HUMAN CANALIZATION AND FEMALE GROWTH BUFFERING WITH *DROSOPHILA* AS A MODEL ORGANISM

by

JASON A. DECARO, COMMITTEE CHAIR
LAURA K. REED
LESLEY J. WEAVER
SONYA E. PRITZKER

A THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Arts
in the Department of Anthropology
in the Graduate School of
The University of Alabama

TUSCALOOSA, ALABAMA

2018

ABSTRACT

Child health is a central concern in populations experiencing economic, environmental, and nutritional stress. Adversity, however, does not affect individuals uniformly as preferential child investment and underlying biological processes may lead to instances of differential growth outcomes among boys and girls. The causes of such differences may be misinterpreted when examining health and nutrition survey data and are deserving of inspection. This research utilizes an evolutionary female canalization model to broadly contextualize observed instances of sex-specific growth outcomes. The objectives of this research are to: (1) investigate sex-specific differences in growth and development; (2) address contributing cultural factors of the target population; (3) create a biological framework for understanding female canalization; and (4) create a robust understanding of sex-specific growth outcomes that can be used to interpret health and nutrition survey data. To complete these objectives, this research uses the Cebu Longitudinal Health and Nutrition Survey of the Philippines as a database for analysis. *Drosophila melanogaster* was employed as a model organism to investigate female canalization as an ancestral biological and evolutionary mechanism present in both *Drosophila* and humans. Human results indicate that girls are less sensitive to adverse environmental conditions and show more stable patterns of growth and development than boys. *Drosophila* results suggest there to be significant sex, diet, and genotype interactions that contribute to differential male and female phenotypic outcomes. These results show there are shared, sex-specific developmental characteristics between humans and *Drosophila* and that an understanding of contributing factors is crucial to future interpretations of health and nutrition survey data.

LIST OF ABBREVIATIONS AND SYMBOLS

WHZ	Weight-for-height z-score
HAZ	Height-for-age z-score
WAZ	Weight-for-age z-score
ZBMI	Body mass index z-score
WHO	World health organization
LBW	Low birth weight
AEL	After egg laying
SES	Socioeconomic status
INC	Iglesia no Cristo
L1	First instar larvae
L2	Second instar larvae
L3	Third instar larvae
%	Percent
+	Plus
-	Minus

:	Ratio
>	Greater than
<	Less than
=	Equal to
~	Approximately
SD	Standard deviation
p	Probability of result
n	Sample size
df	Degrees of freedom
F	Test of ratio of variance
Sig.	Significance
E	Exponent
t	t test
ANOVA	Analysis of variance
g	Grams
dL	Deciliter
cm	Centimeter
mg	Milligram

kg	Kilograms

ACKNOWLEDGMENTS

First, I would like to thank my advisors Jason DeCaro and Laura Reed for their continued assistance and guidance throughout my graduate career. Without their support this research would not have been possible. Second, I would like to thank my committee members Lesley Weaver and Sonya Pritzker for their contributions in making this research possible and for providing insight into specialties outside my realm of expertise. Third, I would like to thank The University of Alabama Department of Anthropology and all the wonderful faculty, staff, and students that contribute to such an outstanding department. Additionally, I thank The University of Alabama College of Arts and Science for creating a truly special place where students can achieve their goals and for fostering an environment conducive to the pursuit of academic excellence. I would also like to personally thank my friends and family for their continued support in helping me achieve my personal goals. Without them this research would have been all the more arduous. Finally, a big thank you to my wife, Kaitlin Spangler, for encouraging me to pursue my dreams and for her patience in enduring the long hours of seclusion that came with my graduate schooling.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Many health and nutrition surveys collect anthropometric data as a way to determine the health and nutritional status of a population. In some cases, there are data reflective of differences in male and female growth and development outcomes. This is especially true in populations experiencing economic adversity or malnutrition where females appear to be doing better than males. It is critical to understand the mechanisms behind observed differences in male and female health outcomes so an accurate interpretations of survey data can be made. Data showing growth closer to the international reference standards among females do not reflect the fact that they too are experiencing chronic malnutrition despite having anthropometric measurements that suggest otherwise.

My research posits that evolutionary canalization mechanisms have led to a female buffering effect where phenotypic variation is dampened against environmental perturbations. Furthermore, this research stresses the importance of understanding the cultural elements of a particular population that contribute to differential growth and development outcomes of males and females. Culture plays a major role in determining sex-specific anthropometric outcomes as differential son or daughter preference, for instance, may lead to unequal parental investment and biases. My research also builds upon previous theories by contextualizing them within a broader evolutionary canalization framework and incorporating them within a cultural context. A biocultural synthesis will create a more holistic model that can be applied to interpretations of anthropometric and biological outcomes of males and females in a population.

To investigate the impact of female canalization and culture on growth outcomes, I used the Philippines as a focal population for analysis. The Cebu Longitudinal Health and Nutrition Survey used for this analysis provided socioeconomic, environmental, and anthropometric data that can be used to analyze differential male and female growth and development outcomes. (Adair, L. S., & Popkin, B., 2001). I chose the Philippines as a focal population because longitudinal research in the area provides cultural and anthropometric data on women and their children. Additionally, the Philippines offer the opportunity to examine data within the context of a developing country where variation in local conditions can be studies in relation to sex-specific growth and development outcomes. Conducted in 1984, with follow-up surveys occurring in the years following, the health and nutrition survey collected health and nutrition data on 3,327 mothers and their children from birth. I aim to use secondary analysis to investigate the relationship between adversity and differential growth and development outcomes of Filipino boys and girls from infancy to age eight. Additionally, a thorough ethnographic literature analysis of the Philippines was conducted for this research. My research assesses factors including socioeconomic status, gender roles, gender preference, and other cultural conditions of the Philippines to see how they affect the growth and development of children who live there. It is my intent that a biocultural approach to research will enable a more robust interpretation of the data. The longitudinal aspect of the survey also enables the analysis of infant conditions that may contribute to future growth and development outcomes. In addition, my research focuses on the culture and history of the Philippines and examines how culture affects not only male and female childhood development, but also the general conditions of the women and mothers who live there. Anthropometrics combined with ethnographic literature creates a biocultural synthesis that allows for more robust interpretations of data.

Another element of my research is the use of model organism *Drosophila melanogaster* to analyze the biological mechanisms of differential male and female growth outcomes. This creates a model that addresses the possibility of shared ancestral evolutionary biology between humans and *Drosophila* that provides insight into observed differences in male and female canalization. The use of a model organism also enables the phenomena of canalization to test in a controlled experimental setting that allows for genetic homogeneity and precise nutritional manipulation. The short reproduction and growth time of *Drosophila* will also allow for a real-time model of female growth buffering to be constructed (Ashburner, 1989). Additionally, the genetically homogenous lines of *Drosophila* used in this research will help to contextualize evolutionary principles of canalization in genetically heterogenous human populations. The biological outcomes of female growth buffering will be the primary focus for this portion of my research. In *Drosophila,* altered experimental diets will be the primary source of introducing environmental stress to the experimental population. The data on *Drosophila* can be compared to that of the human data to identify similarities and differences among males and females subjected to environmental stress. My research aims to utilize variables of adversity in both *Drosophila* and humans to create a more holistic model of how males and females respond to conditions of environmental change. The use of a model organism in conjunction with human longitudinal data allows for female canalization to be analyzed as a cross-species, evolutionarily shared biological function.

My research aims to expand upon previous theories by contextualizing and incorporating them within a broader evolutionary canalization framework. This theoretical synthesis will create robust model that can be applied to interpretations of anthropometric and biological outcomes. Many studies conducted on health and nutrition survey data have not incorporated a female canalization model into their analysis. My research also aims to investigate underlying causes that potentially lead to differential growth and development outcomes between males and females. It is my hope to provide insight into female growth buffering and provide clues as to how culture and the environment operate on sex-specific phenotypic outcomes. In doing so, a more complete interpretation of female canalization can be constructed to better understand how evolution has operated on populations to maintain fecundity. Additionally, it is my hope that a comprehensive canalization model and biocultural approach will provide context to observed differences in male and female anthropometrics present in health and nutrition surveys and contribute to meaningful interpretations of data.

