Beals 1946
	Duration of the Weaning Process	11.5	Beals 1946
Teda	Complementary Liquids	-	-
	Complementary Solids	6	Chapelle 1957
	Complementary Liquids or Solids	6	Chapelle 1957
		36	Chapelle 1957
	Cessation of Breastfeeding	30	Chapelle 1957
	Duration of the Weaning Process		
Tibetans	Complementary Liquids	-	-
	Complementary Solids	11	MacDonald 1929
	Complementary Liquids or Solids	11	MacDonald 1929
		11	MacDonald 1929
	Cessation of Breastfeeding	0	MacDonald 1929

	Duration of the Weaning Process		
Tiv	Complementary Liquids Complementary Solids Complementary Liquids or Solids Cessation of Breastfeeding Duration of the Weaning Process	0.3 6.0 0.3 24 20.9	Bohannon 1958 Bohannon 1958 Bohannon 1958 Bohannon 1958 Bohannon 1958
Toda	Complementary Liquids Complementary Solids Complementary Liquids or Solids Cessation of Breastfeeding Duration of the Weaning Process	- - - 36 -	- - - Marshall 1873 -
Trobriands	Complementary Liquids Complementary Solids Complementary Liquids or Solids Cessation of Breastfeeding Duration of the Weaning Process	0 12 6 24 18	Malinowski 1929 Malinowski 1929 Malinowski 1929 Malinowski 1929 Malinowski 1929
Truk	Complementary Liquids Complementary Solids Complementary Liquids or Solids Cessation of Breastfeeding Duration of the Weaning Process	- 3 3 18 15	- Gladwin 1953 Gladwin 1953 Gladwin 1953 Gladwin 1953
Turkana	Complementary Liquids Complementary Solids Complementary Liquids or Solids Cessation of Breastfeeding Duration of the Weaning Process	- - - 36 -	- - - Gulliver 1951 -
Tzeltal	Complementary Liquids Complementary Solids Complementary Liquids or Solids Cessation of Breastfeeding Duration of the Weaning Process	9 3.5 3.5 18 14.5	Nash 1970; Stross 1970 Nash 1970; Stross 1970 Nash 1970; Stross 1970 Nash 1970; Stross 1970 Nash 1970; Stross 1970
Warao	Complementary Liquids Complementary Solids	- -	- -

	Complementary Liquids or Solids	- 24	- Hill 1956
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process		
Woleai	Complementary Liquids	-	-
	Complementary Solids	3	Spiro 1949
	Complementary Liquids or Solids	3	Spiro 1949
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process		
Yahgan	Complementary Liquids	-	-
	Complementary Solids	4	Gusinde 1937
	Complementary Liquids or Solids	4	Gusinde 1937
	Cessation of Breastfeeding	24	Gusinde 1937
	Duration of the Weaning Process	20	Gusinde 1937
Yap	Complementary Liquids	-	-
	Complementary Solids	6	Hunt 1949
	Complementary Liquids or Solids	6	-
	Cessation of Breastfeeding	3	-
	Duration of the Weaning Process	24	-
Yokuts	Complementary Liquids	13	Gayton 1948
	Complementary Solids	1	Gayton 1948
	Complementary Liquids or Solids	1	Gayton 1948
	Cessation of Breastfeeding	24	Gayton 1948
	Duration of the Weaning Process	22.9	Gayton 1948
Yurok	Complementary Liquids	-	-
	Complementary Solids	6.5	Erikson 1943
	Complementary Liquids or Solids	6.5	Erikson 1943
	Cessation of Breastfeeding	12	Erikson 1943
	Duration of the Weaning Process	5.5	Erikson 1943
Zuni	Complementary Liquids	24	Leighton 1963
	Complementary Solids	-	-
	Complementary Liquids or Solids	24	Leighton 1963
	Cessation of Breastfeeding	24	Leighton 1963
	Duration of the Weaning Process	0	Leighton 1963

