A Behavioral Ecology Approach to Trade-offs in Reproduction: Modelling Women's Reproductive Strategies and Empirical Studies of Post-partum Amenorrhea

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Abstract

Reproductive behaviors are shaped by a plethora of selective pressures, past and present. On an ecological time scale, reproductive “decisions” are made by balancing life-history trade-offs that are dependent on intrinsic and extrinsic factors, such as resource availability and age. Mathematical models are powerful tools that allow for the systematic investigation of such factors, and to test whether selective forces thought to be responsible for particular traits had been correctly identified. In this thesis, I present a dynamic state variable model for the optimization of reproductive scheduling under a range of family and environmental contexts. Next, I test one of the model’s simplifying assumptions, that sons and daughters cost the same to produce and to raise, via secondary data analysis of two existing data sets. These results are discussed in parallel to the benefits of applying principles of evolutionary ecology to public health problems.

Keywords: Human reproduction; behavioral ecology; state-dependency; dynamic state variable model

Dedication

To my grandfather, the most generous and humble person I know.

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I accrued a trail of debt over the 3.5-year making of this thesis, and the *n*-year making of Gigi as a scientist. Here, I express my gratitude to this large group of generous folks in reverse chronological order, where T=time of defense.

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Table of Contents

List of Tables

List of Figures

List of Acronyms

BMI	Body mass index
CI	Confidence interval
DSVM	Dynamic state variable model
DT	Demographic transition
HBE	Human behavioral ecology
HR	Hazard ratio
IBI	Inter-birth interval
LHT	Life history theory
NS	Natural selection
PA	Post-partum amenorrhea
SES	Socioeconomic status
TW	Trivers-Willard hypothesis

Chapter 1.

Introduction

The health and well-being of women are a global public health mission. Investments into this cause has a ripple effect extending beyond providing for half the human population, to ensuring a healthy and strong next generation. Unfortunately, women worldwide face elevated health hazards for biological and gender-based reasons. A vast majority of these risks are related to their reproductive roles (Tinker, 2000). Childbearing is a highly risky endeavour for multiple reasons. Certain medical conditions, such as anemia and malaria, can be exacerbated during pregnancy. Pregnancy itself is associated with a number of potential health complications for both mother and child, such as gestational diabetes and obstructed labor. These risks are further increased as a mother ages (Naeye, 1983; Sauer, 2015). In populations where fertility is high but basic maternity care is limited, women are particularly vulnerable to injury, infection, or even death, during gestation and childbirth. Maternal and child health have both been identified as United Nations (UN) Millennium Development Goals, which expired in 2015. This global movement seeks to lower maternal and child mortality, increase access to reproductive health, and to improve coverage of antenatal care and immunization rates. The latest UN report has suggested that, although there have been significant achievements in these areas worldwide, progress has been uneven across regions and countries (United Nations, 2015). Maternal mortality was reported to be one of the largest gaps in health outcome between developed and developing countries at the turn of the millennia (Hill et al., 2001), and these gaps remain to date.

Governments and NGOs have been hard at work with policies and programs to improve conditions for women and children. These initiatives include promotion of safe sex and family planning, advocating for women’s dignity and choice, reducing violence against women and children, improving nutrition and the social position of women and children, and empowering women via education (Tinker, 2000). Most of these policies aim at changing the attitude and behavior of a target population through education and punishments (Gibson & Lawson, 2015). Since behavior (reproductive behavior in this case) is often the focus, effective policy needs to be backed by robust behavioral theory: people are less likely to drop out or refuse to participate when a project is in line with their values, and more importantly, constraints (Gibson & Lawson, 2014).

Evolutionary ecology is a useful framework for understanding human reproductive behavior in a social and economic context. Ecology is of particular importance here, because the relationship between behavior and outcome (e.g., profitability of investment in a certain activity) varies with context (Hill & Kaplan, 1999; Voland, 1998). For instance, if the risk of contracting an infectious disease is low, investment in immune function will have little utility. As a species we are currently experiencing dramatic changes in our lifestyle, family structure, diet, and health challenges. Applying evolutionary ecology can provide new insights into the causes and consequences of behavior and behavioral shifts, and holds great potential to guide the design and implementation of effective social and public health policies. The focus of this thesis will be on applications of evolutionary ecology to reproductive behavior. Life history theory will be central to this discussion.

1.1. A brief history of human behavioral ecology

Evolutionary ecology is conventionally termed behavioral ecology when applied specifically to studies of “behavior”, defined here as observable response to external stimuli. Human behavioral ecology (HBE) is thus the study of how behavior evolved, with a particular focus on the ecological conditions under which it occurred (Nettle et al., 2013; Winterhalder & Smith, 2000). “Ecological conditions” refer to an organism’s physical environment, interactions with conspecifics and other species, and its internal state. Essentially, human behavioral ecologists seek to understand how past selective pressures and current challenges shape diversity in biological and behavioral phenotypes in contemporary human populations. HBE is anchored in the basic principles of evolution by natural selection (NS). The fundamental assumption here is that, humans, like all other organisms on earth, are expected to maximize fitness given the socioecological context to which they are exposed. This expectation that organisms exhibit behaviors that are close to optimal allows researchers to generate hypotheses regarding the types of behaviours expected under different conditions. In addition, behavioral plasticity (e.g., in the form of social learning; Henrich & McElreath, 2003) is also expected to be favored by natural selection. Plasticity is favored because individuals experience diverse life circumstances, such that there is not one universal superior strategy, but sets of strategies will be available under constraints. Here, optimization is defined as choosing the best strategy from the available subset in each context. Humans are indeed remarkable in their ability to adapt to new niches much faster than the time required for genetic change (Laland & Brown, 2006; Nettle, 2009). HBE has been particularly concerned with explaining this rapid adaptation and diversity, and considers behavior as a result of tracking local ecological conditions rather than being strictly a “playback” of routines that were adaptive in the past (Winterhalder & Smith, 2000). This assumption distinguishes HBE from other disciplines that apply evolutionary theory to the study of human behavior, such as evolutionary psychology (Winterhalder & Smith, 2000).

Pioneers of HBE were anthropologists who applied optimal foraging theory to studies of hunter-gatherer societies in the 1970s. These early studies predominately concerned hunting band formation (Wilmsen, 1973), foraging patterns (Dyson-Hudson & Smith, 1978), and shifts in diet as a response to technology change (Hames, 1979). The focus of HBE broadened in the 1990s to include studies of social structure and reproductive behavior in non-foraging subsistence populations and industrialized populations. Representation of non-anthropology fields, such as biology and demography, also increased since the inception of HBE (Nettle et al., 2013).

HBE conceptual models are characterized by having a goal (something to optimize), a currency (for measuring costs and benefits), a set of constraints, and decisions (behavioral options to be evaluated) (Winterhalder & Smith, 2000)**.** These models are formulated under the assumption known as the phenotypic gambit: that there are no important phylogenetic or developmental constraints over the range of strategies that individuals are able to evolve and perform (Grafen, 1991). Decisions regarding the thought process, or neural circuitry, involved in decision making are also typically avoided.

Studies are often framed in terms of decision rules or conditional strategies: in context *a*, do *x*, otherwise, do *y*.

Evolutionary models holds great potential in generating new predictions and unifying diverse empirical observations, without being incompatible with proximate theories (Nettle, 2009). However, it is also important to consider alternative, non-NS, explanations to the same observed outcome. As an example, when low fertility is observed in a particular population, it could be a result of adaptive choice (having fewer children is the better strategy), or insufficient resources (unable to reproduce regardless of optimal strategy). Rigorous testing of these hypotheses is necessary to avoid evolutionary explanations being discounted as being "just-so stories" (Gould, 1978; Voland, 1998). This criticism points straight at the core of the greater field of evolutionary ecology: the ingrained idea that traits are results of adaptations have led researchers to overlook the fact that evolutionary hypotheses were rarely actually tested. While these "stories" were often elegant, compelling, and good starting points for setting up theory, many were not supported by evidence, and were erroneously accepted as being robust merely because they were told over and over again (Durrant & Haig, 2001; Gould, 1978; Lennox, 1991; Olson & Arroyo-Santos, 2015).

1.1.1. Life history theory

Life history theory (LHT) is a framework under which questions regarding the timing of an organism's life events are explored (Roff, 1992; Stearns, 1992). One fundamental principle of LHT is that of resource allocation: resources are needed for multiple competing functions, and resources used for one function cannot be used for another. Biological functions can be broadly separated into two categories: somatic and reproductive effort. Somatic effort represents growth and maintenance while reproductive effort can be further separated into mating and parenting efforts. When two traits share the same resource pool, increased allocation to one would necessarily decrease allocation to the other. These traits would thus appear to be negatively correlated and pose trade-offs to the organism (Rosenheim et al., 2010). An exception occurs when there is more variation in the input of energy from the environment than there is in the internal competition for energy, in which case the traits would appear to be positively correlated (van Noordwijk & de Jong, 1986; Zera & Harshman, 2001).

The main postulate of LHT is that the ontogeny (i.e., developmental trajectory) and behavior of an organism has been shaped by natural selection such that resource allocation is optimized across its life span in order to maximize fitness. Different resource allocation patterns are expected during different life stages due to changing, context-dependent, costs and benefits (Stearns, 1976). For example, human babies focus their resources on somatic growth and maintenance as opposed to reproductive processes. Life-history transitions, i.e. going from one life stage to another, are often accompanied by changes in energy allocation regimes. Puberty marks the transition into sexual maturity, and therefore energy allocation priorities are expected to shift from growth towards reproduction.

Two trade-offs prevail when considering reproduction, namely that of quantity vs. quality of offspring, and current vs. later reproduction. These trade-offs can be understood in the context of *r*/*K* selection, where *r* stands for intrinsic growth rate of population size (quantity) and *K* for carrying capacity (quality becomes important when the population size is close to carrying capacity and competition is intense). *K*-selected organisms tend to invest in parenting effort, mature later, and give birth small litters of higher quality offspring. On the other hand, *r*-selected organisms tend to invest in mating effort and consist of opposite life-history and family characteristics. The former is often described as a slow life history, and the latter, fast. These reproductive strategies are mutually exclusive, as resources used for mating and production of offspring cannot be used for parenting, and vice versa. Mortality risk was thought to play an important role in the evolution of life history strategies (Chisholm et al., 1993). Regardless of how salubrious the environment, there is always some non-zero probability that the individual will die before reproduction. Investment into the future would be a poor decision if the chances of surviving till then is low (Williams, 1966). In this case, organisms are expected to trade some of their potential fitness in order to prevent total failure.

1.2. HBE and human reproduction

Evolutionary theory posits that variation in reproductive effort across human populations can be understood as the local optimization of life history trade-offs, constrained by past evolution and current challenges. Mating systems, inheritance patterns, gender roles, and other cultural phenomena can be viewed as the result of selective pressures acting on earlier generations (Alexander, 1987), which in turn act as constraints on the available subset of behavioral options in the present day. Reproductive effort can be separated into three categories: 1) mating effort (courtship and competition for mates), 2) parenting effort (producing and raising offspring), and 3) nepotistic effort (investments into genealogical sidelines for the purposes of enhancing inclusive fitness (Ellison, 2001). Here, I focus on parenting effort and relevant life history strategies (e.g., age at first birth and birth spacing). In the following sections, various aspects of resource allocation pertaining to parenting effort are discussed.

1.2.1. Life history strategies

This section concerns the optimization of maturation rates, reproductive rates and timing, mortality patterns, and senescence. I begin the discussion with the trade-off between allocation towards reproductive and other somatic efforts. Based on the simple principle that energy allocated towards reproduction cannot be used for other biological functions, such as maintenance, one would predict women's longevity to be inversely correlated with fertility (after excluding deaths due to pregnancy events). This effect has been studied extensively in insects (e.g., Roitberg, 1989; Patridge & Barton, 1993) and mammals (e.g., Moyes et al., 2006). However, tests of this prediction in humans have generated mixed results. Some studies report that high-fertility women have shorter lives (Doblhammer & Oeppen, 2003; Müller et al., 2002), others only find the relationship in harsh environments (Lycett et al., 2000), and yet other studies report a positive relationship between fertility and longevity (Hayward et al., 2015; Korpelainen, 2000; Smith et al., 2002; Westendorp & Kirkwood, 1998). These results may be confusing due to differences in methodology and characteristics of the populations sampled, ranging from church records from Scandinavian villages, open-source data of European monarch family history, to surveys mailed to German physicians. Exclusion of childless women (either from statistical analyses or that they simply could not have been picked up in retrospective surveys) appear to be common practice, but this could contribute to the over-estimation of the cost of fertility (Gavrilova & Gavrilov, 2007). The counter-intuitive positive association between fertility and longevity could have been a result of phenotypic correlation: high quality individuals tend to have both higher longevity and fertility (Harshman & Zera, 2007). Another possible explanation for these observations would be reverse causality: high mortality risk lead individuals to adopt a high-fertility, *r*-selected, life history (Störmer & Lummaa, 2014).

Perceived life expectancy and the prospects of reproduction during early life were thought to have the biggest influence on determining an individual's life history strategy along the *r*/*K* continuum (Chisholm et al., 1993). A number of theories with roots in the attachment theory of psychology were formulated to address this proposition. The most commonly discussed of these theories include psychosocial acceleration theory (Belsky et al., 1991; 2010), and the child development theory (Ellis, 2004). The psychosocial acceleration theory posits that insecurities experienced during childhood signal that future prospects are grim and thus predispose the individual to adopting an opportunistic reproductive strategy (*r*-selected). The child development theory similarly predicts accelerated maturity and reproduction in individuals who experienced a poor childhood, but attributes the "decision" to accelerate maturity to the lack of benefits of remaining in childhood (i.e., parental investment is low). A lot of studies have tested and provided support for the predictions generated by these hypotheses, however, most of them consisted of only observational data (Ellis, 2004; Nettle et al., 2011). These studies cannot, for example, rule out the possibility that some social setting might cause the parents to invest less and, at the same time, kids to mature faster. Researchers have attempted to address this potential confounding by taking advantage of natural experiments. Pesonen and colleagues (2008) studied the reproductive strategies of individuals from Helsinki who had been evacuated from their birth families during WWII, compared to those who remained. As evacuation happened at random (with respect to family characteristics) this can be considered a quasi-experimental design. They found that evacuee women had earlier menarche and more children than controls (though not earlier age at first birth), in line with predictions from the psychosocial acceleration and child development theories.

Another class of hypotheses focused on different constraints faced under various early life circumstances (Ellis, 2004). The main postulate is that in chronically-poor environments (e.g., in terms of nutrition), children should experience slow growth, delayed pubertal development, and achieve smaller adult size due to energetic constraints. Examples of threshold traits include fat reserves, nutrition, chronic stress and illness (Ellison, 1982). This hypothesis also predicted that such children will have lower reproductive capacity than those who grew up in better conditions.

Adaptationist vs. constraint hypotheses often generate opposite predictions regarding early life exposures and life history strategies. This is because the hypotheses are formulated in a mutually exclusive manner: adaptationist models typically do not take into account the physiological regulation in the timing of puberty and reproduction, while “constraint” models rarely consider adaptive delays and abstinence. Empirical evidence in support of predictions generated by both classes of hypotheses has been found, not surprisingly, often by their own proponents (Ellis, 2004). The result is that both good and bad environments in early life have been associated with both accelerated and delayed pubertal development. It was thus proposed that there should be a quadratic (i.e. U-shape) relationship between early-life experience and the timing of sexual maturity (Ellis, 2004). Both low and high levels of adversity would predict late age of sexual maturation, but for different reasons. Under poor environmental conditions individuals develop slowly due to energetic constraints, while in good environments delaying maturation is the adaptive strategy. This hypothesis not only marries the concepts of adaptive choice and constraint, it also provides an explanation for those studies that failed to reach consistent conclusions regarding the relationship between environmental conditions and the onset of sexual maturity. Depending on where the adversity level of the study population sit along the “U”, different conclusions of the strategies adopted by the relative good and poor can be generated. This hypothesis can be tested via meta-analyses of the plethora of existing studies and should shed light on the association between these factors.

In addition to developmental programming (early life stimuli altering an organism's development and adult phenotype), two other mechanisms modulating the pace of reproduction have also been proposed. The first is social learning, which is the simple case in which women observe the behavior of other women in the same situation and relate that to their own reproductive goals (Wilson & Daly, 1997), or they attempt to mimic the behavior of the perceived fittest women they know (e.g. copying their mother). The second one is context evocation: situations where evolved, domain-specific psychological mechanisms respond to a particular class of environmental input by producing an appropriate motivational response. In this case, the observation of mortality cues psychological mechanisms that increase the desire to reproduce. This latter view is often discussed in the context of psychological studies where study subjects were asked to think about death and then interviewed regarding their desire to have children (Wisman & Goldenberg, 2005; Zhou et al., 2009). In a less hypothetical setting, there has been evidence of localized spikes in birth rates following spikes of death rates (Cohan & Cole, 2002; Rodgers et al., 2005) and exposure to crime (Davis & Werre, 2007).

While the onset of sexual maturation marks the beginning of a women's reproductive career, at the other end, women face senescence and terminal investment. As women age, it becomes more pressing to produce another child, but probability of successful pregnancy drops (Holman & Wood, 2001). At menopause, women cease to reproduce yet on average they continue to survive for around 20 more years (Robson et al., 2006). Humans are the only primate in which an extended post-reproductive life span is observed in females, even in hunter-gatherer populations (but some primate species have been reported to experience menopause when reared in captivity) (Paul, 2005). A proximate explanation for menopause is oocyte depletion, resulting in the inability to continue ovulation. Ultimate explanations are formed based on the facts that risk of birth complication increases significantly with mother's age, and that there is a trade-off in her ability to continue to reproduce vs. caring for existing offspring. Individual fitness gained from continuing to reproduce often diminishes, and inclusive fitness gains from helping close kin (children or grandchildren) increase, as women age. This ultimate explanation of menopause is known as the grandmother hypothesis (Hawkes et al., 1997; Hawkes & Coxworth, 2013). The negative effect of death of a relative on the survival of a child has been used as indirect support for this hypothesis. For instance, Mace and Sear (2005) found that the death of a mother is much more costly in terms of a child's survival and nutrition than a father's, and that the presence of maternal and paternal grandmothers are strongly associated with positive childhood outcomes. These types of studies, however, do not actually demonstrate that gains in inclusive fitness from helping children and grandchildren outweigh the cost in individual fitness if the mother had maintained fertility. Unfortunately, no direct evidence exist because women cannot reproduce past menopause. Mathematical models are useful tools in studying these kinds of hypothetical questions, and indeed, Shanley and colleagues were able to demonstrate that menopause can evolve if maternal mortality is high and increases with age, and that the presence of mothers and grandmothers were effective in lowering child mortality and increase fertility (Shanley & Kirkwood, 2001; Shanley et al., 2007).

1.2.2. Offspring quantity vs. quality

Classic life history posits that there is a trade-off between offspring quantity and quality, as resources allocated towards producing more offspring cannot be invested into improving the quality of the existing ones. Going back to the pioneering work on optimal clutch size in birds by Lack (1954), there appears to exist an optimal (given the circumstance) number of offspring an individual should attempt to raise in order for fitness to be maximized. When the optimum is exceeded, overall reproductive success is reduced as a result of thinning resources and increased offspring mortality. On the other hand, cessation of reproduction below the optimal number represents wasted reproductive opportunities.