Under conditions of environmental stress, the following are hypothesized: (1) boys at age eight will have lower height-for-age z-scores (HAZ), lower BMI z-scores (ZBMI), and lower weight-for-age z-scores (WAZ) than girls at age eight; (2) there will be an interaction between adversity and sex-specific childhood growth outcomes; (3) girls at age eight will exhibit reduced sensitivity to economic adversity in the form of growth markers (ZBMI, HAZ, WAZ); (4) 3rd instar female *Drosophila* raised on high-protein diets, low-protein diets, and nutrient restricting low-protein/low-carbohydrate diets will have greater diet-specific measures of weight, leanness and adiposity than 3rd instar male *Drosophila* raised on the same diets; (5) There will be significant sex, diet, and genotype interactions that contribute to sex-specific phenotypic outcomes in *Drosophila*. Despite the complexity of cultural influences on phenotypic outcomes, the following are several explanations regarding how scenarios of cultural conditions impacting human biology can be interpreted: (1) no observed difference in height-for-age z-scores (HAZ), BMI z-scores, and weight-for-age z-scores (WAZ) can be interpreted as culture and biology offsetting themselves or operating in opposite directions; (2) in conditions of male preference, girls continuing to fare better can be interpreted as biological mechanisms being strong enough to overcome cultural male-preference; (3) in conditions of egalitarian treatment of boys and girls, girls exhibiting similar phenotypic variation to that of boys can be interpreted as egalitarian cultural norms offsetting differential biological outcomes among boys and girls; (4) males and females both showing positive HAZ and WAZ scores despite nutritional stress can be interpreted as compounding cultural and biological influences.

CHAPTER 2

LITERATURE REVIEW

2.1. Theoretical Overview

Environmental stress can impact the fertility of males and females of a human population during growth and affect future population fecundity. Trivers and Willard (1973) stated that parental investment in sons of good quality will have greater reproductive returns than investment in daughters of good quality, while parental investment in sons of poor quality has lower reproductive returns than investment in daughters of poor quality. They predicted that mothers in good condition are likely to give birth to sons and mothers in poor condition are likely to give birth to daughters. This can lead to a distortion in sex ratios within the population as more females will be produced than males in times of stress. During times of environmental stress, selection will favor one sex over the other based on reproductive costs and benefits. Trivers and Willard proposed that in poorly nourished populations, sex ratios become distorted and reflect an increase in the number of females because female offspring will have a greater future reproductive potential than males Myers (1978) provided another explanation for sex ratio distortions. Myers proposed that female birth rates will increase during times of nutritional stress because females are smaller and reproductively less expensive than males due to sexual dimorphism (Myers, 1978). This theory is based off reproductive costs and benefits rather than maternal condition, but still provides an explanation for increased female births during food shortages.

However, sex ratios at birth alone do not provide an explanation for possible origins of increased female fitness during times of environmental and nutritional stress, and only reflect that such conditions are possible. While studying rates of diabetes mellitus in modern populations, Neel (1962) formulated the thrifty genotype hypothesis, which posits that genetic factors favor the storage of adipose tissue in populations under certain environmental conditions. In populations subjected to nutritional stress in the past, the thrifty genotype increased in frequency as natural selection favored individuals with an increased insulin response to ingested food. This facilitated the deposition of adipose tissue and enabled "thrifty" individuals to better persist during periods of nutrient restriction (Neel, 1962). Additionally, it has been suggested there are sex-specific responses to nutritional stress due to reproduction-based differences in energy metabolism. Females require greater fat storages than males to carry out successful gestation and lactation. Natural selection, acting on the reproductive potential of females, may have led to increased metabolic efficiency among females in order to maintain reproductive functions during times of food shortages (McGarvey, 1994).

The theories mentioned above, however, only cite increased female fitness as specific functions and do not discuss them in terms of a broader evolutionary framework. This research expands upon previous theories proposed by Trivers and Willard, Myers, Neel, and McGarvey by incorporating them into a more comprehensive examination of female growth buffering using an evolutionary canalization model. The theory of canalization refers to the dampening of phenotypic variation in populations subjected to perturbations in environmental conditions (Waddington, 1957). Genetic canalization operates in populations by restricting heritable phenotypic variation under natural selection and, over time, creates a degree of insensitivity to changes in environmental conditions. This is referred to as environmental canalization and is evident when members of a population display reduced phenotypic variation when subjected to environmental change. Canalization occurs as stabilizing selection conserves genes that restrict phenotypic variation and increases the frequency of such genes in a population. Under stabilizing selection, genes that reduce phenotypic variation in response to environmental change increase the mean fitness of a population by maintaining their adherence to optimal baseline conditions (Wagner et al., 1997). This research posits that females will exhibit increased canalization over males to maintain an optimal phenotypic condition that supports costly reproductive success.

Differences in sex-specific growth and development outcomes are dependent on a number of conditions and factors that deserve consideration. Instances of increased female canalization during times of environmental stress can occur during prenatal growth. In such cases, the physical condition of the mother differentially affects the prenatal growth of her offspring depending on if they are male or female. Maternal undernutrition has been observed to result in greater decreases in male birth weights than female birth weights when the mother is subjected to periods of food shortages (Stinson, 1985). Additionally, maternal anthropometric characteristics can affect prenatal growth and lead to differences in child birth sizes. Maternal arm circumference and stature has been found to influence male birth length and weight while not contributing to the length and weight of female infants (Frisancho et al., 1977). It has also been suggested that prenatal stress under conditions of hypoxia affects males more than females. Males born at high-altitude have been found to have lower birth lengths and weights than those born at low-altitude with no significant differences among female infants (Haas et al., 1980). Overall, studies suggest that males have higher occurrences of prenatal mortality and growth retardation than females but also have greater increases in growth when maternal conditions improve (Stinson, 1985).

Postnatal sex-specific growth outcomes, however, are more complicated. This is in part due to male and female children being differentially exposed environmental stressors that impact growth and development. Past studies which focus on undernutrition as a stressor are divided on whether or not females are more buffered than males with some studies reporting supportive evidence of female canalization and others reporting no significant differences. This may be due to cases where male children receive preferential treatment over female children making it difficult to determine the degree to which males show increased sensitivity to environmental stress over females. Similar to studies on postnatal nutritional stress, studies on climatic stress do not reveal consistent evidence of increased male sensitivity. Although climatic stress has been found to affect the prenatal growth of males more than females, it has not been found to significantly affect postnatal growth. Some studies suggest that levels of sexual dimorphism are reduced among children in high-altitude conditions but this is not supported by later growth patterns during childhood and adolescence. This is perhaps due to delayed maturation in high-altitude children where sexual dimorphism does not become as apparent until after puberty. In response to the inherent complications surrounding past growth and development studies, it has been noted that local conditions and the exact nature and timing of environmental stressors need to be considered when making interpretations regarding increased male sensitivity (Stinson, 1985). The above-mentioned complications surrounding measures of postnatal growth and development illustrate the importance of determining which local cultural conditions, such as preferential child treatment, may influence growth outcomes.

2.2. Evidence of Adaptive Sex Ratio Adjustment

Apparent shifts in human population dynamics have been observed historically as evidenced demographic examinations of China during the Great Leap Forward Famine. The famine occurred during the Great Leap Forward Movement, initiated in November 1957, and had disastrous consequences for the Chinese population. The Great Leap Forward Movement lasted until January 1961 and resulted in 30 million deaths (Peng, 1987; Aston et al., 1984). A study conducted by Shige Song used data from the 1982 one-per-thousand fertility survey conducted by the Chinese State Family Planning Commission, which generated birth histories of 310,101 Chinese women aged 15-65 from face-to-face interviews. Song's sample consisted of 83,045 children born from the initial 310,101 women who took part in the 1982 survey. An examination of sex ratios between 1929 and 1982 revealed a decline in male births during the years of famine (1959-1961). In the years leading up to the famine, nutritional availability was steady and sex ratios were less distorted. However, when food insecurity became widespread, China saw a decrease in male births. Between September 1929 and April 1960, male births declined steadily at a rate of 0.00011 per month. Male births rapidly declined over the course of the following 42-month period from April 1960 to October 1963; declining from 0.521 to 0.51 at a rate of 0.00103 per month. As food availability improved, the rate of male births rebounded from 0.51 to 0.518 in just two years following the famine. By 1982, the proportion of male births slowly rebounded to pre-famine proportions of 0.520. Song suggested that famine-induced variation in maternal nutrition leads to a decrease in male birth rates and is responsible for the abrupt changes in sex ratios during the period of famine. He also noted that famine-induced fetal attrition could have caused the distortions in sex ratios as male fetuses may be more sensitive to nutritional deficiency, but cautions that more research in this area is needed (Song, 2012).

Distortions in sex ratios favoring female survivability under nutrient-deficient conditions have been observed in non-human animals. An examination of 46 Peruvian spider monkey infants conducted by Symington (1987) revealed adaptive sex ratio adjustments biased towards female offspring. Mothers were divided into high and low-ranking groups based on their social standing. Social rank was determined by agonistic encounters involving displacements and agonistic threats. Dominant individuals displayed open mouth threats to which subordinate individuals would retreat. The ranks were reported to remain stable over the course of the study. Between July 1981 and June 1986, two communities of spider monkey were observed with a total of 31 adult females and 11 adult males. Over the course of 21 months, 44 infants were born and sexed. 12 males and 11 females were born to high-ranking mothers, while 0 males and 21 females were born to low-ranking mothers. Among high ranking mothers, the average time between a male infant reared to weaning and the birth of another infant was 36 months. Conversely, high ranking mothers who gave birth to females had shorter birth intervals at an average of 29 months. High ranking mothers also carried male infants an average of 3 months longer than female infants (Symington, 1987). This indicates differential sex-based parental investment depending on the mother's social rank, and agrees with the adaptive sex ratio adjustment theory proposed by Trivers and Willard that mothers in good condition will invest more heavily in sons than daughters.