	Process		
Shona	Complementary Liquids	8	Simango 1997
	Complementary Solids	2	Simango 1997
	Complementary Liquids or Solids	2	Simango 1997
	Cessation of Breastfeeding	24	Kuper 1954
	Duration of the Weaning Process	22	Kuper 1954; Simango 1997
Umbundu	Complementary Liquids	0	Childs 1969
	Complementary Solids	0	Childs 1969
	Complementary Liquids or Solids	0	Childs 1969
	Cessation of Breastfeeding	36	Childs 1969
	Duration of the Weaning Process	36	Childs 1969
Komachi	Complementary Liquids	-	-
	Complementary Solids	0	Bradburd 1998
	Complementary Liquids or Solids	0	Bradburd 1998
	Cessation of Breastfeeding	-	-
	Duration of the Weaning Process	-	-
Rendille	Complementary Liquids	-	-
	Complementary Solids	-	-
	Complementary Liquids or Solids	-	-
	Cessation of Breastfeeding	12	Spencer 1973
	Duration of the Weaning Process	-	-
Samburu	Complementary Liquids	0.3	Spencer 1973
	Complementary Solids	-	-
	Complementary Liquids or Solids	0.3	Spencer 1973
	Cessation of Breastfeeding	11	Spencer 1973
	Duration of the Weaning Process	10.7	Spencer 1973
Dinka	Complementary Liquids	1	Deng 1988
	Complementary Solids	-	-
	Complementary Liquids or Solids	1	Deng 1988
	Cessation of Breastfeeding	72	Deng 1988
	Duration of the Weaning Process	71	Deng 1988



**APPENDIX 2, SOURCES FOR ALLELE FREQUENCIES PROXY POPULATIONS**

<b>Population</b>	<b>Proxy</b>	<b>Source</b>
!Kung	(no proxy needed)	Cavalli-Sforza et al. 1994
Amele	Papuans	Smith et al. 1994
Arapaho	Blackfoot/ Cheyenne/ Algonquin avg.	Goddard 1981
Aymara1	(no proxy needed)	Cavalli-Sforza et al. 1994
Aymara2	(no proxy needed)	Cavalli-Sforza et al. 1994
Azande	Eastern Bantu	Westermann 1952
Badaga	Toda	Vishwanathan et al. 2003
Bang Chan	Bangkok Thai	Ethnologue? (Raymond 2005)
Bella Coola	Haida	Ward et al. 1993
Bhil	(no proxy needed)	Cavalli-Sforza et al. 1994
Cayapa	(no proxy needed)	Cavalli-Sforza et al. 1994
Chipewyan	(no proxy needed)	Cavalli-Sforza et al. 1994
Chuckchee	(no proxy needed)	Cavalli-Sforza et al. 1994
Datoga	Hadza; Nilotes	Ehret 1971
Dogon	Fulani; Niger-Congo	Greenberg 1955; Raymond 2005
Dorobo	Maasai; Nilotes	Gordon 2005; Raymond 2005
Fang		Dembo 2007
Gainj	no proxy needed; New Guinea Melanesians	Cavalli-Sforza et al. 1994
Garo	no proxy needed; Burmese	Cavalli-Sforza et al. 1994
Goajiro	no proxy needed; Arawak	<i>Encyclopedia Britannica Online</i> 2009
Hare	Athabaskans; Dogrib	Raymond 2005
Igorot	no proxy needed; Ifuago	Raymond 2005
Ila	Zimbabwe Tonga	Raymond 2005
Javanese	Luanguia; Solomon Islanders	Raymond 2005
Jivaro	(no proxy needed)	Cavalli-Sforza et al. 1994
Kapauku	no proxy needed; Kapauku	Raymond 2005
Kogi	Colombia Chibcha	Raymond 2005
Kpelle	(no proxy needed)	Cavalli-Sforza et al. 1994
Kwoma	Sepik (Abelam)	Raymond 2005
Lolo 1	Szechuan/ Sichuan; Chinese avg.	Raymond 2005
Lolo 2	Szechuan/ Sichuan; Chinese avg.	Raymond 2005
Maasai	(no proxy needed)	Cavalli-Sforza et al. 1994
Marshalls	(no proxy needed)	Cavalli-Sforza et al. 1994
Micmac	Ojibwe	Raymond 2005
Nahane	Athabaskans; Nahane	Raymond 2005
Navaho	(no proxy needed)	Cavalli-Sforza et al. 1994
Okayama	no proxy needed; Japanese	Cavalli-Sforza et al. 1994