Empirical evidence for the quality vs. quantity trade-off in humans has been mixed. The predicted unimodal, optimal number of offspring was found in the Dogon women in Mali, West Africa, where the maximum number of offspring surviving until age ten occurred at a fertility of 7-8, and not when fertility was maximized (>10) (Strassmann & Gillespie, 2002). Similar results were observed in a preindustrial Finnish population (Gillespie et al., 2010) and in the Kipsigis of Kenya (Borgerhoff Mulder, 2000). In a contemporary US military and German physician sample where data on family history was obtained via mailed survey, however, a positive relationship between fertility and long-term fitness (measured by number of grandchildren) was observed (Mueller, 2001). The author of the study concluded that even if there is a high fertility where overall fitness actually decreases, few people seem to reach that fertility in the first place. The same study also included fertility information for ~1500 European royalties from public sources, where a positive association between fertility and fitness was also observed. However, results drawn from this extremely privileged sub-population with access to virtually unlimited resources is hardly relevant. Severe negative consequences to having more children than parents can support can also assumed to be lacking in the US and German populations, which could also contribute to the absence of a trade-off. No relationship between fertility and number of grandchildren were detected in the Aché people of eastern Paraguay (Hill & Hurtado, 1996). Data compiled from three generations of pre-industrial Finns suggested that the relationship between fertility and fitness in that population depends on whether these families owned land: negative relationship observed in landless families and vice versa in families which owned land (Gillespie et al., 2008). This emphasizes the importance of context when evaluating costs and benefits of reproductive strategies, in this case, wealth.

Another approach to examining the quantity vs. quality trade-off is to test the prediction that offspring mortality increases with mother’s fertility. Results have been rather consistent on this front. Demographic surveys from 27 contemporary, sub-Saharan African populations found a robust negative correlation between fertility and child survival, and it was thought that the relationship was primarily driven by offspring competition for parental resources (Lawson et al., 2012). Similar results were seen in Dogon children, where the odds of death by age 5 increased 25% per additional child in the family (Strassmann, 1997). The association persisted even after controlling for wealth of the family, which suggested that higher mortality risk for children born in high fertility families were not results of dilution of wealth and resources.

1.2.3. Parental investment theory

As resources are often finite, parents are tasked with making strategic investments in their children. Parental investment is defined as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving at the cost of the parent’s ability to invest in other offspring” (Trivers, 1972, p. 139). Parent care is expected to decline as cost to parents’ fitness increase, such as when access to mates is easy and individual can increase fitness by investing in mating and having more offspring instead. Conversely, individuals are predicted to increase investment into offspring as they age and residual reproductive value decreases (Beaulieu & Bugental, 2008). An extreme manifestation of parental selectivity is infanticide. This practice has been observed in hunter-gatherer societies. Children born under circumstances where the appropriate care needed to properly raise said child is not forecoming are more likely to be killed (Strassmann & Mace, 2008). Hill and Hurtado (1996) found that in the Aché of Paraguay, children without living fathers were 3.9 times more likely to be killed and children of divorced parents were 2.8 times likely to be killed.

In mammals, energy expenditure into offspring care peaks at lactation, requiring approximately three times more energy than gestation (Clutton-Brock, 1991). Lactating females commonly lose weight, and their energy intake can increase by up to 200% during this time (Canale et al., 2012). Given that lactation is one of the milestones in mammalian evolutionary history, it is unsurprising human females have evolved resilience in their ability to nurse their infants (Sellen, 2007). Even under conditions of malnutrition, lactation is rarely affected: the protein and carbohydrate contents of milk are virtually unaltered, although lipid content and total volume of milk produced may decline (Sellen, 2007). Mother’s reproductive function is usually traded off as the nutritional drain imposed by lactation could lead to ovulatory failure and amenorrhea (Short, 1976).

Children can be viewed as being both assets and burdens. Having kids not only enhances one’s fitness, children are often capable of taking on small chores starting at a young age, relieving a portion the mother’s energetic stress (Kramer, 2011; Mattison & Neill, 2013; Nitsch et al., 2013). However, children are costly to raise, and there are constant competition with siblings over parents’ attention and resources (Nitsch et al., 2013; Stockley & Parker, 2002), which typically result in disagreements with parents over investment patterns (Haig, 2000). Parent-offspring conflict refers to the differing interests in terms of resource supply and demand between parent (usually mother) and child. Although the profitability of investment varies depending on the timing of the birth and sex of child, a mother is nonetheless equally related to all of her children. A child, however, is always more related to itself than to its siblings. Thus, it is in a mother's best interest to distribute her resources in a relatively even manner among her children, but children are expected to monopolize resources.

Selective allocation of resources into offspring is often studied under the Trivers-Willard hypothesis (TW) (Trivers & Willard, 1973). According to life history theory, if sex affected offspring fitness, then reproductive effort should be concentrated on the particular sex that gives the highest fitness returns per unit of parental investment (Trivers, 1972). Parents would therefore benefit from investing into the more variable sex (in terms of fitness potential) when resources are plentiful, as there is a higher chance that they could help their child achieve high reproductive success. Given that in humans males are the sex with more variable reproductive success, TW predicts that mothers in relatively good conditions should preferentially invest in sons, while those in relatively poor conditions should engage in the opposite (Trivers & Willard, 1973). These effects are observable only within a population, as sex ratio is subjected to stabilizing selection at the local population level.

There are two ways in which parents can adjust their investment into offspring of different sexes. One is to adjust sex ratio prior to birth (favor the production of children of one of the sexes), and the other is to adjust investment after sex is determined. Two mechanisms have been proposed for sex ratio adjustment in humans: male fetuses are more susceptible to elimination by spontaneous abortion under stressful conditions compared with female ones (selection in-utero hypothesis; Catalano et al., 2012), or via hormone-controlled receptivity to sperm carrying a different sex chromosome (reduced conception hypothesis; James, 1997). In terms of flexible investment during gestation (fetus growth rate, birth weight) and the pre-weaning period, most of the evidence was gathered from studies of mothers' nursing behavior where the mothers' conditions were typically classified by measures of their SES (e.g., income). Surprisingly, none of the published studies appear to include the mother's intrinsic condition (e.g., BMI) as a metric for her general condition. Rather, the focus has been on the role of maternal investment, such as birth weight, breastfeeding duration, breastmilk energy content, and interbirth-interval. The interaction between sex of child and maternal condition was found to influence birth weight and inter-birth interval (IBI) (Gaulin & Robbins, 1991), breastfeeding duration (Koziel & Ulijaszek, 2001; Wander & Mattison, 2013), and fat content of breastmilk (Fujita et al., 2012) in the manner predicted by TW. However, Quinn (2013) found no correlation between the aforementioned predictor variables on breastfeeding frequency nor milk fat content. These studies have so far generated inconsistent results. A better understanding of TW (i.e., correlates of parental investment behavior) would be of great interest and utility across disciplines.

1.2.4. Demographic transition

The demographic transition (DT) refers to the rapid decline in family size in a given population, as observed throughout Western Europe in the late 18th and early 19th centuries (Lee, 2003). In Western Europe, this period was characterized by declines in mortality and fertility, and increased levels of material investments into each child. The fact that increased wealth is coupled with decreased fertility in post-DT populations is a paradox for evolutionary models of fertility and parental investment. This is also in disagreement with data that show in pre-DT populations, wealth and fertility are positively correlated (Hill & Kaplan, 1999). It was proposed that people in affluent societies could have had many more grandchildren and great-grandchildren by having more children, but yet they do not appear to do so (Goodman et al., 2012). Historical and economic demography has revealed several socioeconomic factors correlated with post-DT reproductive behavior, but has failed to converge on a hypothesis addressing the spatial and temporal variations of DT. Hypotheses aimed at explaining the DT phenomena can be broadly separated into two camps: the maladaptive camp posit that reduced fertility is an undesirable, lagged response to the rapidly-changing environment, whereas the adaptive camp posit that DT represent a shift from an *r*- to *K*-selected life history (Borgerhoff Mulder, 1998).

The key idea that governed adaptive studies of DT is that rather than maximizing the number of offspring raised, under at least some circumstances, humans might adaptively lower fertility in order to maximize longer-term fitness (Borgerhoff Mulder, 1998). Kaplan (1996) developed an explanation of fertility reduction that focuses on parental investment to prepare offspring for successfully competing in skill-based labor markets where “human capital” (education and acquired skills) is a prime determinant of success. Indirect evidence was provided in Mace’s (1998) model where it was shown that an increase in the cost of raising children could lead to a marked reduction in the optimal fertility rate, as well as an increase in average inheritance and average wealth, all features associated with post-DT societies. Another model predicted reduced fertility as an adaptive strategy when stochastic mortality risk is lowered (Winterhalder & Leslie, 2002). The use of mathematical models had been a great asset in understanding DT, however, modellers were only occasionally successful in capturing the negative relationship between wealth and fertility, suggesting that the precise mechanisms of DT remain elusive.

1.3. HBE, human reproduction, and health?

The application of evolutionary principles to public health and social welfare can be done at multiple levels: identifying the concerns and needs of marginalized or disadvantaged peoples and/or assisting with the design and critique of policies that seek to implement changes to environment (Gibson & Lawson, 2015). Its application brings along the extremely important and fundamental realization that human life history and behavior have been shaped to maximize reproductive success, not health, financial gain nor other measures of personal or societal well-being (Williams & Nesse, 1991). This represents an important paradigm shift in how public health and medicine are to be approached: instead of just treating symptoms, one should also seek to understand the ultimate explanations for why these symptoms exist and find means to manage these roots causes. With respect to maternal and child health, studies of breastfeeding behavior and motivation to use family planning in immigrant populations and societies experiencing economic shifts have provided important insight in designing aide programs and policies

(Leonetti et al., 2007; Nunez-de la Mora, 2014). A thorough understanding of evolutionary theory would also prevent the implementation of policies that have unintended effects. One such example was given by labor-saving development projects (via installation of water taps at villages) in rural Ethiopia (Gibson, 2014). Following the implementation of said program, there was an unexpected shift in local demography towards larger family sizes, coupled with deteriorating child health. The unintended, negative child health outcome was thought to be a direct consequence of women's workload decreasing, and the "excess" energy being reallocated towards fertility. This work brings forth an intuitive, yet often neglected, insight regarding development policies that aim at improving the well-being of a population needs to be paired with promotion of family planning.

1.4. Purpose of study

This brief discussion of life history strategies and reproductive behavior reveals abundant inconsistencies in empirical evidence for HBE theories. Also lacking are means to study the many factors that influence complicated behavioral traits under one unifying roof (but see Kaplan, 1996). My thesis contributes towards filling some of these gaps. The ultimate goal of this project is to promote HBE to a wider audience, and to create a tool for the study of reproductive behavior and health that is useful across disciplinary boundaries.

My project consists of theoretical and empirical components. In Chapter 2, I describe a first-principle model for the optimization of a young woman's reproductive behavior. First-principle models describe established laws and biophysical properties with mathematical equations, and attempt to "reconstruct" a system of interest with a minimal set of equations. Models are useful on many fronts: 1) identifying optimal strategies (it is necessary to know what the optimal is before passing judgement on any observed behavior) , 2) testing whether selective pressures responsible for the evolution of a trait have been correctly identified, and 3) providing a platform for asking questions that are difficult to study in real life (Maynard Smith, 1978; McNamara et al., 2001). Modelling should be seen as a way of opening up an enquiry, not the end game. For my study of the optimization of reproductive behavior, I will be making use of a class of models known as dynamic state variable models. The formulation of these models follows remarkably closely the logic of HBE: evaluating competing strategies by considering the costs and benefits of each one under different ecological contexts. The contexts of interest here are energy reserve, stochasticity, and kin structure. I describe the formulation of this model, demonstrate model performance with examples, and discuss in depth its current limitations and, on moving forward, what it can potentially achieve. I follow this model with an epidemiologic study of the influence of sex of offspring in mothers' post-partum condition. For that study, I performed secondary analyses on existing data taken from two populations, the Kaqchikel Maya women of Guatemala (Nepomnaschy et al., 2004) and Toba women of the Nomqom village, Argentina (Valeggia & Ellison, 2004). Duration of post-partum amenorrhea (PA) was chosen as a proxy for mother's post-partum condition. These two chapters complement each other in approach and utility, but at the same time are stand-alone studies. The model has the potential to become widely useful for purposes ranging from policy evaluation to the study of hypothetical scenarios. The epidemiologic study was not only a test of an HBE hypothesis and model assumptions, but quantification of PA differences should be useful to other human reproduction scholars.

Chapter 2.

A generalized dynamic state variable model for the optimization of reproductive behavior in human females

2.1. Introduction

Humans, like all other organisms, face trade-offs in resource allocation towards competing biological processes: growth, maintenance, and reproduction (Roff, 1992; Stearns, 1992). Resources necessary for these processes (e.g., food and time) are finite and resources invested into one function cannot be used for another. Relative allocation to these functions are expected to vary over the course of an individual's life. For instance, menarche marks the shift in the allocation of energy from growth to reproduction. Understanding how optimal allocation changes with age and other factors is the central focus of the study of human life history.

Two key life-history trade-offs are related to reproduction: 1) now vs. later reproduction, and 2) quantity vs. quality of offspring. These trade-offs are hypothesized to depend on extrinsic (e.g., disease risk, mate availability) and intrinsic (e.g., age, energy reserves) factors, altogether modulated by resource availability and mortality risk (Chisholm et al., 1993; Holland Jones, 2005). High-fertility-low-quality strategies are thought to be optimal when offspring mortality risk is high due to limiting and unstable environmental conditions. Conversely, low-fertility-high-quality strategies are thought to increase parents' long-term reproductive success when parents invest into producing few yet high quality offspring. Importantly, negotiation of said trade-offs can involve conscious decisions as well as biological mechanisms. In the context of this thesis, and representing standard terminology in the field of human behavioral ecology and reproductive ecology (Lawson & Mace, 2011; Nettle et al., 2013; Winterhalder & Smith, 2000), I will use the terms decision, decision making, behavior and strategy interchangeably to represent responses to a particular situation or stimulus. They do not reflect conscious planning nor one's desire to have children. A "response" could take the form of a cultural tradition or social rule, as human culture can be perceived as the outcome of fitness-maximizing behavior from earlier generations exposed to similar selective pressures (Alexander, 1987; Voland, 1998). For example, the practice of natural fertility (absence of deliberate birth control) could be considered an adaptation in response to particular environment. Responses could also be a biological mechanism to shut down reproductive function under certain situations, such as secondary amenorrhea in female athletes under intense training (Nichols et al., 2006).

Reproductive strategies not only influences an individual's reproductive success, but also have important implications for the health and wellbeing of the mother and child. For instance, women who reproduce before the age of 19 suffer higher risk of pregnancy-related complications, increasing morbidity and mortality for both themselves and their baby (Fall et al., 2015). Additionally, both short (<18 months) and long (>59 months) inter-birth intervals are associated with elevated risks of preterm birth, low birth weight, and perinatal death (Conde-Augudelo et al., 2006). Studies that seek to better understand correlates of reproductive decision making in humans are thus valuable from both theoretical and public health perspectives.

Mathematical models are powerful tools that allow for the systematic investigation of factors that may influence traits of interest and to test whether selective forces thought to be responsible for a particular trait have been correctly identified (Maynard Smith, 1978). Theorists study human life history, behavior, and reproduction via a variety of mathematical approaches. Game theoretical models solve for optimal strategy by evaluating payoffs of different actions in relation to what others in the population might do. These models has been often applied to studies of conflicts of interest between the sexes and their effects on parental investment strategies (e.g., Houston et al., 2013) and mating system evolution (e.g., Alonzo, 2007). Network models provide insights regarding population level effects of individual behavioral changes (Nakaoka et al., 2009; Pearce, 2014). Neither of these approaches, however, take into account an individual's internal state, which could be an important driver of behavior (e.g., reproduction and energy; Ellison, 1994). Dynamic state variable models fill this gap and provide a flexible framework for studying how an individual's behavior can be regulated by its internal state (Clark & Mangel, 2000; McNamara & Houston, 1996).

Dynamic state variable models (DSVM, or stochastic dynamic programming) are primarily used for finding the best option among a set of competing strategies. They were first developed and used in applied mathematics and economics to solve problems of utility maximization and cost minimization. Since the 1980s, ecologists and evolutionary biologists have been using this technique to study a variety of behavioral optimization problems, including foraging (e.g., Mangel & Clark, 1986), clutch size (e.g., Charnov & Skinner, 1984) and dispersal in birds, fish, and insects (e.g., Purcell & Brodin, 2007; Roitberg & Mangel, 2010). When applied to biological systems, an organism's strategy is evaluated in terms of its impact on expected accumulated fitness throughout and/or at the end of an organism's life (Clark & Mangel, 2000). The behaviors of individual organisms are assumed to have evolved (i.e. to have changed over time) as a result of their positive effects on reproductive fitness. Dynamic state variable models are distinguished from other modelling techniques in their ability to take into account sequential decision making, the organism's "knowledge" of its environment, and most importantly, the "state" of the organism. State here refers to a particular element of an organism's biological status. The state should be measurable empirically, and when studying biological processes, be connected to the fitness of the organism. Different state variables can be formulated according to the purpose of the model, possibilities include parasite load, wealth, and education level. Energy state is a common state variable employed in DSVMs (Houston et al., 1988).

Economists (e.g., Siow & Zhu, 2002; Soares, 2005) and anthropologists have studied various aspects of human life history evolution using dynamic stochastic programming techniques. Beauchamp (1994) provided one of the earliest examples of such studies, showing that the classic economics concept of "utility" (i.e., a currency derived from balancing costs and benefits of having a child) alone cannot explain why wealth is often negatively correlated with fertility, unless one takes into account evolutionary fitness and the trade-off between offspring quantity and quality. Mace (1996, 1998) studied optimal birth spacing in Gabbra pastoralists of Northern Kenya, and showed that wealth, cost of marrying off a child, and the number of existing children all influenced the parents' subsequent reproductive efforts and the probability of the father remarrying. In her models, reproductive decisions were made every two years, which was unrealistic, yet, inevitable given the limited computing power at the time. Recently, Thomas and colleagues (2015) revisited the optimal reproductive scheduling question by asking whether competition among closely-spaced siblings will counter the effect of having abundant “helpers at the nest” early on in a couple’s reproductive career. Their model predicted that child mortality risk interacted with sibling competition to lengthen inter-birth interval (IBI).

This thesis chapter describes a DSVM for optimal reproductive scheduling in humans under a range of contexts. I developed an optimality model to determine the age-, energy-, and offspring-dependent sets of reproductive strategies for a young human female. The optimal strategy was one that allowed the focal female to achieve the highest expected lifetime fitness calculated based on her energy reserves and quantity and quality of offspring. A single behavior was under optimization in this model: whether to attempt pregnancy or not. The previously discussed life-history trade-offs apply to the focal female, and the optimal strategy maximizes the number of children she can afford to produce, without depleting herself nor neglecting existing children, under imposed extrinsic and intrinsic conditions.