2.3. Feeding Practices, Childhood Morbidity, and Growth and Development

Infant feeding practices can have implications for the growth and development of offspring, and has consequences for infant health (Cunningham, 1995). One health consequence of formula-feeding is that it does not provide anti-infective agents found in breast milk to the infant. The underdeveloped immune system of infants is particularly susceptible to infection, which can be improved by the anti-infective agents found in breast milk. The agents include antibodies, proteins, white blood cells, carbohydrates, and fats that are passed to the infant through the mother's milk (Institute of Medicine, 1991). The world Health Organization (WHO) recommends that infants be fed exclusively breast milk until 6 months of age and should continue to be breast fed with additional, nutritionally adequate complementary food until 2 years of age. VanDerslice et al. (1994) investigated feeding practices and diarrheal prevalence among children of the Metropolitan Cebu area of the Philippines using the Cebu Longitudinal Health and Nutrition Survey. The study found a high prevalence of mixed infant feeding with 38% of infants being mixed-fed and 19% being completely weaned by 2 months of age. An additional 20% of infants were given non-nutritive liquids complementary to breast milk during the first 2 months of age. Infants who were fully breast-fed dropped to less than 10% by the end of the first 6 months of life. In relation to diarrheal disease prevalence, non-breast-fed infants were almost three times more likely to suffer from diarrhea than breast-fed infants. The prevalence of infants suffering from diarrhea was 7.2% a week after the interview was given and rose to 20.4% over the first 6 months of life. This study suggested a clear relationship between feeding practices and susceptibility to diarrheal disease. They also noted that while good community sanitation, such as running water and excreta disposal reduced diarrhea prevalence, breast-fed and mixed-fed infants still had much lower rates of diarrhea. Interestingly, this study also found that female infants showed a lower prevalence of diarrhea than males with 12.3% of females and 13.1% of males being afflicted with diarrhea at 4 months of age. This could contribute to observed differences in the prevalence of growth stunting among males and females in other studies (VanDerslice et al., 1994).

Adair and Guilkey (1997) investigated the prevalence of growth stunting in relation to morbidity among children of the Philippines. Using the Cebu Longitudinal Health and Nutrition Survey, they defined stunting as an outcome of long-term growth retardation in individuals with z-score lengths that fell -2 standard deviations below the age and sex-specific WHO reference median. To test the relationship between stunting and morbidity, they developed a hazard model which defined individuals with "high morbidity" as those with a 50% chance of diarrhea, a 33% chance of febrile respiratory infections, inappropriate feeding (not breast feeding), and no preventative health care. Overall, infants with low birth weight (LBW) comprised 11.5% of the sample and 31% of LBW infants were stunted at 24 months of age. At 12 months, 37.7% of rural and 35.1% of urban children were stunted. This increased to 68.8% of rural and 61.9% of urban children being stunted at 2 years of age. Males were more likely to be stunted than females at 12 months of age, with ~17% of males and ~10% of females falling below the Filipino 5th percentile of length-for-age. However, the number of stunted males began to decrease after the first year of age and stunting among females became more prevalent. This study found that morbidity increased the likelihood of stunting as diarrhea increased the probability of stunting by 9.8% and febrile respiratory infection by 11.19%. Preventative healthcare reduced the probability of stunting by 10.42%. They cited VanDerslice's (1994) findings of differences in diarrhea prevalence as one possible factor in differential growth and development between males and females. They also suggested that unaccounted factors such as parental care investment and sex-differences in diet may also contribute to perceived differences (Adair & Guilkey, 1997). These studies provide evidence indicative of a population experiencing some infant morbidity and nutritional deficiency and highlights the importance of analyzing such data with these considerations in mind.

2.4. Nutrition and Growth and Development

Children under adverse or disadvantaged circumstances typically see a decline in growth after 4-6 months of age and are substantially shorter than advantaged individuals by two years of age (Martorell & Habicht, 1986). This type of growth retardation is referred to as growth faltering and is prevalent in many low-to-middle income countries. Growth faltering is evident in data concerning height-for-age and weight-for-height z-scores of children in nations where food security is not equal to that of developed nations (Stinson, 2012). Weight-for-height z-scores can sometimes approximate those of developed nations because when exposed to nutrient-deficient conditions, children will stop growing in height and weight, but will not be become especially thin. Typically, in extremely stressed populations, linear growth in height can slow down as maintaining weight becomes a priority. This may be indicative of reserving fat stores in order to maintain the energy needed for metabolically costly brain development that occurs in childhood (Leonard et al., 2009). Height-for-age reflects stunting while weight-for-height reflects wasting. Growth faltering typically occurs when breast milk cannot adequately support growth of the individual or when supplementary foods given post-weaning are not be nutritionally sufficient to support growth and may lead to a reduction in growth (Stinson, 2012).

Growth and development patterns regarding nutritional intake have been observed among Tsimane' populations of the Bolivian Andes. Foster et al. (2005) analyzed patterns of growth and nutritional status of Tsimane' children from the Bolivian Andes in the Department of Beni. Anthropometrics were collected on one child per household and included stature, weight, mid-arm circumference, and the sum of triceps and subscapular skin folds. These anthropometric measurements were used as indicators of child nutritional status. Descriptive variables included village distance to major towns, number of households, distance to forest, number of teachers, number of healers, and village road access. Height-for-age z-scores (HAZ) of Tsimane' male and female children showed high levels of linear growth retardation when compared to National Center for Health Statistics values. Mean HAZ scores for males were lower than that of females (HAZ= -1.96 vs. -1.65; $p < 0.05$). Mean weight-for-age z-scores (WAZ) for males and females did not differ significantly (-1.14 for males and -1.06 for females) but did fall ~1SD below U.S. averages. Skinfold scores indicated that Tsimane' children were leaner than children in the United States but only fell -0.58 SD below U.S children, suggesting that they were not suffering from severe energy stress. Lower-arm circumferences indicate that Tsimane' children were not experiencing protein malnutrition (-0.21 for males and 0.05 for females) as low arm muscularity did not fall below 2SD of U.S. averages. Levels of stunting had an overall prevalence of 47% among Tsimane' children and indicated long-term moderate nutritional stress in children under nine years of age. 52% of male and 43% of female children showed growth stunting. Low weight-for-height z-scores (WHZ) were used to measure long term nutritional stress and represented sever short-term nutritional stress in the form of wasting. This figure was low with a prevalence of 4% for males and 6% for females. Correlations between village characteristics and child nutritional status (HAZ, WAZ, WHZ, skinfold summation, and arm muscularity) were performed. Skinfold measurements of males and females were significantly correlated with the number of houses in the village (0.20 for males and 0.18 for females; $p < 0.01$). Similarly, skinfold measurements were significantly correlated with the number of teachers in the village (0.29 for males and 0.14 for females; $p < 0.001$) and was the strongest correlation between village characteristics and child nutritional status. This indicated that access to education was the strongest determinant of childhood nutritional stress and affected adiposity more than any other village characteristic. Additionally, the prevalence of stunting indicated that post-weaning nutritional provisions were not adequate to sustain childhood growth. This study suggested this was evidence of a poor diet lacking in key nutrients needed in early childhood development (Foster et al., 2005).

2.5. Economic Influences on Child Growth and Development

The influence of culture on growth outcomes between males and females is another central focus of this research. One such factor of interest to this research is socioeconomic status (SES) and household condition. It has been posited that factors such as social class and economic status can impact diet and infection rate and can indirectly lead to adverse childhood growth patterns (Martorell & Habicht, 1986). To examine the effects of household conditions and SES on childhood growth outcomes, Pebley and Goldman (1995) analyzed data from the National Survey of Maternal and Child Health conducted in Guatemala in 1987. In total, 5,160 women aged 15-44 and their children took part in the health survey and answered questions concerning household conditions, family SES, the use of health services, prenatal care, delivery assistance, and immunization. A total of 2,437 children aged between 3 and 36 months participated in the survey and data on weight and height was collected and anthropometric measurements were taken. Height-for-age index scores represented a measure of chronic malnutrition and were evidenced by stunting. Parent education greatly impacted average height-for-age distributions. Fathers with no education made up 32.1% of the sample with children falling -2.86 SD under WHO reference medians. Fathers with secondary education made up 11.9% of the sample with children falling -1.47 SD under WHO reference medians. The occupation of the father also had implications for average height-for-age distributions. Fathers who were unemployed made up 1.1% of the sample population and had children who fell -2.57 SD below reference standards. Conversely, fathers in the technical and professional field made up 5.4% of the population and had children who fell -1.35 SD below reference medians. The largest occupational category was self-employed agriculturalists who made up 34.5% of the sample population and had children who fell -2.88 SD below reference medians. Household quality also influenced average child age-for-height standard deviations (running water= -2.15 SD vs no water= -2.83 SD/ refrigerator= -1.36 SD vs no refrigerator= -2.69 SD/ cement floor= -1.99 SD vs dirt floor= -2.90 SD/ electricity= -2.10 SD vs no electricity -2.88 SD/ traditional pregnancy care= -2.96 SD vs modern pregnancy care= -2.11 SD) (Pebley & Goldman, 1995). This study provides evidence that parental education, occupation, and household living conditions as markers of socioeconomic status can severely affect childhood growth outcomes.