Okinawa	Japanese	Raymond 2005
Pygmies	(no proxy needed)	Cavalli-Sforza et al. 1994
Quechua1/2	(no proxy needed)	Cavalli-Sforza et al. 1994
Quechua3/4	(no proxy needed)	Cavalli-Sforza et al. 1994
Saami	(no proxy needed)	Cavalli-Sforza et al. 1994
Senoi	no proxy needed; Malay Aboriginies	Cavalli-Sforza et al. 1994
Siriono	no proxy needed; Brazilian Guarani	Raymond 2005
Tallensi	Mende	Pocklington 1992
Tarahumara	no proxy needed; Nahua	Raymond 2005
Tarasco	no proxy needed	Cavalli-Sforza et al. 1994
Teda	no proxy needed	Cavalli-Sforza et al. 1994
Tibetans	no proxy needed	Cavalli-Sforza et al. 1994
Tiv	no proxy needed	Cavalli-Sforza et al. 1994
Toda	no proxy needed	Cavalli-Sforza et al. 1994
Trobriands	no proxy needed	Cavalli-Sforza et al. 1994
Truk	no proxy needed	Cavalli-Sforza et al. 1994
Turkana	Bantu avg.	Raymond 2005
Tzeltal	no proxy needed	Cavalli-Sforza et al. 1994
Warao	no proxy needed	Cavalli-Sforza et al. 1994
Woleai	Micronesian	Raymond 2005
Yahgan	no proxy needed; Indigenous Chileans	geography
Yap	no proxy needed	Cavalli-Sforza et al. 1994
Yokuts	Tlinglit	Raymond 2005
Yurok	no proxy needed; Ojibwe/ Cree/ Blackfoot avg.	Raymond 2005
Zuni	no proxy needed	Cavalli-Sforza et al. 1994
Shona	Bantu avg.	Raymond 2005
Umbundu	no proxy needed	Cavalli-Sforza et al. 1994
Komachi	Iranians, Iranian Kurds	geography
Rendille	no proxy needed	Cavalli-Sforza et al. 1994
Samburu	no proxy needed	Cavalli-Sforza et al. 1994
Dinka	no proxy needed	Cavalli-Sforza et al. 1994

### APPENDIX 3, SOURCES FOR ECO-GEOGRAPHIC DATA

Population	Variable	Data Point	Source
!Kung	Latitude (oN or S of equator)	20	Murdock 1981
	Elevation (m)	1100	Tanaka 1980
	Variability in Precipitation (mm)	32	Lee 1966
	Effective Temperature (o C)	16.1	Lee 1966
Amele	Latitude (oN or S)	5	<i>Google Earth</i>
	Elevation (m)	300	Smith et al. 1994

	Variability in Precipitation (mm) Effective Temperature (o C)	270 26.5	Mehlotra et al. 2000 Leps et al. 2002
Arapho	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	40 ----- 46 7.8	Murdock 1981 ----- Walter et al. 1975 Walter et al. 1975
Aymara 1	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	16 3850 205 11.4	Murdock 1981 Broncle Carreon 1964 Carter 1965 La Barre 1948
Aymara 2	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	16 4000 205 11.4	Murdock 1981 Broncle Carreon 1964 Carter 1965 La Barre 1948
Azande	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	5 244 298 22.7	Murdock 1981 Junker 1891 Culwick 1950 Culwick 1950
Badaga	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	11 2250 178 21.3	<i>Google Earth</i> Hockings 1980 Hockings 1980 -----
Bang Chan	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	14 ----- 135 22.3	<i>Google Earth</i> <i>Google Earth</i> Hanks 1964 Hanks 1964
Bella Coola	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	52 305 225 12.2	Murdock 1981 Kendrew & Kerr 1955 Kendrew & Kerr 1955 Kendrew & Kerr 1955
Bhil	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	22 500 160 18	Murdock 1981 Koppers 1948 Nath 1960 Naik 1956
Buka	Latitude (oN or S) Elevation (m) Variability in Precipitation	5 225 304	Murdock 1981 Blackwood 1935 Blackwood 1935