My ultimate goal is to create a tool that is valuable on both theoretical and practical fronts. The aim is to help anthropologists investigate the effects of environmental factors on a woman’s general condition, reproductive decision making and fitness potential. This tool will be most useful in scenarios where data collection are difficult and experimentation is not permitted due to logistical difficulties and/or ethical concerns. From an applied perspective, this tool could help identify target populations and critical time spans where intervention would be most effective, as well as to evaluate competing care programs. This model thus distinguishes itself from others in that it was not formulated to investigate a specific life-history question, but was designed to be general enough to handle a range of questions and needs. Therefore, in this dissertation, I provide examples of questions that could be asked to demonstrate the flexibility and potential utilities of generalized DSVM of human reproduction.

2.2. Model description

The first step taken when formulating a dynamic state variable model is to define the state variable(s) to be included. Then, specify a number of options for actions that the organisms must take at each time step, along with dynamics (i.e., equations) that describe the relationship between actions and subsequent states. Lastly, formulate a function that specifies an organism's expected reproductive success based on its current state (Houston et al., 1988; Marescot et al., 2013). Stochastic elements, such as resource availability and mortality risk, are also typically included in these models to reflect uncertainties in environmental conditions.

2.2.1. A month in the life of the focal woman

This model concerns a single woman and her monthly reproductive decision making. This woman must "perform" two "tasks" every month: foraging (obligatory) and making a decision regarding whether to attempt pregnancy (under optimization). First, she forages for food with her helpers. Foraging returns depend upon the time of year and stochasticity (luck), and helpers contribute all their yield to the focal female. For simplicity's sake, she distributes the pooled resources evenly between herself and her dependents. She then makes a decision regarding whether or not to reproduce (can be thought of as whether or not to engage in intercourse vs. abstain). Again, that the term "decision" (along with "behavior" and "strategy") is used here to represent the "best" response to a particular situation and does not reflect conscious choice nor her desire to have children. The best response is one that maximizes her expected fitness returns, which is formulated as a function of the woman's current energy reserve and number and quality of offspring. When reproduction is determined to be the optimal strategy, the woman attempts pregnancy and conceives at a certain probability (i.e., fecundability, described in detail below).

2.2.2. State variables

The woman considered in this model was characterized by the state variables time, energy reserve, kin structure, and pregnancy status. Table 1.1 summarizes the symbols used, and details of state dynamics (i.e., equations that describe transition between states over time) are described in Appendix A.

Time. In the original conception of the study, I planned a model for a woman's entire reproductive career (age 20 to 50). However, due to severe shortage in computing power, the longest time span that I was able to work with, while still keeping essential state variables (described below) was 72 time steps. Each time step in the model translates into one month, reflecting the fact that women have one opportunity to conceive a child per month. Thus, I constructed a model for the study of reproductive decision making in six years of a young woman's life, from age 20 to the end of age 25. The model can easily be modified to consider women of different age groups by adjusting parameters (e.g., natural mortality risk) and assumptions regarding her pre-existing family structure and terminal fitness (i.e., what happens to the woman beyond the modelled time period based on her state at the time).

Energy reserve $E(t)$ at time t. "Energy" was used here as a surrogate to describe the general condition of the woman. This can be conceptualized as a woman's biological capital. Throughout her life she makes decisions on how to invest with this capital. Energy reserves are used for somatic maintenance of bodily function, foraging, caring for a pre-weaning child, etc. Resources brought back from foragers (focal female and helpers) are pooled, then evenly distributed amongst subjects in need (focal female and dependents). She adds to her reserves if her share of foraging returns exceed her energy expenditure for that time step, and experiences a net decrease in energy reserve otherwise. If the depletions are sustained and her reserves fall below a certain critical value, the woman starves to death.

Kin vector $\vec{k}$. I formulated a three-dimensional vector to store age and quality information of up to three children produced during the modelled six-year period. Children were tracked using a "feed-to-mature" system: a certain minimum amount of resources must be supplied in order for the child to complete growth and development, and advance to the next state. This design simplifies calculations of the woman's fitness returns as the child's probability of survival to maturity (and future fitness potential) is better described as a function of both the child's quality and age, rather than simply age (Lummaa & Clutton-Brock, 2002). All children produced over the course of the modelled time period remain dependent in that the oldest possible child will only be five years of age at the end of the modelled time period. Post-weaning children were assumed to require an equal amount of resources regardless of age. In addition, I made the simplifying assumptions of zero risk of infant and child mortality and miscarriage.

Pregnancy state. This state variable serves as a tracker for the pregnancy status of the woman. Her possible pregnancy states were: 1) not pregnant, 2) in gestation (locked for nine months), or 3) caring for a pre-weaning child (24 months). I assumed the focal female to be experiencing postpartum amenorrhea while breastfeeding her pre-weaning child, and thus, there was a constraint in place to prevent her from becoming pregnant during this period. This variable does not carry information that distinguishes between the scenarios where abstinence is optimal vs. she failed to conceive.

2.2.3. Fitness functions, decisions, and dynamic programming equation

The fitness function was defined as an adult female's expected reproductive success from time *t* to *T*, given the states the organism was in at time *t*. I define

$$F\left(E,\vec{k},t\right) = maximum\ expected\ fitness\ return\ from\ reproduction,$$
$$given\ E(t) = E\ and\ \vec{k}(t) = \Sigma\, k_i(t)$$

Decisions to attempt reproduction were based on the trade-off between maximizing offspring production and risk of starvation of the mother when the number of dependents exceed the female's capacity for care-giving. Fitness values associated with the possible behaviors for the woman, attempt pregnancy vs. abstinence, were evaluated indirectly after taking into account fecundability, the probability of becoming pregnant per ovarian cycle where an attempt was made (Weinstein et al., 1990). For the purposes of my model, I modified the definition of fecundability to include the probability of successfully maintaining a pregnancy past the first time step (one month). The fitness functions for the decisions to attempt pregnancy and to abstain were denoted as $V_p\left(E, \vec{k}, t\right)$ and $V_a\left(E, \vec{k}, t\right)$, respectively, and were given by

$$V_p\left(E, \vec{k}, t\right) = \lambda F\left(E', \vec{k}'', t+1\right) + (1-\lambda) F\left(E', \vec{k}', t+1\right)$$

$$V_a\left(E, \vec{k}, t\right) = F\left(E', \vec{k}', t+1\right)$$

E' denotes the energy reserve status of the focal female in the next time step, $\vec{k}'$denotes her new kin state without the addition of a new pregnancy event, $\vec{k}''$ denotes the different kin state the female would assume if she successfully conceives a child. As previously discussed, the kin vector tracks both the number of dependents the woman has and the quality of these kids. Thus, in the scenario where the mother did not become pregnant, her kin state will be updated to reflect changes in the quality of her offspring.

At the end of the modelled time period, the focal female will be 26 years of age. She has the potential to produce more offspring in her remaining life, and this ability is estimated here by her condition at that time (i.e., age 26) as a means of anticipating what might happen to the female after the model terminates. The terminal (end of modelled time period) fitness of the focal female can therefore be expressed as a function of her energy reserves and existing kin structure at time *T*:

$$F\left(E, \vec{k}, T\right) = \Phi\left(E(T), \vec{k}(T)\right)$$

The optimal strategy can now be found by computing the dynamic programming equation

$$F\left(E, \vec{k}, t\right) = (1-\gamma) \max_{f} \left\{V_p\left(E, \vec{k}, t\right), V_a\left(E, \vec{k}, t\right)\right\}$$

where the focal female adopts the behavior that was projected to give her the highest expected fitness return, provided that she survives to the next time step with probability $(1-\gamma)$.

2.2.4. Model assumptions

In formulating this model, a number of simplifying assumptions had to be made due to limitations in computing power, to avoid the risk of generating incomprehensible results from an overly-complicated model, and also simply because no model is capable of capturing the full richness and intricacies of biological systems (Clark & Mangel, 2000). Model outputs must always be interpreted in the context of its assumptions. Here, I reiterate all the assumptions I made regarding the modelled human female reproduction process. The validity of these assumptions is considered in more detail in the discussion section of this chapter.

1. The focal female experienced constant background mortality and fecundability throughout the modelled time period.
2. Risk of pregnancy loss was negligible after the first month post-conception. Child mortality was also negligible.
3. No assumptions were made regarding the fate of the children should the mother die of starvation during the modelled time period – the female's total accumulated fitness is determined by her states right before her death.
4. The focal female does not suffer from pregnancy-related mortality risks.
5. The focal female was not required to maintain a minimum energy reserve in order to conceive, meaning that she was either dead, or alive and fully fertile, but does not experience secondary amenorrhea (the cessation of ovarian cycles as a result of physical or psychosocial stress independent of a previous pregnancy).
6. Offspring were not distinguished as being male or female.
7. The focal female experienced an obligatory two-year post-partum amenorrhea, during which she is not able to become pregnant, regardless of her energy reserve status during that period.
8. The focal female received additional fitness if she maintained a certain high reserve at the end of the modelled time period.

2.2.5. Computation details and model outputs

DSVMs are solved (i.e., optimal strategy is derived) via a backward iteration process analogous to working through a *choose-your-own-adventure* book backwards and always knowing the best option at each stage due to the benefit of hindsight. Formally, the analytical procedures taken to solve a DSVM are as follows:

1. A terminal fitness function for end of time ($t=T$) is set for all values of state X ($X_1 \ldots X_n$).
2. Based on pre-determined dynamics and fitness functions, calculate fitness gains for all possible decisions for state X_1 at the previous time step ($t=T$-1).
3. “Select” the decision that returns the highest expected fitness for each state and update maximum expected fitness value for state X_1 at $t=T$-1.
4. Repeat for states X_2 through X_n.
5. The process repeats itself as the current/T-1 state becomes the future/T state.

The code to execute the above commands was prepared in Python. An *n*-dimension matrix is obtained when the DSVM is solved, showing optimal strategies for all values of every state variable (n) in each time period. The obtained decision matrices were then handled using R statistical software version 3.2.2 (R Core Team, 2015) for further analyses and visualization.

A few points should be emphasized regarding model outputs. First, the focal female’s decision to attempt pregnancy might not necessarily translate to an actual pregnancy event, because fecundability is not 100%. The optimal strategy is solved with this uncertainty taken into consideration (see dynamic programming equation described above). Second, decision matrices provide a guide for optimal behavior if and when a woman finds herself in the specific combination of states listed on the matrix. These matrices should not be read in a continuous manner and provide no information on how a woman should behave over time. The decision matrices also provide no information regarding the fate of the individuals adopting these decisions, i.e. adopting the optimal strategy does not automatically mean you and your lineage is then going to prosper. To study the performance of a population forward in time, decision matrices solved by the DSVM would be used in a Monte Carlo Markov Chain simulation. A population would be simulated and parameters of interest (e.g. energy reserve/health state, fertility rate, interbirth-interval) could be tracked over time.

2.2.6. Sensitivity analyses

Sensitivity analyses refer to methods that explore the effects of changes in parameter values on model outputs. This allows us to identify “important” parameters on which model predictions may be disproportionately relying. I investigated the effects of variation in resource availability, number of helpers at the nest, and fecundability on a woman’s reproductive decision making. Details of functions and parameter values used in these analyses are provided in Appendix B.

Number of helpers. I varied the number of helpers available (0-3) to the focal female and investigated the extent to which her reproductive decisions change across the state space. These values were chosen to simulate the situations where the female is on her own or is receiving help from other people, such as a male partner or a sister. I predicted that the female would begin reproducing at a younger age and attempt another conception sooner after she weaned a child when there are more helpers at the nest.

Resource availability. Resource availability was formulated here as the product of seasonal resource abundance and stochasticity. This meant that, for example, it was possible to have a relatively bad foraging day even when food is abundant. These two aspects were investigated via manipulations to the function describing seasonality and a random number generator that simulate “luck”. I predicted that the female would begin reproducing at a younger age and attempt another conception sooner after she weaned a child with increasing resource abundance and increasing certainty of foraging returns.

Fecundability. Fecundability was defined as the probability of conceiving a baby per ovarian cycle where attempts were made (Weinstein et al., 1990). In this model, I adopted a more refined definition: the probability of a live birth per ovarian cycle where attempts were made (Weinstein et al., 1990). This is commonly referred to as effective fecundability (Weinstein et al., 1990), and it depends on a woman's physiology and frequency of intercourse. Human females have been estimated to have a peak effective fecundability of ~30% around age 25, and decline after that due to changes in physiology and coital behavior (Weinstein et al., 1990). Low effective fecundability has been attributed to high risk of spontaneous abortions in the first month following conception (Holman & Wood, 2001), with the risk decreasing rapidly in the following months (Baird & Strassmann, 2000; Holman & Wood, 2001) This low probability of having a successful pregnancy event has been hypothesized to be a mechanism allowing women to reinvest limited resources in herself (and existing offspring) and wait for another reproduction opportunity either when environmental conditions or the quality of the fetus were subpar (Baird, 2009; Kozlowski & Stearns, 1989). In formulating this model, I began with a low default fecundability value and asked the hypothetical question: what if human females were to have higher effective fecundability? I predicted a decrease in the frequency of pregnancy attempts with increasing effective fecundability, due to the increased probability of actually getting pregnant per attempt.

2.3. Results

The analytic solution of the model consisted of roughly a million data points entered into a six-dimensional object. For simplicity, I present a small subset of the data extracted under two distinct family contexts where the woman 1) has no dependents and 2) her previous child just weaned. These two family contexts were chosen to mirror previous modelling attempts that seek to better understand the ecological correlates of the timing of first birth and birth spacing (Mace, 1996, 1998; Thomas et al., 2015). I investigated optimal decision making of a young female in these situations, given a range of extrinsic conditions: 1) access to help; 2) resource abundance; 3) degree of stochasticity in resource availability; and hypothetically, 4) increased effective fecundability. These analyses were carried out by manipulating one variable at a time while holding the rest constant. I focused on the qualitative differences in decision-making across the range of scenarios rather than quantitative ones (i.e. general trends as oppose to picking on particular parameter values), as the parameters need to be more fine-tuned to achieve meaningfully-accurate quantitative predictions.

2.3.1. Number of helpers

The model predicted that it would be optimal for the woman to attempt pregnancy for most of the state space when she did not have access to helpers, the results being very similar for both family contexts under consideration (Figures 2.1A & 2.2A). When there was some help available, the woman should attempt pregnancy but only when her reserves were low (Figure 2.1B). Age of the female influenced pregnancy-attempt decisions in that pregnancies appear to be less desirable in older ages but only when help was scarce (Figures 2.1A&B, 2.2A). The female was predicted to abstain when at least some help was available (Figures 2.1C&D, 2.2B&C&D).

2.3.2. Resource abundance and stochasticity

Stochasticity refers to the degree of irregularity in obtaining resources, in other words, the degree of uncertainty in foraging returns. For all the intrinsic conditions considered (age, energy reserve, family structure), stochasticity does not play a big role in the female's reproductive decision making, as the decision space looked extremely similar across the variation in uncertainty (Figures 2.3 & 2.4).

Model predictions obtained for various levels of resource abundance is fairly similar to that of varying access to helpers. The woman should attempt pregnancy under impoverished conditions (Figures 2.5A & 2.6A). The optimal strategy switches to that of abstinence in all other environments (Figures 2.5C&D, 2.6B&C&D), with the exception of the scenario where the female who does not have any dependents find herself in a low resource abundance situation, in which case her optimal decisions were dependent on her age and energy reserve levels (Figure 2.5B).

2.3.3. Fecundability

The decision space for all the fecundability levels considered, across the female's age, energy reserve and both family context, do not appear to be significantly different from each other under visual inspection (Figures 2.7 & 2.8).

2.4. Discussion

In this thesis chapter I set out to model optimal decision-making over the course of a woman's reproductive life span. The ultimate goal of the project is to create a tool that would be of interest to theorists and practitioners alike. A successful DSVM-based program would be a great asset to evolutionary anthropologists for the study of selective landscapes that shape human reproductive behavior, as well as to public health professionals for the evaluation of maternal and child health programs. This thesis chapter provided the theoretic backbone for such a goal, along with a preliminary formulation of a DSVM attempting to model optimal human reproductive behavior to demonstrate the potentials of such analyses and the difficulties ahead.

Dynamic state variable models solve for optimal behavior by evaluating expected fitness returns for all possible combinations of all possible values of all of the state variables. This task can be extremely RAM-demanding. Thus, one of the foremost difficulties encountered when constructing DSVMs is limitations in computing power, making it the primary reason for the shortening of time span in this model. This phenomenon was coined the “curse of dimensionality” (Clark, 1991; Clark & Mangel, 2000): although one could write DSVMs for complex decision-making problems, practical limitations will be reached rapidly as the number of state variables increases. Computation requirements go up roughly in magnitudes of n^m, where m is the number of state variables and n is the number of possible values assigned to each state variable. As a result, state variables have to be chosen with care, and only those essential to the problem at hand will be included. This is when modelling becomes more art than science (Shannon, 1975), in the quest to find the smallest set of biological rules sufficient to describe the system of interest. The blind desire to create ever more complex models with the hopes of capturing the “real complexities” of nature will only result in models that, even if our computers are capable, our brains cannot comprehend (Clark, 1991).

The current version of the model concerns a young woman’s monthly reproductive decisions over the course of six years. Decisions on whether to attempt pregnancy or abstain were made based on expected future fitness values after considering her current energy reserve and family structure. This model differs from previous attempts to study human reproduction under the same theoretic (life history theory) and technical (DSVM) frameworks in a number of ways. First, my model includes the mother’s biological status as one of the state variables while previous models considered her wealth instead. I used the blanket-term “energy reserve” in my formulation as a surrogate for a woman’s general condition. Energy can easily be conceptualized as representing a combination of the woman’s health and psychosocial wellbeing, or even wealth with appropriate parameter modifications. This is an important step forward not only because energy is known to be a crucial regulator of women’s reproductive function (Ellison, 1994, 2008), but also a variable that is useful across discipline boundaries from anthropology to public health. Second, my model functions on a monthly time scale as opposed to yearly, the practice adopted by other researchers (Beauchamp, 1994; Mace, 1996, 1998; Thomas et al., 2015). This design allowed for the examination of short-term behavior at the expense of the ability to follow the female over her entire reproductive career. I made the decision to implement the former out of practical considerations. A higher resolution of a female’s energy (health) state over a shorter period of time would be more helpful to public health practitioners. From a theoretical perspective, this is also a biologically accurate representation of women’s physiology as most women ovulate monthly, and thus reproductive decisions also need to be made on a monthly basis. Another important distinction between my model and others is that my modelled women make decisions on whether to attempt pregnancy (i.e., engaging in intercourse) and not whether to become pregnant. This was a necessary modification as it is a known fact that fecundability (probability of conception per ovarian cycle where an attempt was made) is in fact quite low in humans, and optimal, monthly, decision making should only be solved with consideration of this variable.