Gender inequality among children can lead to differential health outcomes due to differences in parental investment. Son preference in some parts of South and East Asia has led to increased mortality rates among female children (Sudha & Rajan, 1999) as societies with sex discrimination favoring male children often show evidence of skewed sex ratios favoring males within the population. It has been argued that in societies with a strong son preference, daughters will be marginalized in their access to rare goods and services such as health care, luxury food items, and other provisional resources (Li, 2004). For example, female infanticide, sex-selective abortions, and sex-selective birth misreporting are prevalent in rural areas of China and may be responsible for unbalanced sex ratios at birth, increasing from 1.08 in the early 1980's to 1.18 in the early 2000's (Scharping, 2003). Similarly, sex ratios of infant mortality in China also reflect son preference, increasing from 0.95 in the early 1980's to 1.15 in the early 1990's (Attane, 2005). It has been suggested possible son preference in China may stem from economic reform and decollectivization during the late 1970's that placed increased value on male child labor and emphasized the role of males as household heads in rural China (Li, 2004). Family planning policies of the 1970's which placed strict limits on family size may also reinforce sex discrimination at birth, though these policies have changed over time and vary from region to region (Graham et al., 1998).

Song and Burgard (2008) used the China Health and Nutrition Survey and the Cebu Longitudinal Health and Nutrition Survey to conduct a comparative study of gender preference in China and the Philippines. This study investigated the impact of son preference and growth outcomes among Chinese and Filipino children using sex difference in height and longitudinal anthropometric data to measure potential son preference as parents may not accurately report stigmatized behaviors in surveys. This enabled the generation of data reflecting possible discriminatory resource allocation in the household and differential parental investment. Results showed that at two years of age, Filipino boys are ~1.09 cm taller than Filipino girls, while Chinese boys are ~0.86 cm taller than Chinese girls. These data indicated that there was no definite advantage in overall height for Chinese boys at age two when compared to Filipino boys of the same age. The linear growth rate component reflected a more definitive male advantage among Chinese boys when compared to Filipino boys. In China, the linear growth rate for boys was 0.03 cm faster per year than that for girls ate age two. Conversely, the linear growth rate for Filipino boys was 0.11 cm slower per year than that for girls at age two. Additionally, there was a rate of growth advantage of 0.15 cm per year of age for Chinese boys after two years of age; equating to 2.4 cm over 16 years of growth with about one-third of a standard deviation in height distribution at age 16. Song and Burgard determined that Chinese boys have a growth advantage over Chinese girls evident after early childhood and becoming stronger during adolescence. Moreover, son preference in China was evidenced by Chinese boys having significantly higher height-for-age z-scores than Chinese girls at ages 2-9 (+.11, $p<0.001$). Among Filipino children of the same age, there was no statistically significant difference in height-for-age z-scores between boys and girls (Song & Burgard, 2008). These studies demonstrate the need for a careful analysis of political and societal conditions which may lead to differential treatment of boys and girls within a particular culture.

Economic adversity can also affect childhood growth and development outcomes and is another focus of this research. Undernutrition at the family or household level can be precipitated by lack of basic sanitation, hygiene, and access to other resources. The underlying causes behind lacking resources at the family level can be attributed to the economic conditions of the household at differing levels of society (Kavishe, 1995). To examine the effects of household income on childhood growth, Yang et al. (2009) analyzed household and village income and child nutrition status in rural Yunnan, China. They conducted surveys from 2002-2007 in which 1731 households and 1,801 children were assessed. Anthropometric measurements included recumbent measurements of children under the age of two years old, height measurement of children over the age of two years old, and child weight measurements recorded to the nearest 0.1 kg. Height-for-age z-scores (HAZ) and weight-for-age z-scores (WAZ) were generated for all children with any score falling -2 SD below WHO reference medians being considered stunted and underweight respectively. Average household income increased from 2002-2007 with 22.1% of households falling below the national poverty line in 2002 compared to 7.7% in 2007. Village income also increased with an average per capita net income of 1904 yuan/person/year in 2002 compared to 2638 yuan/person/year in 2006. Overall, stunting prevalence affected 37% of children with 39.4% of males being stunted and 34.5% of females being stunted. 17.5% of children were found to be underweight with 18.6% of boys and 16.4% of girls being underweight. It was found that average village income had a greater impact on child undernutrition than average household income. Children in villages falling in the 2nd quintile of average village incomes had a 1.3 odds ratio of being stunted while those falling in the 5th

quintile had a 0.3 odds ratio of being stunted. Children in households falling in the 2nd quintile of average household income had a 0.8 odds ratio of stunting while those falling in the 5th quintile had a 0.5 odds ratio of stunting. Yang et al. suggested village income to be a stronger determinant of child undernutrition as village income may have a greater influence on the availability of clean drinking water and hygiene (Yang et al., 2009). These studies show how culture, politics, and economic adversity can have sever implications for childhood growth and development outcomes. This research will examine such factors when analyzing data from the Cebu Longitudinal Health and Nutrition Survey of the Philippines.

2.6. *Drosophila melanogaster* Lifecycle

The lifecycle of *Drosophila melanogaster* begins by the laying of fertile eggs by the female *Drosophila*. Larvae hatch from fertilized eggs 22-24 hours after egg laying (AEL) and begin to feed in the surrounding environment. There are three stages in larval development that are referred to as first instar (L1), second instar (L2), and third instar (L3). The L1 lasts for 24 hours and consists of the larvae feeding on the surface of the food medium and then burrowing after molting into the L2. The L2 lasts for 24 hours in which the larvae remains buried in the food medium as it develops into the L3. The L3 lasts for 48 hours, most of which the larvae spends buried in the food medium. At 110 hours AEL, the L3 cease to feed on the food medium and emerge to find a suitable location for pupariation. Pupariation takes place 120 hours AEL and the pupal stage lasts 4-4.5 days until eclosion, when the adult fly emerges from the pupa. Adult flies emerge with unexpanded wings and little pigment in their bodies. 1-hour post-eclosion, the wings begin to expand and full pigmentation occurs within 2-3 hours (Ashburner, 1989).

2.7. *Drosophila melanogaster* as a Model Organism

Drosophila melanogaster, or fruit fly, has been used as a model organism in biomedical science for over a century and provides a means to overcome the practical and ethical limitations of using humans as research subjects (Bellen et al., 2010). The fully sequenced *Drosophila* genome revealed that 75% of known human disease genes are conserved in *Drosophila*, making their utility as a model organism in biomedical research apparent (Reiter et al., 2011). Moreover, it has been found that many of the genes responsible for embryonic development from a single cell to a mature multicellular organism are present in *Drosophila* and humans as many of these building blocks have been conserved across species through evolution (Jennings, 2011). Genetic experiments that would take months or years in other vertebrate models can be accomplished in weeks using *Drosophila.* In the laboratory, *Drosophila* are relatively inexpensive and convenient to maintain. Each female *Drosophila* can lay ~100 eggs per day for up to 20 days, making it easy to create research populations of substantial numbers. Additionally, *Drosophila* diets can also be easily manipulated to suite a range of experimental designs. In the lab, their diets consist of a jelly-like substance typically created from a mix of cornmeal, water, yeast, corn syrup, agar, soy flour, and malt extract and can be manipulated to create a variety of recipes (Stocker & Gallant, 2008). Genetic conservation between humans and *Drosophila*, practicality in research, short generation times, and the ability to easily manipulate experimental diets make *Drosophila* a good model organism for human biological research.