	(mm) Effective Temperature (o C)	24.0	Blackwood 1935
Cayapa	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	1 263 ----- 24.4	Murdock 1981 Barrett 1935; <i>Google Earth</i> ----- Larrea 1924
Chipewyan	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	49 213 68 10.8	Murdock 1961 VanStone 1961 Irimoto 1981 Irimoto 1981
Chuckchee	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	66 215 83 10.1	Murdock 1981 Alaska Planning Group 1978 Alaska Planning Group 1978 Borogas 1909
Datoga	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	3 1031 260 20.0	<i>Google Earth</i> Sellen 1999 Sellen 2001 Sieff 1997
Dogon	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	14 450 46 22.0	Beirerle 2000 Griaule 1938 Chenevix-Trench et al. 1997 Chenevix-Trench et al. 1997
Dorobo	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	0 1435 201 25.0	Murdock 1981 Huntingford 1953 Huntingford 1953 Cronk 2004; Mutundu 1999
Fang	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	2 625 260 21.3	Murdock 1981 Dugast 1949 Tutin et al. 1995 Alexandre and Binet 1958
Gainj	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	5 1125 203 25.7	<i>Google Earth</i> Wood 1987 Anas 1960 Cotes et al. 1973
Garó	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm)	26 214 75 25.8	Murdock 1981 Playfair 1909 Majumdar 1978 Hunter 1879

	Effective Temperature (o C)		
Goajiro	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	12 358 460 25.2	Murdock 1981 Simons 1885 Green 1978 Green 1978
Hare	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	66 389 0 11.4	<i>Google Earth</i> <i>Google Earth</i> Savishinsky 1976 Savishinsky 1976
Igorot	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	17 1210 277 23.0	Bodner & Gerrau 1988 Bodner & Gerrau 1988 Bodner & Gerrau 1988 Bodner & Gerrau 1988
Ila	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	16 914 350 16.8	Murdock 1981 Jaspen 1953 Scheppe 1972 Payne 1979
Javanese	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	8 16 190 24.9	Murdock 1981 Castles 1967; <i>Google Earth</i> Selosoemardjan 1962 Sievert & Flanagan 2005
Jivaro	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	4 2500 0 -----	Murdock 1981 Reyes and Teran 1939 Bennet et al. 2002 -----
Kapauku	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	4 1676 0 17.5	Murdock 1981 Pospisil 1958 Pospisil 1958 Pospisil 1958
Kogi	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	9 1500 250 22.8	Reichel-Dolmatoff 1982 Reichel-Dolmatoff 1982 Aide & Cavelier 1994 Aide & Cavelier 1994
Koryak	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	62 300 52 10.3	Murdock 1981 Jochelson 1908 Jochelson 1908 Jochelson 1908

Kpelle	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	8 320 762 25.6	Murdock 1981 Gibbs 1965 Lancy 1984 Gibbs 1965
Kwoma	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	4 232 180 25.6	Murdock 1981 Whiting 1941 Muller et al. 1988 Whiting 1941
Lolo1	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	29 2100 225 13.6	Murdock 1981 Tseng 1945 Poling et al. 2003 Poling et al. 2003
Lolo2	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	29 2100 225 13.6	Murdock 1981 Tseng 1945 Poling et al. 2003 Poling et al. 2003
Maasai	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	4 1219 70 23.4	Murdock 1981 Sanford 1919 Sanford 1919 Hayashi 1996
Marshalls	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	7 1.4 361 26.1	Murdock 1981 Chave 1948 Spoehr 1949 Spoehr 1949
Micmac	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	45 88 86 12.1	Murdock 1981 LeClercq 1910 Silva et al. 2003 Walter et al. 1975
Nahane	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	61 1158 ----- 12.0	<i>Google Earth</i> Teit 1956 ----- Teit 1956
Navaho	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	35 2200 32 13.1	Murdock 1981 Adair 1970 Adams 1963 Leighton and Adair 1963 (Zuni as proxy)
Okayama	Latitude (oN or S)	34	<i>Google Earth</i>

	Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	503 256 13.9	Kakiuchi 1979 Kakiuchi 1979 Ikebe and Oishi 1997
Okinawan	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	26 91 148 16.5	Murdock 1981 Glacken 1953 Glacken 1953 Glacken 1953
Pygmies	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	28 729 0 23.9	Beierle 1995 <i>Google Earth</i> Putnam 1948; Turnbull 1965 Turnbull 1965
Quechua1/2	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	2 2600 126 12.7	<i>Google Earth</i> Gangotena 1982 Green 1982 Forman 1982
Quechua3/4	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	2 2600 126 12.7	<i>Google Earth</i> Gangotena 1982 Green 1982 Forman 1982
Saami	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	66 300 53 10.7	Collinder 1949 Itkonen 1948 Anderson 1978 Ingold 1976
Senoi	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	4 838 425 27.2	Murdock 1981 Dentan 1988 Numata et al. 2003 Corbet 1934
Siriono	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	15 152 350 22.8	Murdock 1981 Holmberg 1950 Wallace and Painter 2002 Holmberg 1950
Tallensi	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	11 198 251 -----	Murdock 1981 Lynn 1937 Lynn 1937 -----
Tarahumara	Latitude (oN or S) Elevation (m)	27 1981	Murdock 1981 Bennett 1935

	Variability in Precipitation (mm) Effective Temperature (o C)	94 13.9	Bennett 1935; Kennedy 1978 Champion 1963
Tarasco	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	19 2159 74 14.1	Murdock 1981 West 1948 West 1948 Descroix et al. 2001
Teda	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	21 892 0 -----	Murdock 1981 Briggs 1958 Briggs 1958 -----
Tibetans	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	30 3750 120 11.6	Murdock 1981 Hermanns 1948 Tian et al. 2003 Tian et al. 2003
Tiv	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	7 655 231 21.9	Murdock 1981 Bohannan 1954 Briggs 1941 Bohannan 1954
Toda	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	12 2057 251 15.6	Murdock 1981 Rivers 1906 Breeks 1983 Breeks 1983
Trobriands	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	9 23 ----- 20.2	Murdock 1981 Austen 1936 ----- Heatwole et al. 1975
Truk	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	7 184 285 24.5	<i>Google Earth</i> Goodenough 1951 Goodenough 1951 Goodenough 1951
Turkana	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	4 550 41 -----	<i>Google Earth</i> Dyson-Hudson and McCabe 1985 Leslie & Frye 1989 -----
Tzeltal	Latitude (oN or S) Elevation (m) Variability in Precipitation	16 1700 226	<i>Google Earth</i> Redfield & Villa-Rojea 1935 Wagner 1962



	(mm) Effective Temperature (o C)	15.3	Wagner 1962
Warao	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	9 8.4 310 26.0	Murdock 1981 Wilber 1958 Echezuna et al. 2002 Echuzuna et al. 2002
Woleai	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	7 3 201 26.7	Murdock 1981 Burrows 1948 Burrows 1948 Burrows 1948
Yahgan	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	55 305 30 10.0	Murdock 1981 Cooper 1946; Lorthrop 1928 Lorthrop 1928 Lorthrop 1928
Yap	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	9 122 260 25.0	Murdock 1981 Hunt et al. 1949 Yu et al. 1997 Salesius 1906
Yokuts	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	36 67 25 14.6	Murdock 1981 Beales & Hester 1958 Germano et al. 1994 Beales & Hester 1958
Yurok	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	41 146 435 12.6	Murdock 1981 Taylor 1982 Taylor 1982 Taylor 1982
Zuni	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	35 1829 8 13.1	Murdock 1981 Bunzel 1932 Balling & Wells 1990 Leighton & Adair 1963
Shona	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	19 914 173 21.0	Kuper 1954 Kuper 1954 Kuper 1954 McAinsh et al. 2004
Umbundu	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm)	13 1500 ----- 14.6	Childs 1969 Childs 1969 ----- Childs 1969

	Effective Temperature (o C)		
Komachi	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	30 1409 67 17.7	<i>Google Earth</i> Bradburd 1990 Iran Meteorological Association 2009 Bradburd 1990
Rendille	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	1 500 197 27.8	Spencer 1973 Fratkin 2004 Spencer 1973 Fratkin 2004; Sun 2005
Samburu	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	0 1981 109 28.5	Spencer 1973 Spencer 1973 Spencer 1973 Kahindi 2001; Kasusya 1998
Dinka	Latitude (oN or S) Elevation (m) Variability in Precipitation (mm) Effective Temperature (o C)	11 1500 200 21.7	Roberts 1956 Mohammad et al. 2004 Mohammad et al. 2004 Mohammad et al. 2004