The results suggest that the optimal reproductive strategy should shift from that of attempting pregnancy to abstinence as environmental conditions improve (increasing resource availability and access to extra help). Stochasticity in resource availability and fecundability did not appear to influence how the female should behave. The same trends were obtained for both the family contexts under consideration: first birth was delayed and birth spacing was prolonged when environmental conditions improved. These results are surprising and counterintuitive. I had predicted opposite trends for the environmental contexts of resource and help availability, decreasing stochasticity (a more stable environment) would be more suitable for reproduction, and decreasing frequency of pregnancy attempts as fecundability increases. Next, I propose and discuss two possible explanations for these results: 1) a direct result of inappropriate simplifying assumptions, or 2) abstinence may be an adaptive behavior under favorable environmental conditions, as interpreted in the context of the model assumptions.

2.4.1. Validity of model assumptions

A number of simplifying assumptions were made in formulating this model. Results should be interpreted in the context of these assumptions, some of which may be more influential than others. Here, I discuss the potential effects of all the assumptions on model outputs, and proposed revisions where necessary.

The assumptions of constant background mortality and effective fecundability should not influence model outputs qualitatively (i.e., changing the direction or shape of trends). While these parameters do vary over a woman's life time, during the relatively short duration of the modelled time period (six years), changes in mortality risk and fecundability are usually minimal to a young female (without influence from external factors such as famine and war). The model was, however, built to handle mortality risk and fecundability as functions of time (woman's age) and/or pregnancy status in the case of mortality. Thus, these assumptions can easily be relaxed as necessary when modelling women in different life stages, such as nearing menopause, or considering populations where pregnancy-related mortality risk is a public health concern. These parameters could be further formulated into being functions of the woman's energy states (or other intrinsic factors of interest, such as disease status) if high resolution data becomes available. The lack of risk of pregnancy loss should not change the model outputs in a qualitative manner either, as the majority of the risk was taken into account when parameterizing effective fecundability. The assumption of zero child mortality, however, was a limitation on both theoretical and practical fronts. Child mortality was considered implicitly by discounting offspring fitness returns under sustained resource deprivation, but the child will remain an energetic burden to the mother unless everybody starves to death together. In other words, children will never "disappear" from the kin vector. Moreover, child mortality risk is, like pregnancy-related mortality risk, an important health statistic, and thus should be formulated into the model before it can be meaningfully applied. Programming strategies to overcome this limitation are currently being explored.

My model did not differentiate the focal female's offspring as being male or female. This was an inevitable simplifying assumption, as I would need to add an additional axis to the kin vector to be able to track offspring sex (and find extra RAM space for this addition). The model would also need to be scaled up to the population level, as optimal offspring sex ratio and optimal investment into the different sexes would depend on what the sex ratio at the population level is at each point. Treating offspring as being completely equal in terms of cost to produce and potential fitness return might be inaccurate from a theoretical standpoint, but whether the differences are significant enough to justify consideration in practice warrant further discussion. In Chapter 3, I explore this proposition with data on the costs of producing sons *vs.* daughters in two populations of different ethnic and social economic backgrounds.

Two assumptions were made in direct relation to the focal female's energy reserve state. First, that she does not experience secondary amenorrhea and second, that she is forced through an obligatory two-year post-partum amenorrhea (PA) following each birth. Both of these phenomena have been known to be highly regulated by a female's energy reserves (Jasienska & Ellison, 2004). Imposing a set/minimal PA (or IBI) on the modelled female has been a common practice, a simplification based on field observations of IBI in small-scale societies (Mace, 1996, 1998; Thomas et al., 2015). I will attempt to relax this obligation in a future development of the model, allowing PA duration to varying depending on the female's energy reserves. Precise quantifications of the female's energetics during PA would be of great asset to the accurate formulation of the dynamics that describe the transition from PA to regular ovarian cycling.

A minimum "functional" energy level will be added to a revised version of the model to represent the threshold energy reserve that the female must maintain for ovulation to take place. In other words, women whose energy reserves fall below this critical threshold would be alive but would not be capable of becoming pregnant. An additional status identifier, secondary amenorrhea, will also be added for the purposes of distinguishing between women who are abstaining and those who are unable to give birth. This added constraint has the potential of altering model outputs in a significant manner, particularly in the regions bordering the threshold (i.e., low energy reserve areas) (Day & Rowe, 2002). However, these changes are unlikely to be reflected in the decision matrix for the short time frame that is modelled. Other than the addition of a band at the bottom of the matrix where women are in secondary amenorrhea, I do not expect the presence of a threshold to have significant influences on the current decision matrices even if the woman's entire reproductive career is to be modelled. The importance of this threshold will be revealed when these matrices are put through forward simulations, as there will now be women who are unable to become pregnant regardless of what the optimal decision might have been. Further, I expect a previously-absent effect of age to be revealed as it takes time to save up resources to meet the threshold.

The way the fitness functions were formulated could have contributed to, and provide an explanation for, the counter-intuitive results of females in good conditions abstaining and those in poor conditions keen on attempting pregnancy. There were two means by which the focal female could gain fitness under the current regime: 1) producing offspring, and 2) achieving high energy reserves at the end of the modelled time period (fitness gain via this method is equivalent to that of having one child), the best case scenario being the achievement of both. In the latter scenario I assume that females capable of maintaining high energy reserves were of high quality and were expected to have high survival prospects in the long term. Thus, they can invest into high-quality offspring at a later time after saving up resources (see Lalonde & Roitberg, 1992). The females under bountiful environmental conditions could have been aiming for this latter case of burden- and starvation-risk-free form of "fitness", while females in poor conditions were "encouraged" to attempt to produce offspring (and suffer increased risk of starvation due to depletion) because they were unlikely to attain high energy reserve anyway. The rationale for this particular set up of the fitness functions was based on the fact that the focal female is only going to be 26 years of age at the end of the modelled time period. It was necessary to consider the reproductive potentials of females beyond the modelled time period, because the alternative would mean that they were unable to accumulate fitness past that point. Moreover, banking resources and delaying reproduction is a plausible alternate strategy (vs. reproducing at maximum rate as soon as resources become available) that I must present to the modelled female (Grand, 1999; Low et al., 2002). The implicit assumption made here was that the banked resources were to be invested in a future reproductive event. Unfortunately, there is no way of knowing if this was to be the case, unless we manage to model the female's full reproductive career. I am confident that it is, however, because the value of banked resources diminish, and mortality risk increase, as the female ages, eventually to a point where it no longer payoff to be saving. Thus, the abstain-and-save strategy that was predicted to be optimal under consistently good environments is only expected to be optimal before certain age.

Lastly, one aspect of the fitness function requires attention when revising the model: fitness returns were tallied at either at the end of the six-year modelled period or when the female dies of starvation, but the two scenarios were not differentiated. In other words, the focal female was rewarded if she maintains a high energy reserve, but not taxed if she did not. A woman who has a pre-weaning offspring but died of starvation would have been given the same fitness score as a low energy reserve female who survived till 26 with the same pre-weaning offspring. There were two inaccuracies in this formulation: 1) the female has the potential for future reproduction as long as she stays alive, and 2) a young child whose mother died would probably have a low chance of survival depending on the population in question (Thomas et al., 2015). This could drive the result where females under poor conditions were attempting to leave behind any sort of offspring in order to obtain a small fitness return. In a revision of the model, the fitness functions will be refined such that the female suffers a discount on expected fitness if she were to starve prematurely. Sensitivity analyses could also be performed on the effects of child survival prospects following the death of the mother on her reproductive behavior (e.g. whether she would adopt high-fertility-high-starvation-risk behavior if she knew that her child would survive just fine without her).

2.4.2. Slow reproduction and low fertility as an adaptive behaviors

The shift from attempting reproduction under poor environmental conditions to abstinence as conditions improve may appear to be counterintuitive behavior at first glance, however, this behavior has actually been observed, experienced, and studied by many. It closely resembles the reproductive patterns seen in a post-demographic-transition population, and it has been puzzling evolutionary anthropologists for a long time (Borgerhoff Mulder, 1998; Vining, 1986). The demographic transition (DT) first took place in the late 19th century in Western societies, and is still ongoing in parts of the world today (Lee, 2003; Lesthaeghe, 2010). The key feature of DT is the shift from a high-fertility-high-mortality situation to one of low-fertility-low-morality, with the decrease of mortality risk leading the curve. In addition to the overall decrease of fertility, a negative relationship between "wealth" and fertility was often observed in post-DT populations (Vining, 1986). This phenomenon was intriguing for the precise reason that its beginning also marked the peak of the industrial revolution, where possibly for the first time in human evolutionary history resources were stably abundant, sanitary conditions were improving, and background mortality risk was low.

Demographers, economists, and ecologists took interest in the DT problem from a proximate perspective. The first stage of DT, mortality decline, was commonly attributed to the decreasing prevalence of infectious diseases brought about by improvements in the quality and stability of nutrition, and advances in preventive and therapeutic medicine (e.g., the invention of vaccines in the late 18th century) (Friedlander et al., 1999; Lee, 2003). Western Europe was the first to experience the second stage of DT, fertility decline, at the turn of the 20th century. From an economics perspective, the changing labor market structures during the DT (from labor intensive to education based) raised the cost of children and also diminished their contribution towards household productivity, leading to a shift in incentive from investment into offspring quantity into quality (Lehr, 2009). In addition, decreasing mortality meant children were more likely to survive until adulthood and thus parents could reduce fertility and still achieve the desired family size (Lee, 2003). Taking a population ecology approach, it was thought that population growth in developed countries were regulated by density-dependent processes: urbanization drove socioeconomic developments which increased the cost of producing offspring greatly and in turn reduced fertility (Bauch, 2008; Bettencourt et al., 2007). This process was thought to be sped up due to information and technology shared between countries (Dang & Bauch, 2010).

The evolutionary explanations that emerged to explain changes in reproductive strategies associated to the DT can be broadly separated into the maladaptive and adaptive camps (Borgerhoff Mulder, 1998). The main supporters of the maladaptive camp posit that reduced fertility was a lagged response to our novel environment. Specifically, the emergence and spread of cheap and effective birth control technology lead to the maladaptive decrease in fertility rates. In support, it was shown in a contemporary population that, without contraception, wealthier males will out-reproduce their poorer counterparts (Pérusse, 1993). This argument, however, neglects the fact that the earliest decrease in fertility rates observed in Western Europe predate the wide-spread use of birth control technology (Borgerhoff Mulder, 1998). Adaptationists, on the other hand, argue that reduced fertility represent an adaptive shift from investing into offspring quantity towards quality for the maximization of fitness over multiple generations. This is achieved by focusing investment into a few offspring to ensure their survival and high fitness potential, as opposed to investing little into a lot of offspring in the hopes that some of them will survive (Boone & Kessler, 1999; Chisholm et al., 1993). Lineages consisting of high-quality individuals were thought to be more fit over time as these lineages will be better able to withstand irregular stochastic events such as natural disasters and famines, and would also have lower inter-generational variation in reproductive success (Boone & Kessler, 1999; Chisholm et al., 1993). This key distinction between the maladaptive *vs.* the adaptive camps may lay in whether or not human reproductive strategies are plastic enough to be able to respond quickly to changes in environmental contexts and selective pressures in the past couple of generations.

Despite the DT phenomena being well documented, theorists have rarely succeeded in generating the negative correlation between “wealth” and fertility using mathematical models (Borgerhoff Mulder, 1998). In other words, the precise conditions and mechanisms under which DT took place remains elusive. What is clear was that “wealth” is a complex socioeconomic construct, and may involve more than simply tallying the amount of resources a person possesses. For instance, wealth begets wealth, and indeed, some of the few examples of investment into resource generation (as opposed to offspring production) being the preferred strategy came from models where wealth accumulated early in life (or in a lineage) were allowed to snowball over time (Hill & Reeve, 2005; Rogers, 1995). Another one of the obstacles to modelling DT could be the technical difficulties preventing the formulation of multi-generational models which also included detailed characterization of environmental and individual states within each generation. This meant that tracking of long-term reproductive success is often traded off against the ability to closely examine the impacts and interactions of factors of interest.

My model, with all its current limitations, may help further our understanding of DT processes as it has led to the unintended discovery of a unique set of conditions that may result on DT-style reproductive strategies. The key lies in my model assumptions. According to my current model formulation, optimal behavior shifts from one of attempting pregnancy to abstinence with improving environmental conditions when the following conditions are also met: 1) negligible child mortality, 2) children being costly to produce and represent a long-term locked commitment, 3) mothers invest equally into offspring, regardless of their sex, 4) fitness potential of offspring were determined based on quality of the individual but not sex, 5) females with very low energy reserves were receptive (i.e. they were rarely affected by secondary amenorrhea), and lastly, 6) should the mother produce more offspring than she could care for and she starves to death as a result, the fitness potential of her children will be greatly discounted, but not reduced to zero.

Some of these conditions were already known to be drivers of DT in 19th century Europe. For instance, the aforementioned decreasing mortality risk in the first stage of DT, particularly in children, and the increasing costs of raising children. Although improved gender equality has been observed to parallel economic and demographic development (e.g., Lagerlöf, 2003), the direct implications of narrowing discrepancies between preferential investing into sons vs. daughters, and their relative contributions to the mother's fitness, were rarely considered in DT studies.

Secondary amenorrhea was well-studied among athletes (Loucks & Horvath, 1985; Nichols et al., 2006) and women suffering from eating disorders (Selzer et al., 1996) and polycystic ovary syndrome (Baird et al., 2012), but had rarely been measured in the general population. One study conducted in Denmark found that the prevalence of secondary amenorrhea was around 5% (women in lower SES being more susceptible) and its effects were usually reversible within a couple of months (Münster et al., 1992). Unfortunately, the earliest, and only other record, on the prevalence of secondary amenorrhea in the general population was in a post-DT Swedish population (Pettersson et al., 1973) which showed similar results. Although there are no data available regarding the trends of secondary amenorrhea over time, it would be conceivable for it to be one of decreasing prevalence under improvement in overall nutrition and health (although potential increases in psychosocial stress may counter some of the positive effects of improving nutrition).

Most studies of how children were affected by the death of their mother were conducted in impoverished populations (Braitstein et al., 2013; Moucheraud et al., 2015; Ronsmans et al., 2010), or retrospectively inferred from historic data (e.g. Pavard et al., 2005). These all point to a drastically elevated mortality risk in orphaned children under the age of two. In contrast, in contemporary, developed nations (post-DT), while children do suffer from the death of a parent, they rarely die as a result (Li et al., 2014). Thus, the weakening of the effects of a mother's death on the survival of children appeared to be a characteristic of post-DT populations. Advances in public health and social support networks to help people through difficult times (women in secondary amenorrhea, orphaned children) might have played an important role in the progression of DT.

Thus, under the contexts of the previously discussed assumptions, abstinence can be seen as an adaptive behavior in a post-DT population. In order to strengthen this claim, one of the biggest obstacles remains the concern that there was no way to tell whether the resources saved up by the female under good environmental conditions were actually going to be invested into making better-quality offspring at a later time, beyond the modelled time period. Ideally, I would build a model that allows me to follow the female over her entire reproductive career, and multiple generations beyond for the tracking of long-term fitness. Although I am prevented from building such a model at the moment due to technical difficulties (RAM limitation), as previously discussed, I predict with confidence that the female in a 30-year model would eventually begin to invest in offspring as the value of banked resources diminish over the course of her life. Interestingly, empowering women and allowing them to invest in herself (e.g., via education) rather than only into producing offspring is considered to be one of the two major driving forces of DT, alongside economic development (Becker et al., 1990; 2010). This phenomenon appears to have been captured in my model, as saving up resources is conceptually similar to investing in oneself.

2.4.3. Future developments and applications

In this thesis chapter I presented a DSVM for the optimization of reproductive strategy in a young human female. After implementing the previously discussed revisions (addition of a functional energy level and child mortality), other utilities of the model can then be explored. Firstly, the sensitive analyses described in this chapter should be repeated to investigate whether model outputs will be modified. In particular, it would be important to perform a sensitivity analysis on the terminal fitness function itself, for the analysis of the degree to which the current high-energy-reserve reward influences the woman’s behavior. Then, I would adopt a factorial design when conducting the sensitivity analyses, to assess whether the factors considered in this current analysis interact to influence reproductive behavior. Perhaps then the intriguingly absence of effect by variations in fecundability and stochasticity in resource availability will be revealed. It is conceivable that these two factors only play significant roles under environments of low resource availability not detected under the more affluent, default settings of the current analyses. Otherwise, it would mean that these factor do not, in fact, affect reproductive behavior in significant ways. I would also prepare the model for the study of women in different age groups, such as nearing menopause. This would involve finding appropriate parameter values and formulating new fitness functions. End-of-life behavior has been a popular area of research within behavioral ecology and anthropology, and a better understand of women's behavior and health at older ages would provide insight into the care of menopausal women. Abundant opportunities lay in the model's ability to "ask" hypothetical questions, or simulate experiments that researchers cannot conduct in the real world. Studying alternative realities could shed light onto why particular traits persist and not others. One such question that would be of great interest to evolutionary anthropologists would be: what if female ovarian cycles were prolonged (e.g., ovulate once every four months)? Presumably, that would increase the opportunistic cost of forgoing pregnancy events and potentially result in an overall increase in pregnancy attempts, even when it is risky to do so.

Once the decision matrices are in place, I would use them in forward simulations in order to study women's behavior over time. As previously explained, decision matrices alone will not allow us to get at an individual's reproductive traits, such as inter-birth interval, or changes in intrinsic conditions such as the focal female's energy reserves over time. All that the decision matrices show is optimal decision in a very particular context (age, energy reserve, and other extrinsic factors), but not how the female's states change over time as she is executing these decisions one by one. Simulations not only will allow theorists to study what happens to a population under different environmental conditions, it would also allow public health practitioners to better prepare for when those conditions become reality, and also as a tool to evaluate maternal and child health programs. Competing approaches such as improving environmental conditions on a population level vs. focusing resources on subgroups that are particularly vulnerable can be compared and contrasted, and critical time frames when an intervention may/could be most effective can also be identified (Målqvist et al., 2013). Program evaluations not only allow policy makers to devote limited resources to meaningful causes, they could also prevent potential, unintended, consequences. The goal of health scientists and practitioners is to improve the health and wellbeing of humans. However, natural selection results in traits and functions that maximize reproductive fitness, regardless of the effects those traits have on health and wellbeing. Public health interventions should therefore be mindful of unintendedly increasing fertility, leading to maternal depletion and worsening child health outcomes, defeating the purpose of care programs. Potentially, the key to achieving this is to “give value” to the mother’s own condition: to empower women.

To achieve the ultimate goal of turning the model into a tool for scientists and practitioners, I will seek further collaboration with programmers. The program would include a guide to help users choose parameter values appropriate for their population and purpose. Solving of the model and generation of forward simulations will be automated. The model need not be scaled up to 30 years for the tool to be useful. In fact, care programs are rarely planned for more than a couple of years (Bhutta et al., 2013). Having a high resolution of individual behavior and energy reserves (health status) over a shorter period of time is arguably more helpful from a practical standpoint than ones that only loosely track the modelled individual over a long time span.

2.5. Tables

Table 2.1. Symbols and their usage.