2.8. *Drosophila melanogaster* Nutritional Geometry

Diet composition can influence variations in *Drosophila melanogaster* phenotype and can impact behavior and physiology. Skorupa et al. (2008) conducted a study to examine how diet composition and overall caloric intake moderate lifespan, consumption, and fat deposition in flies. They manipulated the macronutrient composition of food by altering levels of sucrose (carbohydrate) and yeast (protein) and conducted a phenotypic analysis of adult *Drosophila* raised on such mediums. This allowed for assessments of how triglyceride levels and protein levels interact as nutritional components related to adult obesity. This research focused on adult-specific phenotypes with larvae reared on a control diet to eliminate developmental effects of dietary restriction. Five concentrations of sucrose and brewer's yeast were used to create 25 experimental diets with varying carbohydrate:protein ratios (sugar x yeast concentrations 2.5 $g \cdot dL^{-1}$, 5 $g \cdot dL^{-1}$, 10 $g \cdot dL^{-1}$, 20 $g \cdot dL^{-1}$, 40 $g \cdot dL^{-1}$). Once-mated, adult flies were placed in one of the 25 different adult-specific food mediums and collected after 10 days of exposure. Results indicated a range of interactions between diet and phenotypic responses. It was found that fat storage (triglyceride accumulation) is enhanced by carbohydrates and suppressed by yeast. The level of adiposity in adult flies was significantly related to the amount of sugar in the diet ($p<0.0001$). Conversely, the amount of dietary yeast was inversely related to adiposity ($p<0.0001$). This indicated that increased protein availability limited fly adiposity. The interaction between sugar and yeast was also significant ($p=0.04$). It was also found that protein storage was determined by dietary carbohydrates in the food medium ($p<0.0001$) as yeast increased leanness. High levels of dietary yeast also created heavier flies while increased carbohydrate availability created lighter flies. Overall, it was also found that triglyceride levels were maximized in a low-protein/high-carbohydrate diet and minimized in a high-protein/low-carbohydrate diet. This study determined that sugar:yeast ratios rather than overall caloric content affected the levels of triglycerides and protein adult flies maintained. To assess why caloric intake may not have a significant impact on adult physiology, the authors suggested that nutrient availability may not equate to caloric uptake as some diets may not be palatable or may affect feeding behavior. To assess nutrient uptake rates, they added an inert dye to food and quantified ingestion by spectrophotometrically measuring the amount of dye in homogenized flies. Results indicated that flies tend to consume more when presented with carbohydrate-rich food ($p<0.0001$) while protein-rich food suppressed consumption ($p<0.0001$) (Skorupa et al., 2008).

CHAPTER 3

THE PHILIPPINES

3.1. Spanish Occupation

The Republic of the Philippines is an archipelago lying 500 miles off the Southeast coast of Asia and includes around 7,100 islands surrounded by the South China Sea, the Celebes Sea, and the Philippine Sea. The Philippines consists of a land area totaling 115,830 square miles with Manila, the national capital, being located on the largest island of Luzon (Goetz, 1987). The Philippines is named after Phillip II of Spain during the 16th century colonization of the islands. The Spanish saw the Philippines as critical location to reach the West Indies and Spice Islands and established control over the islands from Luzon to Mindanao by the end of the 16th century (Chandler, 2017). The Spanish, however, faced difficulties imposing rule as the Philippines lacked a common, unified language as the population was spread out over an archipelago. They found it necessary to divide the Philippines into Orders according to individual linguistic groups. These Orders were governed by Spanish friars who had spent considerable amounts of time learning the local dialects and acted as a channel through which Spanish civil authority could be communicated. The Spanish friars, traveling with Spanish soldiers, sought to convert Muslims and enforce Catholicism as the dominant religion as their goal was the Christianization and Hispanization of the Philippines. Additionally, Spanish friars were provided financial support from the *Patronato Real*, or the Royal Patronage, giving them legal authority. Any Filipinos seeking to communicate with Spanish authorities in Manila would have to go through the friars governing their local Order (Woods, 2006). Over the next hundred years, the Spanish levied taxes on farming, imposed Catholicism as the dominant religion, and demanded payment from the indigenous population. This lasted until Spanish friars and Spanish debt collectors (encomienda) abandoned religious instruction and withheld taxes from the Spanish Crown, leading to the conversion of rule by Spanish friars to that of a governor-general by the end of the 17th century (Chandler, 2017).

By the 18th century, galleon trade with Acapulco, Mexico made Manila the center of commerce in the Philippines. During this time agricultural practices changed rapidly as Spanish friars enforced sedentary farming as the principle means of production by local farming communities. There was resistance to this rule as Filipino Datus (old nobility class) took control of their lands by adopting Western concepts of land ownership even though their traditional land rights had been stripped. Furthermore, the galleon trade to Mexico ended in 1815 when the last ship arrived in Manila and the Philippines were open to foreign trade by the mid-1830's. As European demand for sugar and hemp increased with the construction of the Suez Canal in 1869, commercial agriculture further empowered local land owners and led to the creation of a new wealthy upper-class of individuals. Many Filipino land owners now had the means to send their children abroad to seek European education. As a result, this created a growing sentiment for public reform and a passion for Filipino nationalism by the end of the 19th century (Chandler, 2017). The most prominent of these European-educated Filipinos was Jose Rizal, whose many essays and novels focused on critiquing Spanish authority in the Philippines. By 1891, ideas of enlightenment inspired by the French Revolution spread throughout resistance groups with the use of publications such as the newspaper *La Solidaridad* and Rizal's novels *Noli Me Tengere* (1887) and *El Filibusterismo* (1891). This newly-founded sense of liberalism created an independence movement and educated rebels inspired by a nationalistic agenda began to revolt against Spanish rule (Woods, 2006). The Philippine Revolution that followed would see an increase in clashes between rebel groups and Spanish occupiers. In 1892, Rizal and other Filipino revolutionists formed a society called *La Liga Filipina* (The Filipino Union) but Rizal was arrested and exiled to the southern province of Zamboanga. Another member of *Liga*, Andres Bonifacio, formed the secret society *Katipunan* which focused on Philippine independence from Spain. *Katipunan* quickly gained popularity with its use of flags, propaganda, secret codes, weapons, and patriotic indoctrination (Rodell, 2002).

In 1896, the Spanish discovered *Katipunan's* plans and quickly worked to suppress rebel revolts around Manila. Clashes lasted for months until December of 1897 when a truce was made and the rebel leader Emilio Aguinaldo was allowed to flee to Hong Kong with other rebel leaders. The Spanish attempted to make societal reforms to appease rebel groups and end civil unrest but reforms were slow and hardly effective (Chandler, 2017). When the Spanish-American War broke out in 1898 with the destruction of the U.S. battleship Maine in Cuba's Havana Harbor, the Spanish lost control of Manila after a crushing defeat by the U.S. navy. U.S. Commodore George Dewey needed to establish control over Manila and enlisted the help of Filipino rebels. Dewey sought out Aguinaldo and arranged his naval transfer from Hong Kong to the Philippines. On May 19th of 1898, Emilio Aguinaldo returned to the Philippines and was assured by Dewey the U.S. had no interest to establish colonies and encouraged him to resume his quest for independence. Aguinaldo and his rebel forces quickly took back Manila and most of the country from Spanish control and on June 12th declared Philippine independence. A functioning Filipino government was established and a constitution was drafted on January 21, 1899 (Rodell, 2002).

3.2. U.S. Influence

In 1899, President William McKinley sent a commission to the Philippines to confirm the Filipino desire for independence and to investigate political action moving forward (Chandler, 2017). The newly-formed Asian democracy, however, did not persist for long. Relations between the U.S. and the Filipino government began to deteriorate as U.S. ships and troops began to arrive in Manila. On August 13, 1898, American and Filipino forces defeated the Spanish in Manila and as part of a prior secret agreement, the Spanish forces were allowed to surrender to the U.S. as to not admit defeat by the local *Indios* (Spanish derogative term applied to local Filipino populations). The official surrender gave the U.S. international legal rights to the islands as established by the December 10th Treaty of Paris. As relations worsened, fighting erupted among U.S. troops and Filipino forces. Aguinaldo maintained a defensive against American forces but was ultimately defeated and captured in 1901. By 1902, the U.S. officially declared hostilities to be over (Rodell, 2002).

During the conflict the American public became angry at reports concerning mistreatment of Filipinos by American forces. The reelected president William McKinley sought to maintain popularity by incorporating prominent Filipinos into a new governing body under a mission of Filipinization of the archipelago. The Philippine Assembly of 1907 created a legislative body aimed at continuing the pursuit of Filipino independence. Over the next few decades, the U.S. invested heavily in the Philippine economy and introduced a massive amount of American goods to the market. By the 1920's, ~75% of the Philippine trade was done with the U.S. This heavily impacted Philippine culture as American influence spread. The education system of the Philippines was heavily inspired by American liberal educational policy and this has lasting impacts today. English became the primary language for business, government, and education and allowed the intrusion of American popular culture into Filipino society. Despite a strong presence of American culture, the want for independence continued (Rodell, 2002).

In the midst of the great depression between 1932 and 1933, President Herbert Hoover supported legislation called the Tydings-McDuffie Law that granted independence to the Philippines. Under President Roosevelt, the Commonwealth of the Philippines was created on November 15, 1935 and independence was made official. Though World War II interrupted the period of the Commonwealth, U.S. support continued and independence of the Philippines was maintained. This marked the end of U.S. colonization of the Philippines and granted political autonomy to the country that continues to exist today (Woods, 2006).

3.3. Religion of the Philippines

The imposition of Catholicism by Spanish friars and missionaries in the 16th-19th centuries did not always live up to the expectations of Spanish friars attempting the conversion of the islands. It became apparent to Spanish priests that while Filipinos converted in great numbers, their adherence to Christian ideology was not to their expectations. This was due to a variety of factors such as language barriers and the inability of the few Spanish priests in charge of conversion to carry out their daily duties. At the time, local Filipino populations with differing cultural beliefs faced difficulty interpreting the new teachings and reconciling them with their previous beliefs (Rodell, 2002). What resulted was a folk belief of religious thinking that blended Christian ideology with traditional worship systems. This has been referred to as the "Philippinization of Catholicism" and has led to the idea that few Filipinos were traditional Catholics. It was not until the 18th century that Filipinos were allowed to train as Catholic priests by order of the Spanish king. When Spanish friars discovered Filipino priests in their pulpits conflict ensued and religion became a major component of the following Revolution (Woods, 2006).

While the Philippine Revolution of the late 19th century was focused at escaping the abuses committed by Spanish friars, the movement also sought religious autonomy. As the Revolution unfolded, so too did an independent Philippine church. In 1898, rebel leader Emilio Aguinaldo appointed Gregorio Aglipay as the leader of a new religious movement. Aglipay fought to have Filipino priests appointed to all Church positions by the Vatican instead of them being only available to Spanish priests. The roman Catholic Church excommunicated Aglipay in 1899 despite him not being anti-Catholic. However, with the success of the Philippine Revolution came the establishment of the Philippine Independent Church led by the formerly excommunicated Aglipay. Shortly after around a quarter of Filipino Christians were members of the Philippine Independent Church. The Roman Catholic Church lost almost 25% of its members and properties to the Philippine Independent Church and wanted to reestablish dominance in the Philippines. As Americans gained control of the Philippines in the early 20th century, the Roman Catholic Church approved the separation of church and state and began to allow Filipinos into church hierarchies. This provided a huge boost in popularity to the Roman Catholic Church and spelled the end of the Philippine Catholic Church. In 1906, the newly-created Philippine Supreme Court, composed primarily of Americans the Philippine elite, voted to transfer properties controlled by the Philippine Independent Church back to the Roman Catholic Church. This effectively reduced the influence of Aglipay and the Philippine Independent Church as only 5% of modern Filipinos claim to be members (Woods, 2006). Today, the Roman Catholic Church maintains a major role in Philippine politics and advocates for democracy and social justice. Additionally, the Philippines appear to be overwhelmingly dominated by Roman Catholicism despite maintaining a diversity of other religious institutions (Rodell, 2002).

Shortly after the decline of the Philippine Independent Church came another indigenous Christian church called the Iglesia no Cristo (INC). The INC was established in 1914 by Felix Manalo who was raised Roman Catholic but came to adopt various forms of religion. His ability to read the bible led him to question the way Catholicism was being preached in the Philippines. Manalo went on to join various churches including Protestant churches, Methodist Episcopal churches, and Presbyterian churches before joining the Disciples of Christ of America where he learned to introduce baptisms into religious ceremony. The INC stressed that true religious knowledge can only come from the Bible and that Jesus was not a deity but rather an ordinary man. Manalo also maintained that venerations of saints were pagan beliefs held by the Roman Catholic Church (Rodell, 2002). The INC was formed by Manalo as a religious institution for Filipinos and embraced indigenous ideas of religiosity. The INC became massively popular and spread from Manila to nearly all provinces on Luzon by World War II (Woods, 2006). Today, the INC remains popular and as of 1990 had between one and two million members and operates its own radio and television programs (Rodell, 2002).

3.4. Sexual Division of Labor

In Philippine society, work is shared among men and women with some tasks being allocated to only men and others being only allocated to women. Two types of work are involved in this process and are classified as productive work and reproductive work. Productive work covers basic human needs such as constructing shelter, finding food, and providing clothing. Reproductive work involves the production of offspring and the responsibility of child rearing. Historically, the Philippines were agricultural producers where distinctive work roles were not clearly defined. As colonial influence grew, so too did the distinction between men's and women's work responsibilities. Colonialism created a dependency on cash crops in the Philippines and left little room for developing a national income. In the neocolonial era of the Philippines, a wage-labor system separated the home and workplace. Eventually, men were absorbed into the economic side of business and women became responsible for home duties and became economically dependent on wages earned by men. This created a gender hierarchy where women's work was viewed in relation to their subordinate position as household earners (Eviota, 1992).

The contemporary sexual division of labor saw men and women filling wage-work positions in disproportionate numbers. As the cash economy grew in the 1960's and 1970's, unpaid labor positions for both men and women began to decline. Women's labor shifted to wage work on farms and men's labor began to take on non-agricultural employment. By 1975, women occupied only 25% of all industrial sector employment. During this time men and women occupied the commerce sector in similar numbers as women comprised 49% of the workforce. Despite occupying the commerce sector in similar numbers women tended to earn less than men and filled different work roles than men. Women were typically sales people involved in low-income trade and market vending. Men on the other hand were typically employed as merchants and salesmen at the top of the business hierarchy. As a result, in the 1980's there existed a wage gap evident by women earning 46% of men's earnings in sales, 50% of their earnings in technical fields, and 22% in the agricultural field (Eviota, 1992).

The sexual division of labor has undergone considerable change since the mid-1980's as women came to dominate overseas migrant work. Many of these women immigrated to Singapore and Hong Kong as these areas saw economic growth. By 1989, there were an estimated 30,000 Filipina domestic workers in Singapore alone. Filipina migrant workers were likely to earn six times more than what they could earn doing their professions in the Philippines. Women now had the ability to send remittances home and became major contributors to the household economy. As income-earners, women had had a new-found ability to confront the sexual division of labor as working abroad provided higher pay (Eviota, 1992). Despite providing gainful employment, this avenue of financial gain is not without difficulty.

3.5. The Filipina Migrant Worker

Since the 1970's it has been problematic for many Filipinos to find gainful employment despite possessing a degree or having formal education as a teacher. As the economic condition of the Philippines deteriorated in the 1980's opportunities for gainful employment decreased. At the same time, the wealth of the upper and middle-classes in Hong Kong grew and available local workers decreased. This effectively created a demand for domestic migrant workers to fulfill household obligations such as child rearing, child education, and housekeeping. Migrant work became a viable way for women to generate income as they made up 95% of the 150,000 foreign domestic workers that migrated to Hong Kong by 1995. Of these 150,000 foreign domestic workers 130,000 were from the Philippines. Many of the women participating in foreign domestic work are highly educated with 50% of these women possessing a high school education and another 38% having some college or postsecondary education (Constable, 2007).

Filipina migrant workers are often employed through recruitment agencies based in their respective countries of employment. These recruitment agencies sometimes tend to objectify migrant workers and advertise them based on stereotypes to prospective employers. Employers of Filipina domestic workers in Hong Kong value Filipinas for their high level of education and English-speaking skills. Chinese employers, on the other hand, view Filipina domestic workers as less desirable due to cultural traditions of hierarchical worker-employer relationships (Constable, 2007). Another example comes from a recruitment agency in Taiwan that used advertisements aimed at portraying Filipina domestic workers as too Westernized, educated, and hard to manage. This recruitment agency instead recommended Indonesian domestic workers as they were more simple and able to work long hours with no days off. These are examples of a kind of institutionalized stereotyping inherent in the migrant worker profession and are just one of the difficulties all domestic migrant workers face (Lan, 2006).

Filipina migrant workers may also be expected to work in difficult situations and work environments. Recruitment agencies may ask if a prospective worker is willing to work for an employer who cannot provide her with a private room. Employers may also expect long working hours. Some Filipina migrant workers are even asked if they are willing to clean multiple flats, work for multiple employers, or to work outside the home in the office. All of these conditions are illegal as they are not a part of the contract but are sometimes accepted due to applicants feeling pressured to sign a contract (Constable, 2007). While some Filipina women view domestic migrant work as difficult and oppressive, others view it as opportunistic and liberating as they now have the ability to make options for themselves (Eviota, 1992). While the main attraction to migrant work for many Filipinas is money, economic incentive is not always the top priority. Other migrant workers view foreign work as liberating as they get to experience modern affluence and sexual liberation present in more advanced economies (Lan, 2006). Regardless of reasons why Filipina migrant workers take foreign employment, it has led to circumstances that challenge the sexual division of labor and has forced a reconsideration of women’s role in the economy.