Symbol	Usage
T	Time state, each unit represents 1 month
T	End of time
$E(t)$	Energy reserve of focal female
m_b	Daily metabolic cost, including maintenance of somatic functions and foraging activities
m_p	Metabolic cost of gestation, or of breastfeeding an infant
p	Pregnancy counter
R	Pooled foraging returns from all helpers
ω	Proportion of resource distributed to focal female and each kid
c	Minimum energy requirement for the growth and development of a child at each time step
s	Seasonality factor
β	Probability of encountering and obtaining resource ("luck")
$\vec{k}$	Vector describing the existing family (kin) structure of the focal female
k_i	The i^{th} child of the focal female. Value represent age/quality of child
K	Total number of post-weaning dependents
γ	Mortality risk
λ	Fecundability (the probability of becoming pregnant per gonotropic cycle)

2.6. Figures

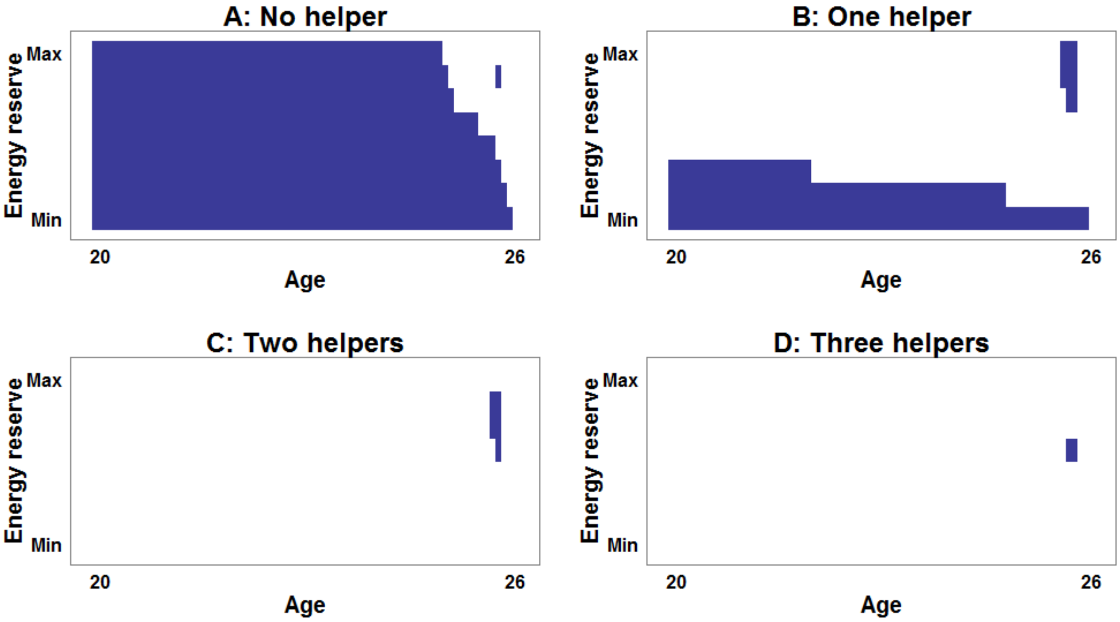

Figure 2.1. Reproductive decisions in mothers without dependents and varying number of helpers.

Decision space is shown for an individual human female as a function of its current energy reserves and age. The extrinsic conditions under comparisons were: access to A) no helpers, B) one helper, C) two helpers, and D) three helpers. The blue-colored regions indicate “attempt pregnancy” to be the optimal strategy whereas the blank regions indicate “abstinence” to be optimal.

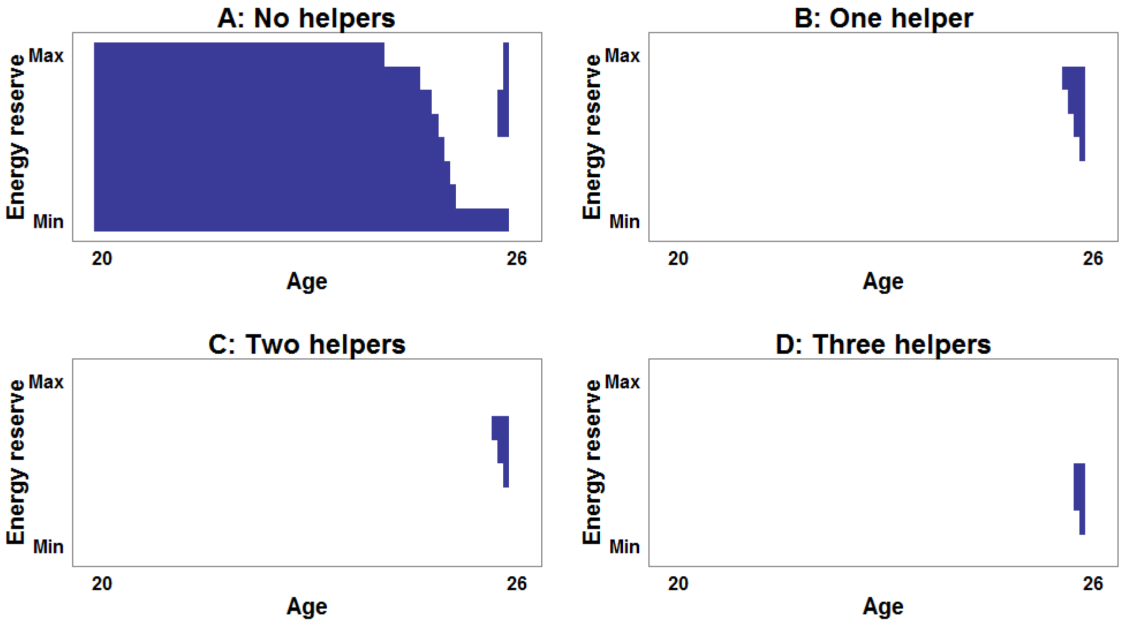

Figure 2.2. **Reproductive decisions in mothers with a weaned dependent and varying number of helpers.**

Decision space is shown for an individual human female as a function of its current energy reserves and age. The extrinsic conditions under comparisons were: access to A) no helpers, B) one helper, C) two helpers, and D) three helpers. The blue-colored regions indicate "attempt pregnancy" to be the optimal strategy whereas the blank regions indicate "abstinence" to be optimal.

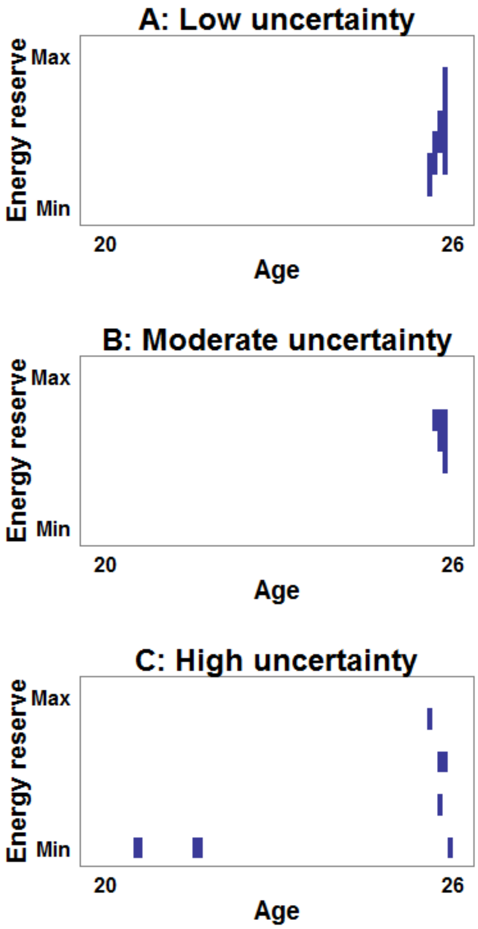

Figure 2.3. **Reproductive decisions in mothers without dependents and varying degrees of stochasticity in resource availability.**

Decision space is shown for an individual human female as a function of its current energy reserves and age. The extrinsic conditions under comparisons were: A) low uncertainty, B) moderate uncertainty, and C) and high uncertainty in resource availability. The blue-colored regions indicate "attempt pregnancy" to be the optimal strategy whereas the blank regions indicate "abstinence" to be optimal.

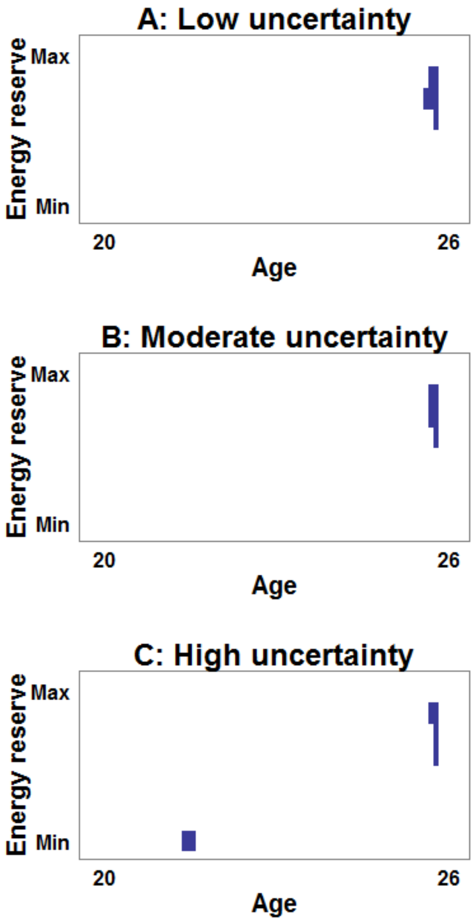

Figure 2.4. **Reproductive decisions in mothers with a weaned dependent and varying degrees of stochasticity in resource availability.**

Decision space is shown for an individual human female as a function of its current energy reserves and age. The extrinsic conditions under comparisons were: to A) low uncertainty, B) moderate uncertainty, and C) and high uncertainty in resource availability. The blue-colored regions indicate "attempt pregnancy" to be the optimal strategy whereas the blank regions indicate "abstinence" to be optimal.

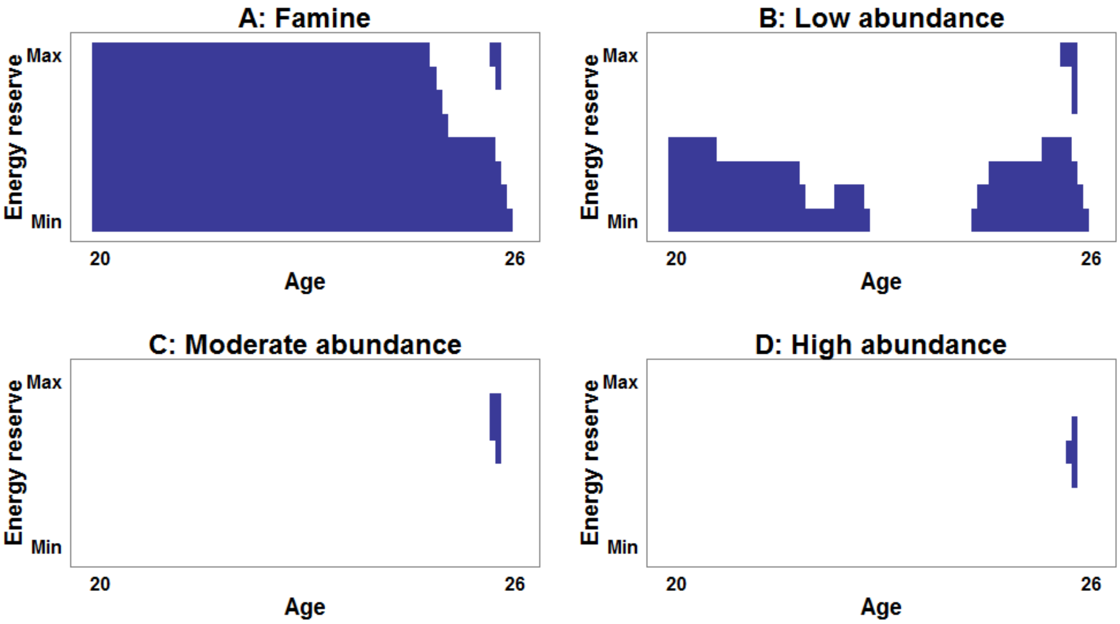

Figure 2.5. Reproductive decisions in mothers without dependents and varying degrees of resource abundance.

Decision space is shown for an individual human female as a function of its current energy reserves and age. The extrinsic conditions under comparisons were: A) famine, B) low resource abundance, C) moderate resource abundance, and D) high resource abundance. The blue-colored regions indicate “attempt pregnancy” to be the optimal strategy whereas the blank regions indicate “abstinence” to be optimal.

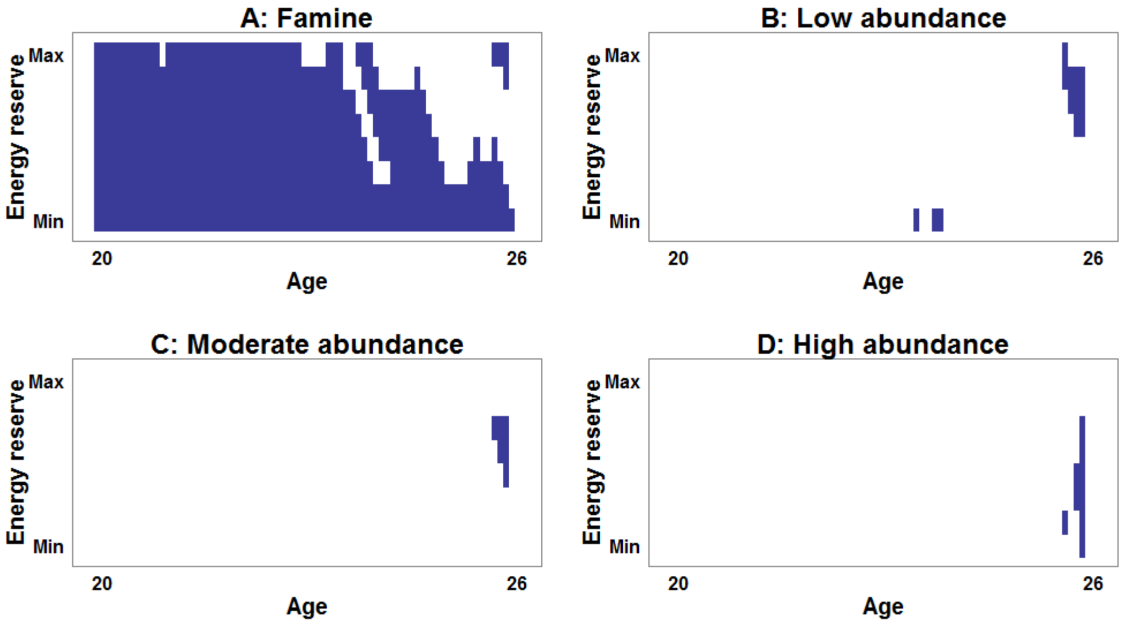

Figure 2.6. **Reproductive decisions in mothers with a weaned dependent and varying degrees of resource abundance.**

Decision space is shown for an individual human female as a function of its current energy reserves and age. The extrinsic conditions under comparisons were: A) famine, B) low resource abundance, C) moderate resource abundance, and D) high resource abundance. The blue-colored regions indicate “attempt pregnancy” to be the optimal strategy whereas the blank regions indicate “abstinence” to be optimal.

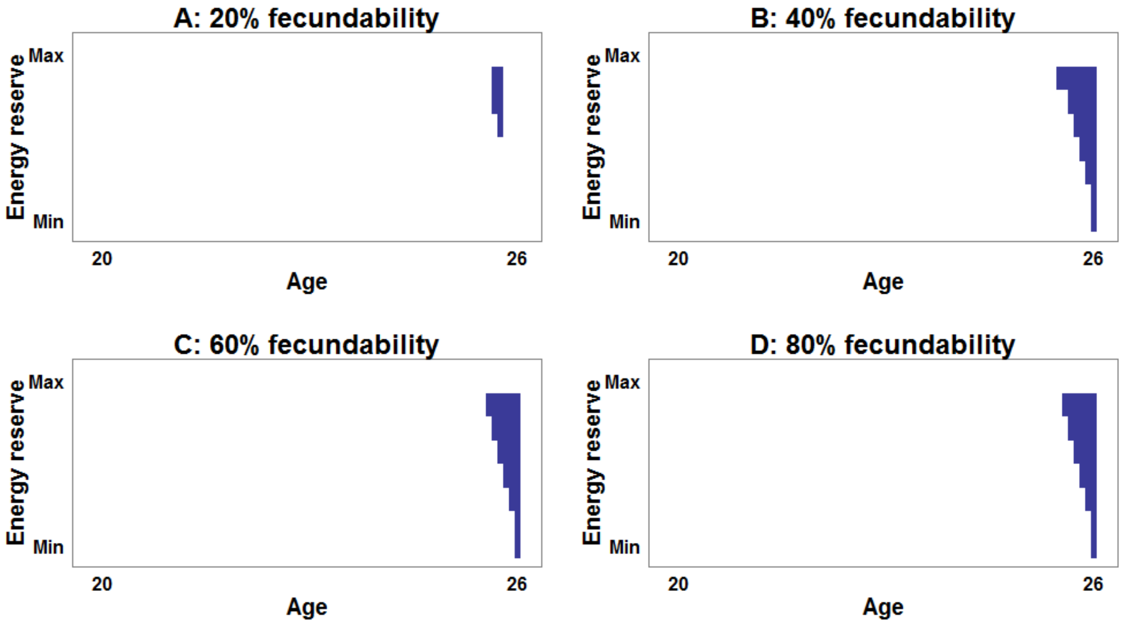

Figure 2.7. **Reproductive decisions in mothers without dependents and varying levels of fecundability.**

Decision space is shown for an individual human female as a function of its current energy reserves and age. The extrinsic conditions under comparisons were: A) 20% fecundability, B) 40% fecundability, C) 60% fecundability, and D) 80% fecundability. Fecundability is defined here as the probability of becoming pregnant, and successfully maintaining the pregnancy past the first month, per ovarian cycle where a woman attempts to conceive. The blue-colored regions indicate “attempt pregnancy” to be the optimal strategy whereas the blank regions indicate “abstinence” to be optimal.