3.6. Gender Ideology and Socialization

The pre-colonial Philippines was defined as a subsistence economy where sexuality was more freely expressed. Both boys and girls could inherit land and power was based on age, not gender. Women held positions of power and were heavily involved in decision-making processes. In the precolonial Philippines cooperation between men and women was highly valued and there were no notions of sexism. Spanish colonization of the Philippines enforced strong Western religious ideologies which redefined Filipino gender and sexuality. Spanish friars introduced *reduccion* (resettlement policy) aimed at consolidating native Filipinos into smaller population centers that were more easily governed. *Reduccion* led to right of lands ownership as a new symbol of wealth and placed men as superior to women in class and rank. Women became subordinate to men and decision-making in the family was no longer a shared enterprise. The Spanish friars' campaign to Catholicize the Philippines also dramatically changed male and female sexuality (Bautista, 1988).

The Judeo-Christian ideology stressed procreation as the sole purpose of sexuality and tied sexuality to morality. Sexual relations outside the family became morally sinful and the importance of chastity was greatly emphasized, primarily concerning women. In a male dominated society, dualities between men and women began to manifest. Chaste women were expected to be sober, modest, and submissive while men were allowed more freedom in their sexuality. Premarital sex was condemned and virginity was highly valued and tied to morality. Women were expected to be faithful to their husbands while only men were allowed to participate in extramarital affairs (Bautista, 1988). What resulted was a male machismo where men were seen as the primary providers for the family while women were seen as care givers. This carried over into ideologies which dictated what work roles were suitable for men and women and what their wages should be for different jobs. Jobs that men did were considered better than those of women and women increasingly took up jobs in the service and caregiving sector. These jobs were seen as less skilled and deserving of lower pay. Men demonstrated fertility with the early production of offspring and denial of contraceptives. The Philippines are a dynamic society as mixed ideological conceptions of sexuality continue to be evident in the sexual division of labor and gender attributes for specific kinds of work (Eviota, 1992).

Today, these ideologies persist to some degree and sex roles of boys and girls becomes more defined during adolescence. Boys can participate in more adult behaviors such as drinking and visiting girls outside the home. Boys are also encouraged to take part in jobs and activities outside the home to avoid household work or any domestic housekeeping duties (Mendez & Jocano, 1979). Girls are encouraged to participate in housekeeping tasks and assist their mothers with taking care of their siblings and other domestic work. Activities such as food preparation and household maintenance are passed from mother to daughter as her domestic skills are seen as a key component in attracting a good future husband. This becomes especially apparent in adulthood when men give all control over household affairs to his wife who is expected to balance the family income, raise the children, and maintain social ties with surrounding households. Men maintain their status in society by demonstrating their ability to be a good provider (Rodell, 2002).

However, the traditional outlook is rapidly changing in modern Filipino society. The unique historical past of the Philippines has shifted gender ideologies as Spanish colonialism enforced male dominance while American colonialism and liberalism relaxed such notions. Education is a primary driver of this change as it became widely available during the American colonial period and further available after World War II. American liberalism in education enforced the idea that women were considered equal to men and were able to take on special roles in society. During American colonialism the plebiscite of April 1937 even granted Filipinas the right to participate in the political arena. Filipinas now take on careers in medicine, education, and industry. Furthermore, nonagricultural employment and women seeking foreign migrant work are also changing traditional gender roles (Bautista, 1988). Modernization and improved transportation allow young men and women to travel to metro areas where they can assume a degree of autonomy. In modern urban settings it is not uncommon to see young men and women comingling and sometimes participating the American-style of dating in couples. There has even been a decrease in traditional views of virginity as it becomes less important an issue for young men choosing a partner. While these changes are taking place in modern Filipino society, young women must still take care to uphold a positive image. Individual dating is often performed in a group setting with multiple couples and the American practice of cohabitation before marriage is heavily frowned upon in even the most progressive sectors of the country. Even today the Filipino woman's social activities are relatively limited compared to those of men (Rodell, 2002).

3.7. Child Gender Preference

Gender preference is not as salient in Filipino society compared to other societies that are patrilineal, such as Chinese society (Rodell, 2002). It has even been suggested that some Filipinos may prefer daughters as they have greater commitment to family and work (Paz, 1974). Filipinas are thought to have positive qualities related to ambitiousness and good managerial skills while Filipino men are sometimes viewed as having ambiguous morals related to gambling and womanizing (Bautista, 1988). Having a son does make things a bit easier on the mother as sons will be expected to spend more time outside the home with their fathers rather than be dependent on the mother's teaching of domestic skills. Until the child is a bit older it is still the mother's responsibility to raise them due to the man's societal role to work outside the home. Boys in rural settings may also be able to perform more arduous tasks on the farm than girls. (Rodell, 2002).

Whether parents highlight the benefits of having either a boy or girl there exists no clear preference for one over the other in Filipino society. Having a child is considered a gift from God and blessing to the family (Bautista, 1988). Additionally, having a child of either gender strengthens familial and social ties as parents become grandparents and gain respect in the community (Rodell, 2002). Children are also valued because of their potential to supplement the family income, especially if they are skilled or educated. Married sons and daughters also provide other resources to the family such as healthcare. Kinship ties known as *pakikisama* (mutual obligation) obligate the husband or wife to provide any assistance possible to their spouse's family. If a son or daughter marry a doctor, it is expected that medical care will be provided to extended family. A child's sense of duty to their parents is reinforced by strong kinship values that place importance on caring for elderly parents (Bautista, 1988).

3.8. Kinship and Family

In pre-colonial Philippines, society focused on kinship ties rather than economic gain. Kinship ties organized social structures into the *barangay* (a local unit of social structure) where private land ownership did not exist. Communal ownership and production was organized by the *Datus* (village chief) and served to fulfill kinship obligations rather than enforce power (Bautista, 1988). However, Spanish colonialism disrupted many families in the archipelago and *compadrazgo* (godparenthood) led to need for extended kinship systems as a means for survival that persist as ritual kinship today. For example, godparents often build relationships with families at baptisms where the Roman Catholic Church requires confirmations and sponsorships. Often times this is how relationships between *ninong/ninang* (godparents) and the *inaanak* (godchild) form. Kinship in Filipino society extends vertically as well as horizontally and spans multiple generations (Woods, 2006).

In Filipino society, the family is a highly valued unit that demands strong commitment. A married couple is not viewed as a productive family unit until the birth of their first child. Filipino families are matrifocal and are centered around the mother in addition to her close relatives and friends. The importance of the mother in family life is highly important as they give to children and subsequently care for, nurture, punish, and educate children in the home. Since the father is expected to perform duties outside the home to provide for the family, the mother takes a central role in her child's life (Rodell, 2002). This can become problematic if the mother needs to travel abroad for work. Though the separation of the mother from her family may be temporary, it can also be prolonged and lead to the abandonment of the family (Eviota, 1992). In the case of Filipina domestic migrant workers, many mothers must rely on networks of relatives to care for the family in their absence (Constable, 2007). This is an example of how beneficial extended family networks created through marriage and ritual kinship can be and illustrates the value Filipino society places on marriage, family, and kinship.

CHAPTER 4

MATERIALS AND METHODS

4.1. Cebu Longitudinal Health and Nutrition Survey

The Philippine Cebu Longitudinal Health and Nutrition Survey consists of data collected between 1983 and 1984 with follow-up surveys conducted in 1991-92, 1994, 1999, 2002, and 2005. The survey was carried out by researchers from UNC-Chapel Hill led by Dr. Barry Popkin, Professor of Nutrition at UNC-Chapel Hill, as well as researchers in the Philippines led by Dr. Florentino S. Solon, Director of the Nutrition Center of the Philippines. Data were made available to the public for analysis and examination. Data were collected on baseline survey mothers and their focal children with data updated in subsequent surveys. The population from which the initial sample of pregnant women was taken is comprised of randomly selected barangays (16 rural, 17 urban) representative of the Metropolitan Cebu area of the Philippines. Initially, 3,327 pregnant women were selected for interview and participation in the 1983-84 Cebu study (Adair & Popkin, 2001).

Baseline interviews were conducted shortly after birth and continued at two-month intervals over the next 24 months. Structured questioners were administered to respondents by trained interviewers with community data provided by key informants in each area where a respondent resided. Completed questionnaires were reviewed for accuracy with questionable data resulting in interviewers returning to that respondent's household. Birth weight was measured in grams and collected from midwives who helped deliver the focal child or hospital records if the infant was born away from home with 85.5% of women reporting their infant had been weighted immediately after birth. Child height was collected in centimeters with Stanley folding measurement sticks while child weight was recorded in kilograms with adult bathroom scales purchased from CIM Weighing Equipment, London. Holtain Tanner Whitehouse skinfold calipers were used to collect all skinfold measurements in millimeters. Arm circumference measuring tapes were used to record arm circumference in millimeters. All focal child anthropometrics were taken according to procedures developed by Habicht. This method involved the measurement being taken twice by a number of observers and once by a supervisor. This method was intended to measure accuracy and precision by comparing the two measures of each observer to those of the supervisor to produce reliable data (Adair & Popkin, 2001).