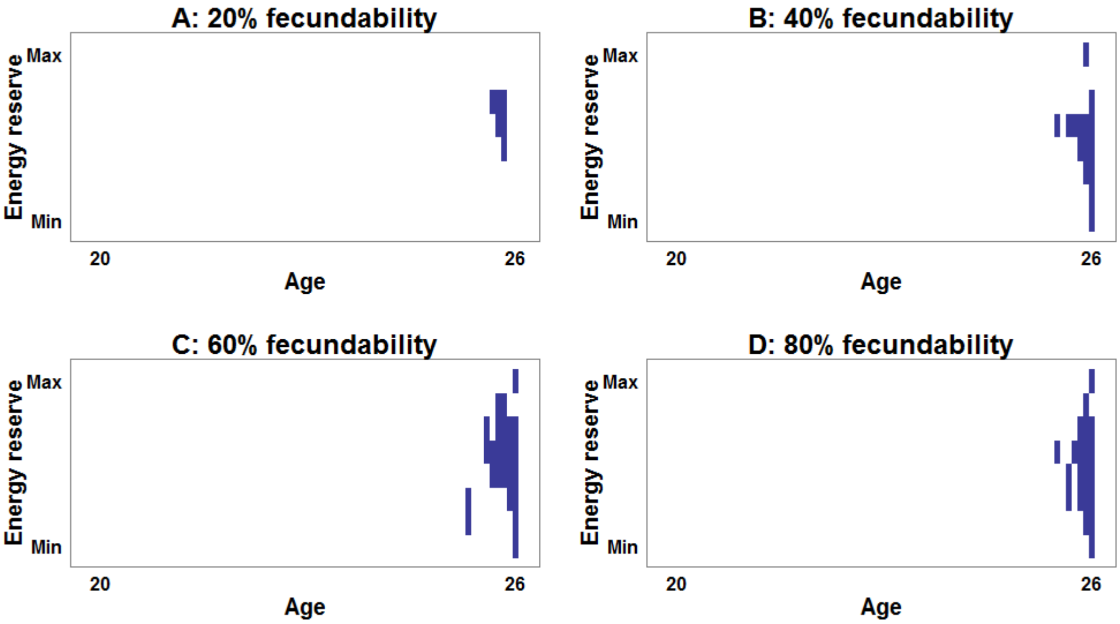

Figure 2.8. **Reproductive decisions in mothers with a weaned dependent and varying levels of fecundability.**

Decision space is shown for an individual human female as a function of its current energy reserves and age. The extrinsic conditions under comparisons were: A) 20% fecundability, B) 40% fecundability, C) 60% fecundability, and D) 80% fecundability. Fecundability is defined here as the probability of becoming pregnant, and successfully maintaining the pregnancy past the first month, per ovarian cycle where a woman attempts to conceive. The blue-colored regions indicate “attempt pregnancy” to be the optimal strategy whereas the blank regions indicate “abstinence” to be optimal.

Connecting statement

I presented a dynamic state variable model for the optimization of reproductive behavior of a young human female in the preceding chapter. In formulating this model, a number of simplifying assumptions were made. One of these simplifications was that offspring was not distinguished into sons or daughters. This was equivalent to assuming the energetic costs of carrying and raising a son vs. a daughters were the same. This may not be a sound assumption, as sons typically have a higher growth rate in-utero and are born larger than daughters. However, what this means in term of actual energetic cost to the mother has never been quantified. Whether sex of child is a meaningful determinate of maternal health thus remain unclear. This next chapter considered these issues via the investigation of duration of post-partum amenorrhea (PA) in women who gave birth to sons and daughters. Post-partum amenorrhea, the time between a women’s birth to her resumption of fertility, was used as a proxy for the total energetic cost to the mother from gestation to early post-partum period. I performed secondary data analysis on two pre-existing data sets from two populations differing in ethnic and socioeconomic backgrounds.

Chapter 3.

Influence of sex of a newborn on mother's resumption of fertility

3.1. Introduction

Gestation and child care are energetically-costly endeavors for women (Ellison, 2003, 2008; Hruschka & Hagaman, 2015; Tracer, 2002). Resources are often finite, women face trade-offs in resource allocation. The classic quantity-quality trade-off is at play during the early post-partum period. A mother could invest resources into herself for maintenance (e.g., focus on recovering from birth and preparing for the next pregnancy soon) or invest into her previous children such that their chances of survival and fitness potential can be increased, but at the expense of possibly delaying subsequent reproduction, and lowering life-time reproductive output and fitness. Closely-spaced births (i.e., inter-birth interval < 2 years), however, increase the risk of infant mortality for both the newborns and preceding siblings (Hobcraft et al., 1983; Mozumder et al., 2000). Mothers themselves may suffer from maternal depletion syndrome, which compromises their health and subsequent reproduction (Shell-Duncan & Yung, 2004; Tracer, 1991). The ability to regulate birth intervals by modulating post-partum investment is thus crucial for the mother's reproductive fitness (Blurton Jones, 1986, 1987; Lawson et al., 2012; Lawson & Mace, 2011).

Interval-birth intervals (IBI) are regulated physiologically by duration of post-partum amenorrhea (PA), and behaviorally by various family-planning practices, such as the use of contraception. PA is a period of subfertility following a pregnancy event. In populations that practice natural fertility (absence of deliberate family planning), variation in IBI is best explained by variation in PA duration (Ellison, 1994). Nursing behavior was initially thought to be the most important predictor of PA duration (Konner & Worthman, 1980). The phenomenon was previously termed lactational amenorrhea when prolactin, a hormone in control of milk production, was thought to be the principal suppressor of post-partum fertility (McNeilly, 2001). Currently, however, energy state is accepted to be the ultimate modulator of reproductive function, and the observed correlation between lactation and amenorrhea durations is understood to be a result of lactation being a major energetic stressor to the mother (Ellison, 2003; Jasienska & Ellison, 2004). The early post-partum period can thus be considered a time when the mother attempts to replenish resources used during gestation and invest in current offspring, including her newborn. The transition from post-partum amenorrhea to normal ovarian cycling represents the baseline recovery from a pregnancy event in terms of energy reserves (Ellison, 2003). Psychosocial stress (Nepomnaschy et al., 2004) and immune challenges (French et al., 2007) are also thought to affect women's resumption of fertility, but the focus of this thesis chapter will be energetics. Other factors that affect the mother's energy level during gestation and the early post-partum period include her age, access to resources and helpers, and the sex of the child.

Most mammalian species are sexually dimorphic in body size, with males being typically larger than females (Armelagos & Van Gerven, 1980). Extreme examples include phocid seals (Galimberti et al., 2007; McCann, 1981) and gorillas (Zihlman & McFarland, 2000), where males can be twice as large as females. Humans are also sexually dimorphic, though to a lesser extent. Sampling from over 70 populations world-wide, men were found to be about 15% heavier and 10% taller than women (Ruff, 1994, 2002). One widely-accepted ultimate explanation for this observed difference is male-male competition for mate access (Armelagos & Van Gerven, 1980; Isaac et al., 2005; Puts, 2016). Females are considered the limiting sex in species where females invest more in reproduction than their male counterparts (e.g., bearing the child, parental care). This lowers the rate of reproduction in females, biasing the operational sex ratio towards males (i.e. increases the ratio of sexually-active males to females), and increases the variance in reproductive success among males (Clutton-Brock & Parker, 1992; Trivers, 1972). Sexual selection theory predicts the evolution of sexual dimorphism under such conditions, as larger males tend to be stronger and advantaged during competition. In support of the relevance of this hypothesis to humans, men's reproductive success was found to be 2-4 times more variable than that of women's in traditional societies (Brown et al., 2009), and men's reproductive performance have been linked to traits associated with dominance (Hill et al., 2013; Puts, 2016). For instance, height has been shown to be positively associated with probability of having a long-term partner and more children (Nettle, 2002; Pawlowski et al., 2000).

In line with the observation that humans are sexually dimorphic in size, in mammalian species male offspring tend to be energetically more costly to produce than females offspring. In red deer and rhesus macaques, subordinate mothers that rear male offspring are more likely to die or fail to reproduce the subsequent winter (Bercovitch & Berard, 1992; Clutton-Brock et al., 1981). In humans, sons grow more rapidly *in utero* (Marsál et al., 1996) and have higher birth-weights than daughters (Tamimi et al., 2003), indicating a higher level of maternal energetic investment in pregnancies involving sons. The higher energetic costs of producing and raising sons were thought to be long lasting and taxing to the fitness potential of his subsequent siblings. Those born after brothers have been found to be lighter at birth than otherwise (Côté et al., 2003; Nielsen et al., 2008; Rickard, 2008), and suffered a reduced probability of reproduction in later life (Rickard et al., 2009). The number of sons a woman has was also found to be inversely correlated with her longevity (Helle et al., 2002).

The sexual selection framework for understanding parental investment patterns was expanded by Trivers and Willard (1973) to include a broader consideration of the ecological context under which these allocation decisions are made. The Trivers-Willard hypothesis (TW) posits that parents would benefit more from investing into the more variable sex (in terms of fitness potential) when resources are plentiful, as they could be more likely that their child will reach the high-reproductive-success end of the spectrum. Given that in humans males are the more variable sex, TW predict mothers in relatively good conditions should preferentially invest in sons while those in relatively poor conditions should invest in daughters. These tactics are expected to be regulated by stabilizing selection of sex ratios at the local population level. This hypothesis has been of great interest to evolutionary anthropologists studying parental investment, but due to limitations in data availability I will not be adopting the TW framework in this thesis chapter. I will instead focus on investigating the implications of sexual dimorphism on a mother’s post-partum condition. Recent work concerning TW in humans was examined in the Introduction of this thesis and further discussed in the Discussion section of this chapter.

As previously mentioned, sexual dimorphism is a well-documented phenomenon across human populations, however, the degree to which these differences affect the mother's condition in the early post-partum period remain elusive. I am interested in this time period because mothers are at elevated risks of undernutrition and depletion during and following a pregnancy. Children's health and well-being are highly dependent on the care they receive during this period. From a public health perspective, this information can help us identify individuals prone to these adverse health outcomes. PA duration is a useful metric for this study, as it takes into account both the costs of producing a child and also investment in the early post-partum stage. Drawing from previously discussed life history and sexual selection theories, I predict that women who had sons will experience longer PA when compared with those who had daughters, reflecting the higher cost of producing sons. To test this prediction, I analyzed post-partum amenorrhea data from two populations.

3.2. Methods

To test the prediction that women who gave birth to sons experience longer post-partum amenorrhea (PA) than those who had daughters, and that this effect is more apparent in under-nourished populations, I conducted a secondary analysis of two pre-existing data sets. The data sets were taken from reproductive ecology studies in the Kaqchikel Maya women of Guatemala (Nepomnaschy et al., 2004) and Toba women of the Nomqom village, Argentina (Valeggia & Ellison, 2004). These two populations were well-studied over time, and are thought to differ in their overall energetic condition due to differences in diet and SES. This is reflected in the difference in mean BMI, a measure of nutritional status, of women from these populations. The Maya women's average mean BMI (±SD) was 21.8 (±3.7). This was calculated from village-wide demographic surveys conducted at the time of data collection (2001). The Toba population has been consistently described as being well-nourished (Valeggia & Ellison, 2003a, 2003b, 2004, 2009). The average BMI (±SD) of Nomqom women was reported to be 26.3 (±3.2) during a pilot study (Valeggia & Ellison, 2003a). In addition, ~50% of the total Nomqom population were considered overweight (BMI > 25) and ~25% obese (BMI > 30) by international standards (Valeggia & Ellison, 2003a).

3.2.1. Study populations

Kaqchikel Maya women of Guatemala. Data for this population consisted of women from two villages in the southwestern highlands of Guatemala, with a population of ~1200 each. Their diet consist mostly of corn, beans and fruits, with freshwater fish and crab being their main source of protein. Women's daily activities involve raising children, household chores, and farm work during harvest (Nepomnaschy et al., 2004). A longitudinal cohort study was conducted between November 2000 and November 2001. Women ages 18-40, married, who had at least one child more than 6 months prior to the onset of the study but were not currently pregnant were invited to participate. A total of 135 women volunteered initially. Data on demographics, anthropometrics, and hormonal correlates of fertility were collected. To monitor changes in reproductive status (PA *vs.* regular ovarian cycling), the participant's first-morning urine specimens were collected every other day, three times a week, for the entire duration of her participation in the study (either for one year, or until the participant became pregnant or no longer wished to participate). Details of immunossays used in determining the fertility status of study subject was reported can be found in (Nepomnaschy et al., 2004). Demographics data were collected via a village-wide survey at the beginning of the study, and anthropometrics data were collected monthly at a local health post.

The observational study described above was not originally designed for the purpose of studying PA duration. As a result, none of the study subjects were followed from parturition to end of PA. Logically, women began PA immediately after birth, and were assumed to remain in PA until the resumption of ovarian cycles was observed. The study subjects included in the data set were: 1) women whose transition from PA to first post-partum ovarian cycle was observed during her participation in the study (events), 2) women who left the study still in PA (right censored), and 3) women who entered the study already cycling (left censored). Observations are considered censored when information on the timing of the phenomenon of interest is incomplete. The usage of censored data, given my choice of statistical model, requires censoring to be “non-informative”, meaning that the censoring time is independent of the event of interest. One example of informative censoring would be patients who withdraw from a drug trial due to negative side-effects. Inclusion of such informatively censored data in my statistical model would result in biased parameter estimates. With respect to this data set, there was no indication that censoring time was associated with women’s fertility status, therefore censoring was assumed to be non-informative. These right and left censored observations provided additional information regarding minimum and maximum PA duration, respectively. The following set of exclusion criteria were applied to this data set:

1. Women experiencing anovulatory cycles and their true fertility status is uncertain (n=4).
2. Women suspected of family planning (n=4).
3. Women whose records were incomplete (n=30).
4. Left-censored individuals whose censored period were over three years long (n=6).

One of the right-censored individuals (subject #44) with a very long, open-interval, observation was considered an outlier and was excluded from the Maya population data set (discussed in Appendix D). The final data set consisted of 91 individuals, with 29 counts of events, 38 counts of right censored data, and 24 counts of left censored data.

Toba women of the Nomqom village, Argentina. This village is situated in northeastern Argentina, and has a population of ~2300. Women from this population were considered well-nourished as their diet consist of calorie-dense food items, such as fried dough (Valeggia & Ellison, 2004). Very few women have paid jobs, and their daily activities include household chores and looking after children. A longitudinal prospective cohort study was conducted from 1999 to early 2000. Study subjects were recruited during a village-wide demographic survey conducted prior to the cohort study using the following criteria: had a full-term (singleton) birth in the last six months, not using contraceptives, still breast-feeding and in PA. A total of 113 participants were interviewed monthly regarding their child-care practices and menstruation. Anthropometry data were also collected during the monthly visits to the local health clinic. The duration of post-partum amenorrhoea was defined as the time from the women’s last birth to her first post-partum menses. The participants were followed till their third self-reported post-partum menses. A subsample of the subjects (n=70) were selected for hormonal assay of ovarian function, and it was determined that first post-partum menses is an accurate indication of PA termination (Valeggia & Ellison, 2004). Data on censored individuals (those who were still in PA at the end of the study and those who left prior to their first post-partum menses, n=7) were unavailable. Thus, the final data set consisted of 106 counts of events.

Ethics approval for the secondary analyses of the Maya and Toba data sets were reviewed and granted by the Research Ethics Board at Simon Fraser University (project numbers 2012s0971 and 2015s0572, respectively).

3.2.2. Statistical analysis

I performed survival analyses on the data to test the predictions that women who gave birth to sons experience longer post-partum amenorrhea (PA) than those who gave birth to daughters, and that this effect will be more apparent in under-nourished populations. Prior to running the analyses, I constructed a direct acyclic graph for the relationships between the predictor, outcome, and potential confounders (Appendix C). Two potential confounders were identified: women's age at birth and condition prior to birth. Pre-pregnancy BMI (surrogate for the latter factor) data were obtained from village health center records or measurements taken during a pilot study in the Toba population, but was unavailable for the Maya population.

Cox proportional-hazards models were used to compare hazard rates of terminating PA between women who gave birth to sons vs. daughters. An adjusted model consisting of the potential confounders, mother's age and pre-pregnancy BMI (Toba only), as additional covariates was built for the purposes of assessing the impact of confounding. In these models, hazard rate refers to the instantaneous probability that, given a woman hasn't terminated PA, she will in the next (infinitely small) time step. Women were determined to have terminated PA when her first post-partum ovulation (Maya) or menses (Toba) was observed. Hazard ratios (HR), the relative likelihood of PA termination in women who gave birth to daughters vs. sons at any given point in time, and median "survival" times (i.e., median PA durations) were also calculated for both populations. Cox proportional hazard models make the assumption that the hazard ratios of the comparison groups remain constant over time. Model assumptions were validated by visual inspection of the log-transformed cumulative hazard functions over (log) time (Appendix E). Kaplan-Meier survival curves, non-parametric estimates of survival probability, were graphed to aide in visualization of the data. All statistical analyses and graphing were completed in R version 3.2.2 (R Core Team, 2015). The R package "icenReg" version 1.3.3 was used to fit Cox proportional-hazards models to the Maya data as its left-censored observations required a special method of error estimation (not available in the popular "survival" package).

3.3. Results

The Maya data set consisted of 90 observations (29 counts of events and 61 censored), of which 38 were from mothers who gave birth to daughters. The median PA lengths for mothers who had daughters and sons were estimated to be 490 and 579 days, respectively. Results of Cox proportional-hazards model were shown in Table 3.1. The association of child's sex with probability of PA termination was found to be statistically significant (unadjusted $p<0.01$, adjusted $p=0.03$). Age of mother ($p=0.19$) was not significantly associated with the probability of PA termination. When assessed visually (Figure 3.1A), the effect appeared to be mainly driven by a proportion of mothers who had sons and took a relatively long time before they resumed fertility (the "tail" of the black/son curve). The adjusted HR of 2.45 is interpreted as follows: for women still in PA, those who gave birth to a daughter have 2.45 (95%CI [1.08, 5.58]) times the chance of PA termination at any given point in time compared with those who gave birth to a son. An alternative way to interpret a HR is to consider the odds that a "treated" individual will "resolve symptoms" before a control subject. In this regard, HR of 2.45 (95%CI [1.08, 5.58]) can be interpreted as a 71% (95%CI [52%, 85%]) chance that those who gave birth to daughters would terminate PA first (conversion formula given in Spruance et al., 2004).

The Toba population consisted of 106 counts of closed-interval observations, and 54 were from women who gave birth to daughters. The median PA lengths for mothers who gave birth to daughters and sons were 279 and 272 days, respectively. No statistically significant difference was found between the probability of PA termination between mothers with daughters when compared with those who had sons (unadjusted p=0.88, adjusted p=0.55). A visual assessment revealed little difference between the survival curves and confidence bands representing the two groups (Figure 3.1B). Mothers who gave birth to daughters were 1.14 times (95%CI [0.75, 1.70]) more likely to leave PA at any given time step, given they are still in PA, when compared with those who had sons. In other words, there is a 53% (95% CI [43%, 63%]) chance that mothers who had daughters will leave PA before those who had sons. Neither age nor pre-pregnancy BMI of the mothers influenced PA termination in this population (p=0.14 and 0.32 respectively, see table 1 for HR and 95%CI).

3.4. Discussion

In this thesis chapter I used data from two well-studied, small-scale societies, to test the following hypothesis: differential investment into sons vs. daughters is reflected in the time that is required for the women to resume ovarian function after a pregnancy (post-partum amenorrhea, PA). I predicted women who gave birth to sons would experience longer PA. Maya population when compared with the Toba. Results from my analyses supported these predictions. With respect to the Maya population, I found an 89 day (~3 months) reduction in estimated median PA duration in women who had daughters vs. sons, and 71% (95%CI [52%, 85%]) chance that those gave birth to daughters would terminate PA before those who had sons. Associations between sex of child and PA termination in the Toba were not found to be statistically significant.

The difference in PA termination between mothers who had daughters vs. sons observed in the Maya population was statistically significant (p=0.03), however, the fact that the estimated 95% confidence interval for HR for sex of child were quite wide (1.08-

5.58) deserves attention. While point estimates represent the best approximation of direction and magnitude of the association between the dependent and independent variables, a confidence interval (CI) is a range estimate of its true value, thus providing insight regarding the inherent uncertainty in the estimation of the parameter of interest. Typically, a confidence level of 95% is selected when using confidence intervals, meaning that the interval captures the value of the parameter being estimated in a study 95 out of 100 times the study is repeated. A wide CI, therefore, points to high levels of uncertainty in a parameter estimate. The relatively large margin of uncertainty in the estimated HR for the Maya population was likely a result of the large proportion of censored observations in the dataset (61/90). This CI estimate was obtained via bootstrapping (default in R software package), which was known to improve (i.e. provide precise estimates) with increasing sample size and decreasing amounts of censoring in the data (Efron, 1987; Hall & Wellner, 1980). Repeating this analysis with data from similar populations consisting of larger samples and less censoring would allow for greater precision in parameter estimate. Ideally, such a study would be designed in a similar fashion to the Toba study (Valeggia & Ellison, 2004) in that women who had recently given birth would be recruited and followed through to the end of her PA. I would also choose to work with populations where detailed records of anthropometrics and health over time of the woman and her child is available. Information regarding the mother's condition prior to her birth would be an asset.

A mother's pre-pregnancy BMI was determined to be a potential confounder in this study (see Appendix C) due to its known associations with sex of child (positively correlated with probability of having a son) and PA duration (negatively correlated). A proper assessment of its effect was not possible due to lack of data. Here, I hypothesize on the likely direction of bias that would result should pre-pregnancy condition be a true confounder by considering the following scenarios (thought experiment adapted from Stürmer et al., 2010):

1. If the distribution of pre-pregnancy BMI was skewed to the right (low BMI) in this population, it means that across the board, women are experiencing longer PA. There will also be an increased proportion of women who had daughters, and thus, there exist a high proportion of women with daughters and long PA. This is opposite to the hypothesized direction of association between these variables, and results in a narrowing of the difference in PA duration between women

who had daughters vs. sons, and thus, biasing the HR estimate towards the null value of no association.

2. If the distribution of pre-pregnancy BMI was skewed to the left (high BMI) in this population, it meant that there exist a high proportion of women who had sons experiencing shortened PA. This is opposite to the hypothesized direction of association between these variables, and results in a narrowing of the difference in PA duration between women who had daughters vs. sons, and thus, biasing the HR estimate towards the null value of no association.

Given the above logical deductions, I hypothesize that pre-pregnancy condition is potentially a negative confounder in this study, meaning that HR would be pulled towards the null value of 1 under influence of this confounder (i.e. effect is weakened).

I attribute the lack of association of sex of child on PA duration in the Toba to the overall better energy levels of women in this population when compared with the Maya. Trade-offs in energy allocation exist when resources are limited. Under conditions of relative abundance, when there are enough resources to satisfy competing functions, trade-offs will be masked (Zera & Harshman, 2001). During PA, a mother's resources are divided between her own maintenance and child care (and other tasks she performs). The higher cost of caring for sons (or recovering from producing a son, or both) could have been compensated for by the higher caloric diet in the Toba when compared with the Maya. This difference was reflected in the mean BMI of women in these populations: 21.8 ± 3.7 for Maya *vs.* 26.3 ± 3.2 for Toba. The interaction between energy status and PA duration in these populations can be formally modelled in a future study by combining the two data sets and use fancy stats.

Future studies should consider making use of multiple measures of energetics, such as energy balance (energy gain minus energy expenditure), energy flux (rate of change of energy balance), percentage body fat, and C-peptide (a physiological market of energetic condition that can be measured non-invasively (Sherry & Ellison, 2007). Detailed observations on mother's child-caring behavior will help quantify energy balance and flux, and also shed light on the origins of the costliness of sons: whether costs were incurred during gestation, or post-partum investment (e.g. breastfeeding intensity). This would also aide in identifying the mediator variable(s) between PA duration and sex of child. In this current analysis, I drew from previous research and hypothesized energy level to be the most important mediator variable (Ellison, 2008). Other potential mediators, such as psychosocial stress and particular diet compositions should be considered in future studies. An analysis of breastmilk energetic content would also be an asset, as it was shown in rhesus macaques that although milk yield was higher in mothers who gave birth to daughters, fat content was significantly higher in the milk of mothers who had sons such that the total energy provided to offspring of the two sexes was the same (Hinde, 2009). This suggests that nursing intensity alone might be an insufficient measure of a mother's investment into breastfeeding.

The Trivers-Willard hypothesis (TW) is a border evolutionary ecology framework that has been popularly applied to studies of context-dependent parental investment. As previously discussed, TW predicts that mothers in relatively good conditions will preferentially invest in sons, while those in relatively poor conditions should engage in the opposite. Studies of TW behavior in mammals and humans have generated mixed evidence (see Chapter 1). Potential TW effects in humans warrant further investigation as correlates of nursing behavior and breastmilk composition have important implications for the health and wellbeing of mothers and newborns (Sellen, 2007). A more in-depth analysis of the data sets described in this chapter (parameterize "maternal condition" with information from demographic surveys and monthly health clinic visits) would be valuable to this body of knowledge. As PA is a more general measure of a women's exertion from her gestation to early juvenile care period, difficulties in finding an appropriate proxy for maternal investment could be alleviated. Meta-analyses would also shed light on some of these contradictory results.

From an evolutionary biology perspective, it remains elusive whether the costliness of sons is a result of adaptive parental investment strategy or differences in the resource solicitation and extraction rates of offspring of the two sexes. Parents and offspring are expected to be in conflict, as it would be in mothers' best interest to distribute resources strategically among her current and potential future offspring according to their respective reproductive value, while the offspring will always want to monopolize resources for itself (Haig, 2010). Ideally, one would compare the observed investment level to the optimal levels of mother's *vs.* that of offspring's, but these parameters are often difficult to measure or estimate in real life. In birds, parental investment was typically studied by comparing the begging intensity of individuals in a brood to the amount each of them was eventually fed (e.g. Stamps et al., 1987). A similar study design could be considered in human studies, by comparing the begging (or crying) rates and rewards obtained between siblings of a different-sex multiple birth.

In summary, sex of child appear to affect mother's PA duration in a subsistence population, but not in one in which energy levels are high. These results highlight the salience of resource availability in shaping the reproductive trajectories of women. With respect to modelling reproductive strategies in humans (Chapter 2), these results indicate that the sex of child was indeed an important variable that should be built in when possible. The difference in cost, as measured by PA here, can potentially be quite large and thus be of importance both clinically and evolutionarily. The estimated HR and median PA durations were also useful quantitative data that would aid in creating a sliding PA window in a mathematical model. From an applied perspective, these results indicate that women with lower SES (or had lower BMI) who had sons are potentially at higher risks of undernutrition and depletion during the early post-partum period. Maternal and child health interventions need to be designed with the consideration of the diversity in the needs of different women and children, and also be mindful that there is no one-size-fit-all care program.

3.5. Tables

Table 3.1. Summary of Cox proportional hazards models for the probability of termination of post-partum amenorrhea (PA) by sex of child, age of the mother, and her pre-pregnancy BMI.

Maya population (n=90, 61 censored)						
	Unadjusted model			**Model with covariates**		
	Hazard ratio	**95%CI**	**p-value**	**Hazard ratio**	**95%CI**	**p-value**
Sex of child (daughter)	2.61	[1.30, 5.25]	<0.01	2.45	[1.08, 5.58]	0.03
Age				0.94	[0.86, 1.03]	0.19
Toba population (n=106, none censored)						
	Unadjusted model			**Model with covariates**		
	Hazard ratio	**95%CI**	**p-value**	**Hazard ratio**	**95%CI**	**p-value**
Sex of child (daughter)	1.03	[0.70, 1.51]	0.88	1.14	[0.75, 1.70]	0.55
Age				1.02	[0.95, 1.07]	0.14
Pre-pregnancy BMI				0.97	[0.91, 1.03]	0.32

Hazard ratios represent the relative “hazard” (i.e. instantaneous probability) that a woman who gave birth to a daughter will terminate PA in the time step when compared with a woman who gave birth to a son, given that neither of them have left PA. Pre-pregnancy BMI data was unavailable for the Maya population.

3.6. Figures

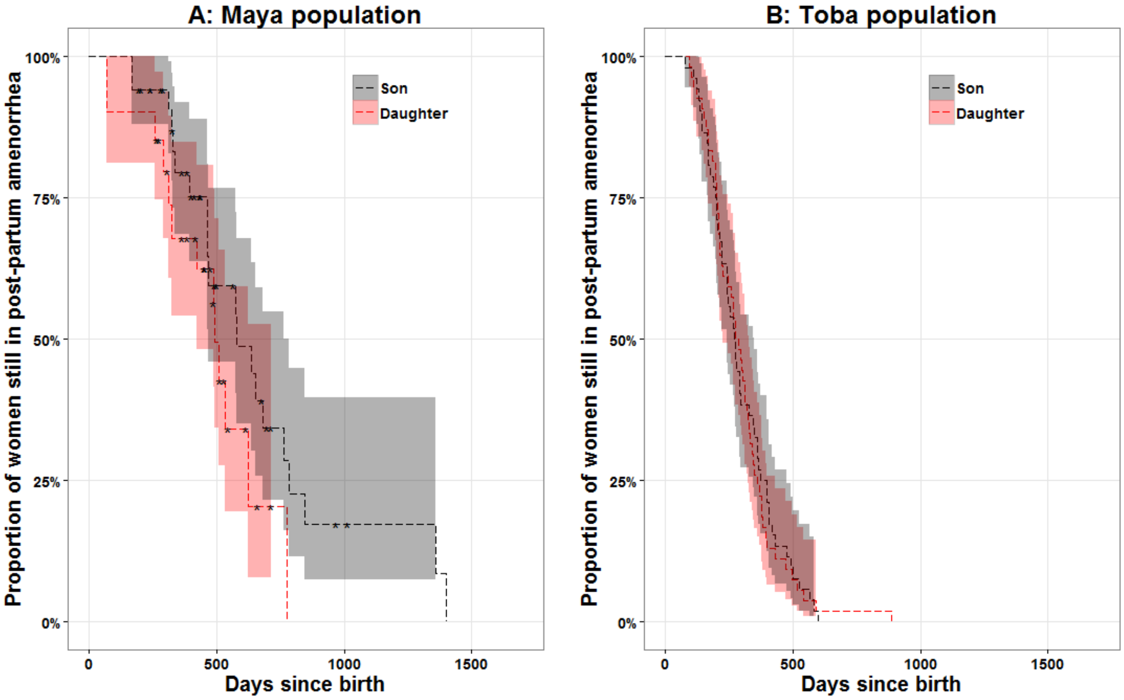

Figure 3.1. **Kaplan-Meier curves depicting proportion of women still in post-partum amenorrhea over time, grouped by sex of child in A) Maya population, and B) Toba population.**

Crosses represent right-censored data points, and shaded area give the 95% confidence band for each curve.

Chapter 4.

Discussion

Human behavioral ecology (HBE) continues to be an active field of research, however, it does not appear to have received the full attention it deserves (Nettle et al., 2013). One of the contributing factors could be that HBE is practiced under different disguises across a number of academic disciplines, spanning the full spectrum of life and social sciences. Being grounded in conceptually-approachable theory (i.e., evolution by natural selection) has made HBE available, and user-friendly, even to researchers with a non-biology background. The elegance of HBE lay precisely in its power to generate predictions to a variety of behaviors observed under diverse settings from simple theory. It is relatively rare in the social sciences for the same set of predictive principles to apply to variation both within- and between-societies and to society types ranging from subsistence populations to industrial states (Winterhalder & Smith, 2000). Thus, HBE brings a sense of conceptual coherence to the study of human behavior, a study that has traditionally been spread across a number of different disciplines each with different conceptual starting points.

The evolutionary approach of HBE argues that huge variation in behavior exists because the payoffs to alternative strategies are dependent on local ecology and individual life circumstances, and is shaped by cultural and evolutionary legacies. The causes and consequences of recent human behavioral and environmental changes (such as urbanization, economic development, and population growth) are recurring themes of HBE studies. Research findings typically converge on the fact that determinants of behavior and health are often multi-factorial and interact in complex manners. Culturally-appropriate study designs, data analysis, and interpretation are emphasized (Gibson & Lawson, 2015). The same applies to policy recommendations: intervention projects should be designed to address local needs, rather than relying exclusively on “blanket” initiatives copied and pasted with little regard to each unique situation (Gibson & Lawson, 2014; Tucker & Taylor, 2007). In applying HBE to policy design, however, the unintended promotion of adaptive behavior being beneficial to society must be avoided. This is known as the naturalistic fallacy: the erroneous belief that natural processes are morally correct.

Hypothesizing that a behavior is, or may have been, adaptive, is not the same as endorsing the behavior. Doing so would be an abuse of evolutionary theory, much like the justification of eugenics and genocide.

Since the birth of the field, HBE has evolved to embrace increased complexity in methodology. The reductionist paradigm is prevalent in HBE. This could be a result of anthropologists dominating this field, and anthropological studies typically consist of field observations from a single population at a single site. The contextual information provided by these studies has been most valuable, but are often difficult to generalize outside of the particular study population (Nettle et al., 2013). In addition, as humans are long lived, measurements of fitness can be difficult to make, and in turn making HBE hypotheses difficult to test. These challenges are being countered with a broadening of the HBE toolkit to make use of more secondary demographic and survey data coupled with advanced statistical methods (e.g., Lawson et al., 2012; Mathew & Perreault, 2015; Sear et al., 2016). In some cases, secondary demographic data allowed for the tracking of multiple generations, providing valuable new insights on the correlates of long-term fitness (Goodman & Koupil, 2009; Lahdenperä et al., 2004).

My thesis research into human reproductive behavior marries ecology, anthropology, and epidemiology, under the theoretic premise of HBE. As context is extremely important to consider when evaluating the causes and consequences of behavior, a means by which optimization of behavior under a variety of circumstances (constraints) can be systematically studied would be a most helpful tool in the management of public health. For this purpose, a dynamic state variable model was constructed for the optimization of reproductive behavior (abstinence vs. attempt to reproduce) under diverse environmental settings. This class of model was chosen as such models handle stochasticity and non-linearity well, and they function in parallel to the logic of HBE: evaluating alternative behavior strategies based on fitness consequences, and from there set up decision rules (if *a*, do *x*; otherwise, do *y*). More importantly, DSVM provides a means ability to track women's biological condition (energy reserve), which allows the model to be useful across disciplines. Energy reserves provides a link between reproductive fitness and medicine as it is both an investment currency and a good proxy for overall health. This model has thus far generated interesting results and conversations.

Moving forward, it would be important to revisit some of the current simplifying assumptions, continue to evaluate model performance, and ultimately, to regenerate interest in the use of first-principle models in HBE. One of the proposed usage for these models is for the evaluation of aide policies and programs and ensure sources of unintended and negative side-effects are minimized. Take the example of the installation of a village water tap that relieved women of hard labor in order to obtain water, but this new-found energy was reallocated towards fertility and a worsening of child health resulted (Gibson, 2014). The model should have been able to capture this result by simply performing a forward simulation under switching environmental conditions (high cost and high stochasticity in resource acquisition to that of low cost and low stochasticity).

In formulating this optimization model, it became clear that certain parameter values were difficult to obtain, and pieces of information regarding the biology of child birth also appear to be missing. One example was that, although it is known that sons are more costly to produce than daughters (Marsál et al., 1996; Tamimi et al., 2003), it was unclear whether this difference should be included in the model (and if so, to what extent), particularly in the post-partum investment stage. I compiled data on women's post-partum amenorrhea (PA) duration obtained from two small-scale societies, and performed secondary data analysis to answer the question whether sex of child influences PA duration. The analysis provides evidence that PA duration is indeed associated with sex of child, but only in the relatively less well-nourished population. This reaffirms the notion that costs and benefits should be evaluated with consideration of local context. With regard to the model, these results suggest that the inclusion of offspring sex would be helpful. The actual biological relevance of a three-month delay in PA termination, however, still remains to be determined.

My thesis work needs to be discussed in the context of assumptions and methodological limitations. Not only is it worth emphasizing that the dynamic state variable model, as discussed extensively in Chapter 2, is built on a number of assumptions, results from the data chapter must also be considered in the context of the correlational nature of the association and limitations in original study design (sampling of the population in particular). Indeed, models, observational studies, and even controlled experiments, all come with their own unique sets of limitations. Models are often criticized for inevitable simplifying assumptions that may render the model unrealistic. Observational studies face issues of bias when making causal inferences. Experiments may suffer from a lack of ecological-validity for being too well controlled. There does not exist a universally superior way of studying any phenomenon. Instead, these different methods complement each other, and can bring the most fruitful study outcomes when coupled with an open-minded discussion regarding the potential sources of uncertainty, error, and bias in each case.

The integrated nature of HBE results in studies that naturally bring together researchers from multiple disciplines (e.g., this thesis research united experts from anthropology, ecology, epidemiology, statistics, and computing science). Adopting an inter-disciplinary approach seems to be a popular trend nowadays. For years, academics have been divided into disciplines characterized by specialization both in epistemology and in methodology. Unfortunately, public health problems are global and complex, and pay no respect to man-made disciplinary boundaries. For example, the AIDS pandemic has become public health problem of massive proportions and requires the expertise of numerous disciplines. We cannot continue to apply disciplined research approaches to undisciplined problems (Rose, 1986).

The key to successful multi-disciplinary research, in my humble opinion, lies in having an open mind. Institutional barriers (e.g., granting mechanisms) (Frost & Jean, 2003; Pfirman et al., 2005) appear trivial in the face of miscommunications regarding study approaches and (realistic) expectations. Reassurance of a common goal is essential in the navigation of disciplinary boundaries (though this can be a challenge of its own as researchers may join the team with their own discipline-specific agendas), but most importantly, researchers must be willing to leave their fixed platforms and consider the influence of a broad variety of factors, and appreciate the utility of methodology they are not necessarily comfortable with. Academic fields often have different standards of proof. Uncertainty over quality of evidence can be a major source of anxiety in the group. Using mutually-developed language, and with complete honesty, limitations in methodology needed to be discussed early on in the project, and continuously throughout. This may involve a self-reflection upon the limitations of methods one is so accustomed to. An agreement regarding what is “the best we can do” must be reached. Compromises and trust (in each other’s skills) are thus necessary for effective inter-disciplinary research and to bridge research gaps (Golde & Gallagher, 1999).

The goal to apply this research to aid policy design is still a long way away. In addition to the need to refine the model and demonstrate its effectiveness, there is a wide gap of differences that needs to be filled between scientists, clinicians, public health officials, and the general population (the “end-users”). The challenge here is that these stakeholders often “inhabit different worlds” and likely not share the same language, culture, and agenda (Caplan, 1979; Jacobson et al., 2003; Lavis et al., 2003). In order to be heard, a direct and tailored message needs to be delivered by a credible messenger. Personal interaction with the target audience would ensure actual needs are understood and met.

As a scientist with an upbringing in a classic hard science (biology), murmured disdain over scientists engaging in policy work, or worse, becoming advocates, ring clear in my head. The concern of one’s ability to maintain objectivity is not unfounded, and will always be present. Advocacy aside though, how many scientists can say that they have never ever been tempted for reasons much less noble? Knowing that one day my work might matter gave me a peace of mind amid the madness inside (and outside) this ivory tower, and shall continue to make up half of the driving force in my future adventures in academia. The other half? A simple desire to learn, of course.

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Appendix A.

State dynamics in DSVM

Energy reserve *E(t)* at time *t*

I characterized the energy reserves of the focal female as a closed, discrete, interval wherein she starves to death if she falls below a certain minimum threshold but will not be able to accumulate anymore after the maximum is reached. Energy requirements for somatic maintenance and foraging activity, m_b, were taken from the energy reserves of the focal female each time step. An additional metabolic cost, m_p, was incurred should the focal female be pregnant, or caring for a pre-weaning child. Foraging returns were pooled from all helpers (including the focal females) and distributed evenly amongst the focal female and her dependents. This value was always positive, meaning that the focal female will always gain some energy. The energy gained, however, may not be enough to cover her energy used in maintenance and foraging, and therefore, it was possible for the focal female to experience a net decrease of energy reserve at any given time step. The dynamics of the energy reserves of the focal female can therefore be described as

$$E(t+1) = \begin{cases} E(t) + \omega - m_b, & p = 0, p > 34 \\ E(t) + \omega - m_b - m_p, & 1 \le p \le 34 \end{cases}$$

and the proportion of resources to be distributed to each dependent and herself in need is given by

$$\omega = \Sigma R \div (K + 1)$$

Foraging returns, *R*, depends on seasonal variations in resource abundance, *s*, as well as the probability (“luck”) of encountering and obtaining said resource, β. Seasonality in resource abundance is described by the function

$$s = 0.75 + 0.25(sin\frac{t\pi}{6})$$

The given sine wave oscillates with a period of 12 time units (12 months), and described the relative abundance of resources in spring and summer when compared with autumn and winter. The amplitude of the curve represents the degree of resource abundance, with 0 begin never available and 1 being always available. Probability of encountering and obtaining resource is generated by drawing uniformly from a pre-determined, closed, range of possible values.

Pregnancy state *p*

Since this state variable is a tracker of the progress of reproductive episodes, it simply advance one unit per time step once the focal female successfully conceive.

Kin state, represented by $\vec{\boldsymbol{k}}$

The kin vector stores information regarding each of the focal female's children acquired during the modelled time span. The vector can hold the age and quality information of up to three children at a given time, $k_i(t)$. When the amount of resources the children receives is above the minimum threshold, *c*, he/she is considered to have successfully grew and developed for that time step, and will advance one unit. Children will remain at their current states should they receive insufficient resources, but it is not possible for them to revert to earlier states nor die. The dynamics of kid state can be therefore be described as

$$k_i(t+1) = \begin{cases} k_i(t), & \omega < c \\ k_i(t) + 1, & \omega \geq c \end{cases}$$

Appendix B.

Functions and parameters used in sensitivity analyses

Number of helpers.

I investigated the difference between having 0-3 helpers at the nest on the reproductive decisions of the focal female. Resource abundance and probability of acquiring resources were set to moderate levels.

Resource availability.

Variations in resource availability were explored from two angles, probability of acquiring resources and resource abundance by season, with the access to two helpers. The former was investigated by manipulating the range of the random number generator used to simulate “luck”. The values used were:

High irregularity in luck: 30-100% chance of obtaining resource.

Moderate irregularity: 50-100% chance of obtaining resource.

Low irregularity: 70-100% chance of obtaining resource.

Four levels of resource abundance were examined, and the following functions describe the changes in abundance over the course of 12 time steps (one year, see Figure B1):

$$High\ s = 0.85 + 0.15(sin\frac{t\pi}{6})$$

$$Moderate\ s = 0.75 + 0.25(sin\frac{t\pi}{6})$$

$$Low\ s = 0.55 + 0.25(sin\frac{t\pi}{6})$$

$$Famine\ s = 0.35 + 0.25(sin\frac{t\pi}{6})$$

Fecundability.

The fecundability values used in this analysis were 0.2, 0.4, 0.6, and 0.8. The focal female has access to two helpers, and were experiencing moderate levels of resource abundance and luck.

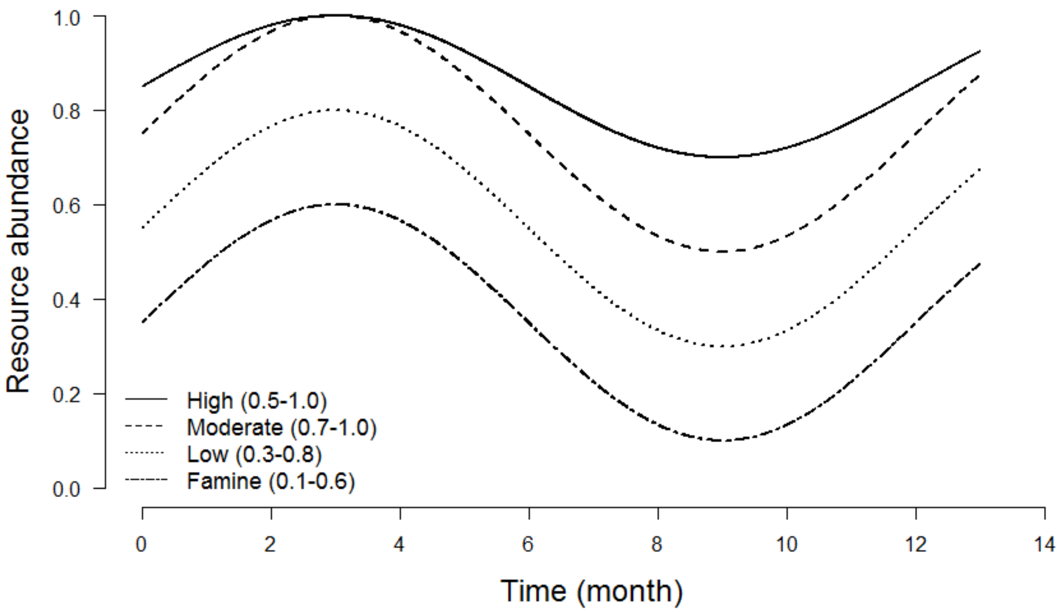

Figure B1. A visualization of the four levels of resource abundance examined.

The sine functions shown consisted of periods of 12 time units (month). The degree of resource abundance was described by a scale from 0 to 1, where resources were never available at 0 and were always available at 1. The range listed in the legend represent the peak to trough distance for each condition.

Appendix C.

Direct acyclic graph and the identification of potential confounders

In studies of causal links one must be cautious to avoid making inappropriate inferences due to confounding. I adopted the counterfactual definition of confounding (Greenland & Robins, 1986). In making an inference regarding a certain exposure and outcome, the ideal comparison group for the exposed group is itself, but “unexposed” (i.e. counterfactual). This is of course impossible, and in reality the exposed can only be compared to some other group that is not their counterfactual selves. This other group may have characteristics that make its experience an inaccurate representation of what the exposed group would have experience if they can be unexposed. As a result, the causal effect of the exposure on the outcome cannot be accurately measure. The “characteristics” that render the comparison inaccurate are known as confounders, and this phenomenon is termed confounding.

For a lot epidemiological studies, multiple potential confounders could be involved, each related with the others in complex manners. The traditional definition of confounding could thus be confusing and difficult to apply in these cases, undermining the correct identification of confounders. Neglecting to adjust for a confounder may lead to biased effect estimations, while unnecessary adjustments of covariates in a model may increase or decrease precision depending on the relationship between the unnecessary covariate and exposure and outcome variables and the sample size (Schisterman et al., 2009). The theory of direct acyclic graphs (DAGs) provide an elegant solution to this problem (Greenland et al., 1999; Shrier & Platt, 2008). DAGs are constructed by summarizing and visualizing causal relationships between study variables, starting with those that affect the outcome and predictors. In general, an arrow on in the direction of A → B represents the assumption that A causes B (intermediate steps may be omitted for clarity if those steps are not involved in another path), a lack of arrow explicitly means A does not cause B, and arrows always have to be unidirectional. The minimal set of required adjustments for an unbiased effect estimate could then be found by following a simply procedure of path analysis (Shrier & Platt, 2008), or by using specialized software (e.g. DAGitty, Textor et al., 2011). DAG analyses are most helpful when conduced at the planning stages, as it encourages researchers to consider very carefully all the behind-the-scene hypotheses and assumptions made, and also would inform researchers of the kind of data that should be collected.

Here I present a DAG constructed for the identification of potential confounders of the hypothesized relationship between sex of child (predictor) and mother’s duration of post-partum amenorrhea (outcome) (Figure C1). The graph was produced and analyzed with DAGitty software. The relationship of interest was shown on the top row. The main mediating variable was believed to be the mother’s condition after birth. In this thesis chapter I focus on the main mediator of reproductive function – energetics (Ellison, 2008). Other aspects of a woman’s condition that could interfere with her resumption of fertility include psychosocial stress (Nepomnaschy et al., 2004) and immune challenges (French et al., 2007), but these will not be considered here. Starting from the top row, the sex of the child was hypothesized to have an influence on a mother's energetic conditions after birth (due to different levels of costliness), which would in turn be reflected in her duration of post-partum amenorrhea. As a plethora of factors may affect a woman's energetics, only the factors that are simultaneously associated with others were shown. On the next row, the mother's energetic condition prior to her birth influences both her condition after birth, and the sex of the child. Several mechanisms have been proposed for the latter association. These include the selection in utero hypothesis (male fetuses were more sensitive to maternal physiological stress and hence were more susceptible to spontaneous abortion (Catalano et al., 2013)) and the reduced conception hypothesis (changing receptivity to X/Y-bearing sperm (James, 1997)). Age of the mother has an effect on her condition both pre- and post-partum: neither young nor old mothers were considered to be in good shape energetically. Age also has an independent effect on sex of the child, hypothesized to be a result of decreasing gonadotrophin levels as a women ages (James, 1997). Two potential confounders were identified: mother's age and pre-pregnancy condition. Pre-pregnancy BMI was used as a proxy for the mother's pre-pregnancy energetic condition, however, this information was unavailable for women in the Maya population due to the lack of records prior to the beginning of the current study. Thus, the proportional hazards models used to estimate the effect for the hypothesize association between sex of child and PA duration consisted of the independent variables sex of child, age and pre-pregnancy BMI for the Toba population, and only the former wo variable for the Maya population data.

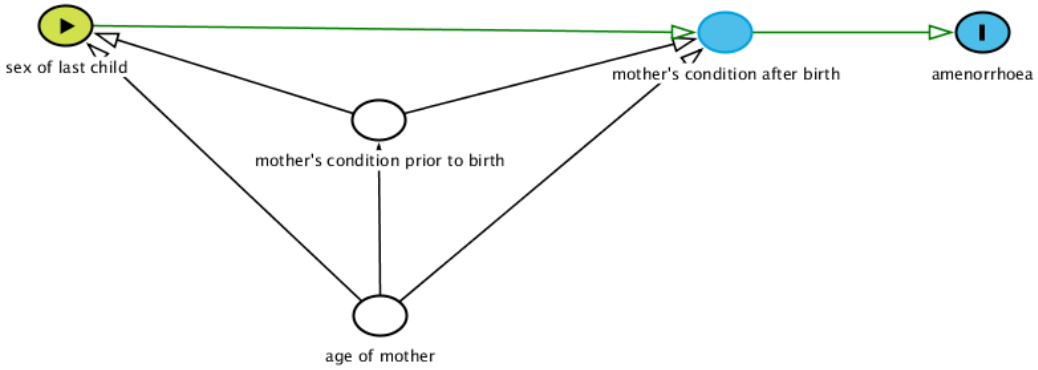

Figure C1. A DAG showing the relationship between potential confounders of the relationship between the predictor and outcome variables.

The minimum sufficient adjustment needed to eliminate bias consisted of mother’s condition prior to birth and her age (white circles).

Appendix D.

Excluded outlier from the Maya population

The subject identified as being an outlier was right-censored observation (Figure D1), with estimated survival time at least three times more than the median value for her cohort (490 vs. >1700 days). When this observation was included in the analyses the median survival time remained the same, however, the estimated HR for sex of child (daughter) on the probability of PA termination significantly differed: 1.26 (95%CI [0.27, 5.93]) compared with 2.61 (95%CI [1.30, 5.25]) when the outlier was excluded. Basically, the outlier narrowed the difference in the hazard rates of PA termination between women who had daughters vs. sons (p=51), introduced uncertainty, and resulted in a less precise estimate of HR (evident from the widened 95%CI). Cox proportional-hazards model assumptions were not met in this case (diagnostic plot not shown), and thus the validity of the report p-value cannot be confirmed.

This individual had only participated in the study for two months (during which she was not cycling) out of the four years and eight months that would have been coded as her PA duration. In other words, she was only observed for 3.5% of the time she was thought to be in PA. This could be a case of secondary amenorrhea, a condition where a woman's reproductive functions were suppressed for reasons other than child birth, such as physical exertion (Jasienska & Ellison, 2004; Nichols et al., 2006). I found no data on the prevalence of secondary amenorrhea in small-scale societies, and thus cannot make inferences regarding how likely this was to be true. In fact, little is known about the prevalence of secondary amenorrhea even in industrialized populations (Münster et al., 1992; Pettersson et al., 1973). Despite this, I would still argue that this data point should be removed from the dataset based on the fact that she was only observed for a small fraction of the very long PA she was thought to be in.

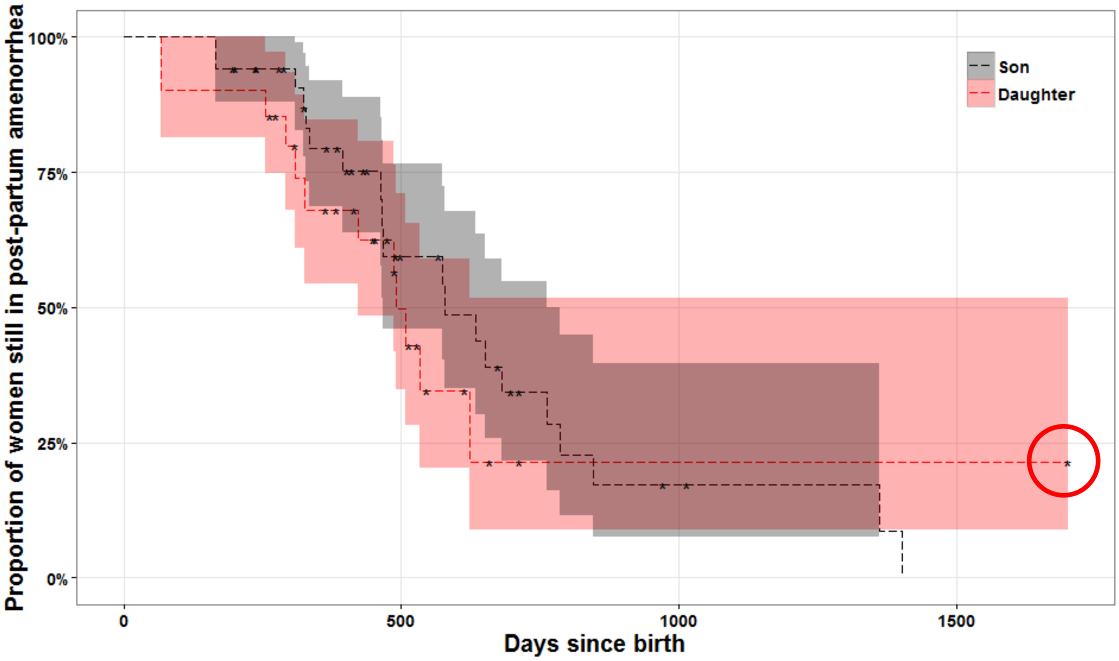

Figure D1. Kaplan-Meier curves depicting proportion of Maya women still in post-partum amenorrhea over time, grouped by sex of child.

Crosses represent right-censored data points, and shaded area give the 95% confidence band for each curve. Red circle highlights outlier.

Appendix E.

Validating Cox proportional hazards model assumptions

The proportional hazards models used to analyze these data sets were semi-parametric and make the single assumption that the hazard ratio, which is the relative likelihood of "symptom resolution" in the comparison groups at any given point in time, is constant over time (i.e. over the course of the trial, or disease prognosis). In other words, "failure rate" (represented by the hazard function) in each category of the predictor variable should be consistently proportional to each other. This assumption can be validated via a visual inspection of log(-log(S(t))) *vs.* log(t) plots, the former referring to the log-transformed cumulative hazard function and the latter log-transformed time. For proportional hazards model assumptions to be met, the curves representing the different strata should be roughly parallel to each other throughout. The plots generated for the Maya and Toba populations (Figure E1) both showed curves (by offspring sex) that were approximately parallel to each other, and therefore model assumptions were considered met.

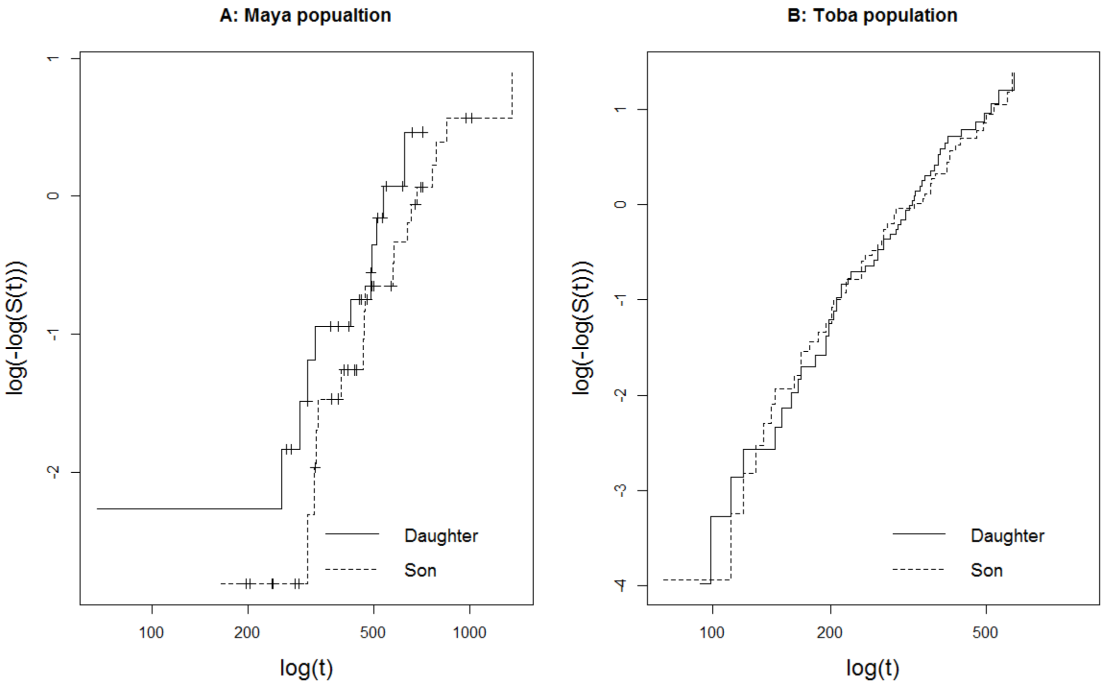

Figure E1. Cox proportional hazard model diagnostic plots for A) Maya population and B) Toba population.

Model assumption were considered to be valid as the curves representing the different strata in both cases remain approximately parallel to each other throughout.