This research used secondary data analysis from the 1983-84 and 1991 follow-up surveys to examine data reflective of individual health outcomes, focal child anthropometric measurements, sociocultural variables, and household economic variables. 1984 anthropometric measurements included focal infant weight, length, and sex as recorded shortly after birth. Variables from the 1984 baseline survey used to measure sociocultural factors included mother's alcohol use while pregnant, mother's intent to breastfeed, and urban or rural strata while economic variables included home value and gross family worth. Other SES variables of interest from the 1983-84 baseline survey included months of maternal vocational training, household cleanliness where food is stored, the possession of material goods such as radios, televisions, beds, electric lighting, and home ownership.

Anthropometric variables from the 1991 follow-up survey included focal child triceps skinfold measurements, arm circumference, subscapular skinfold measurements, sex, height, and weight. These anthropometrics were converted into HAZ, WAZ, and ZBMI scores using the World Health Organization SPSS macro that generated individual-specific scores in relation to standard deviations from international reference medians. Any z-scores under -2 standard deviations from WHO international reference medians were considered as evidence of stunting, underweight, or wasting, and occurring from acute or chronic malnutrition. Infant conditions from the 1983-84 baseline survey were used determine their impact on subsequent growth and development outcomes of boys and girls later in childhood. Secondary data analysis statistical procedures included one-way ANOVAs and least squares linear regression analyses.

4.2. *Drosophila melanogaster*

This research uses *Drosophila melanogaster* as a model organism to examine female canalization as a biological function in a non-human species. This allows for the biological isolation from cultural influences that contribute to sex-specific growth and development outcomes in human populations. This also enables a real-time model of female canalization to be constructed so that comparisons can be made across species. The *Drosophila* portion of this research attempts to construct variables and measures that are analogous to those used in the human portion of data analysis. Variables of study in the *Drosophila* portion of this research include sex, weight, triglyceride storage (measurement of *Drosophila* fat storage and analogous for child adiposity), and protein storage (measurement of *Drosophila* lean tissue storage and analogous for child leanness).

Three naturally derived homogenous genetic lines from Ghana were selected for this portion of the research. Inbred lines GH74, GH06, and GH30 were selected due to their ancestral lineages deriving from the region where *Drosophila melanogaster* originated. The parental generation of adults was raised on a normal control diet consisting of a protein to carbohydrate composition of 9:90. After adequate population numbers had been established, 1st instar larvae from each line were introduced to the control and experimental diets. Experimental diets included a low carbohydrate diet with a protein to carbohydrate composition of 20:80, a low protein diet with a protein to carbohydrate composition of 6:94, and a low calorie diet with a protein to carbohydrate composition of 5:54. All diet ratios were constructed based on the amount of protein and carbohydrates per gram. All diets were constructed using varying amounts of yeast, molasses, cornmeal, agar, tegosept, and propionic acid. Additionally, all diets maintained the caloric value as close to the control as possible to prevent starvation (with the exception of the low calorie diet). All diets were in the form of a solid food medium.

Adult parental generation *Drosophila* were put into laying chambers constructed from a six-ounce bottle with an apple agar plate fixed to the bottom. Females deposited their eggs onto the apple agar plate, which contained a drop of yeast paste to encourage egg-laying, and were changed and stored every 12 hours for 1st instar larvae collection. At 24 hours, once the eggs hatched, 1st instar were microscopically collected from the apple agar plate and placed in the control and experimental diets. 50 1st instar larvae were collected and introduced to each of the four diets contained in solid food medium vials. There were five solid food medium vials per diet, per genetic line, each containing 50 1st instar larvae for a total sample size of 1,000 larvae per genetic line. This procedure was repeated three times to control for changes in seasonality and continuity of environment, generating 9,000 larvae in total. Samples were stored in 1.5 ml microcentrifuge tubes Ringer's solution to maintain a balanced PH and salinity to preserve tissue. Samples were then dried out at 34^{o} Celsius for 12 hours so that protein and triglyceride assays could be performed according to protocols developed by Mendez et al. (2016). Triglyceride and protein levels were normalized to the number of samples stored in each microcentrifuge tube. Weights were recorded by measuring three dried larvae on a microbalance after sexing and drying. Statistical analysis for the *Drosophila* portion of this research included one-way ANOVAs, post hoc tests, and least squares linear regression.

CHAPTER 5

RESULTS

5.1. Cebu Secondary Database Analysis

Analysis of the Cebu Longitudinal Health and Nutrition Survey secondary database consists of data from the 1984 baseline survey of mothers (n=3,327), their children (boys n=1,657; girls n=1,461), as well as data from the 1991 follow-up survey. The 1991 household follow-up survey had a participant retention rate of 75.9% for focal mothers (n=2,525) who participated in the 1984 baseline survey. Mortality rates reported for children in the 1991 follow-up survey were low with only 56 child deaths (boys n=28; girls n=28) reported by interviewed mothers. The average age of death was 3 years old for boys and girls with the primary cause of death being measles (boys n=7; girls n=11) and diarrheal morbidity (boys n=3; girls n=6). The mean infant birth weight for boys was 3.02 kg and 2.97 kg for girls. The mean infant birth length was 49.5 cm for boys and 49 cm for girls. All focal child anthropometrics are shown in table 1. There was a statistically significant difference between focal male and female birth weight ($p<.000$) and birth length ($p<.000$) as determined by a one-way ANOVA (table 2).

Table 1: Child anthropometrics

Mean Anthropometric Measurements	Boys	Girls
1984 Baseline	n= 1.657	n= 1,461
1991 Follow-up	n= 1,163	n= 1,032
1984 Infant Weight (kg)	3.04	2.97
1984 Infant Length (cm)	49.53	49.04
1991 Child Weight (kg)	20.66	20.4
1991 Child Height (cm)	117.69	117.63
1991 Child Arm Circumference (cm)	16.83	17.03
1991 Child Subscapular Skinfold (cm)	5.27	6.1
1991 Child Triceps Skinfold (cm)	6.29	7.28
1991 Child WAZ	-1.99 SD	-1.83 SD
1991 Child ZBMI	-.82 SD	-.8 SD
1991 Child HAZ	-2.1 SD	-1.99 SD

Table 2: One-way ANOVA of focal child birth weight and length

	Sum of Squares	df	Mean Square	F	Sig.
Birth weight (kg)	2.825	1	2.825	14.277	.000
Between groups					
Birth length (cm)	152.592	1	152.592	33.597	.000
Between Groups					

The average age of the focal children in the 1991 follow-up survey was 8.5 years old. The mean height for boys was 117.7 cm while the mean height for girls was 117.6 cm. The mean weight for boys was 20.7 kg and 20.4 kg for girls. The mean arm circumference for boys was 16.8 cm and 17 cm for girls. Mean subscapular skinfold measurements for boys was 5.3 cm and 6.1 cm for girls while the mean triceps skinfold measurement for boys was 6.3 cm and 7.3 cm for girls. Mean weight-for-age z-scores (WAZ) for boys fell -1.99 SD below WHO international reference medians while girls fell -1.83 SD below the same reference medians. Mean BMI-for-age z-scores (ZBMI) for boys fell -.82 SD and girls fell -.8 SD below WHO international reference medians. Mean height-for-age z-scores (HAZ) for boys fell -2.1 SD below WHO international reference medians while girls fell -1.99 SD below the same reference medians. As evidence of being underweight at age eight, 27.3% of boys and 19.6% of girls had WAZ scores below -2SD. Similarly, 4.8% of boys and 3.8% of girls had ZBMI scores below -2SD. Stunting prevalence indicated that 28.9% of boys and 24.5% of girls had HAZ scores below -2SD at age eight. A one-way ANOVA (table 3) indicated statistically significant differences between boy and girl WAZ ($p<.000$) and HAZ ($p=.009$) scores with results shown. A one-way ANOVA (table 4) also indicated statistically significant differences in mean triceps ($p<.000$) and subscapular skinfold measurements ($p<.000$) and arm circumference ($p=.005$) between boys and girls.

Table 3: One-way ANOVA of focal child HAZ, WAZ, ZBMI

	Sum of Squares	df	Mean Square	F	Sig.
Weight-for-age Z Between Group	14.269	1	14.269	14.706	.000
BMI-for-age Z Between Group	.181	1	.181	.228	.633
Height-for-age Z Between Group	6.144	1	6.144	6.828	.009

Table 4: One-way ANOVA of child subscapular and triceps skinfold measurements and arm circumference

	Sum of Squares	df	Mean Square	F	Sig.
Triceps Skinfold Between Groups	526.006	1	526.066	136.555	.000
Subscapular Skinfold Between Groups	365.521	1	365.521	121.355	.000
Arm Circumference Between Groups	17.072	1	17.072	7.894	.005

Sociocultural and economic variables were used as a measure of adversity. Child gender, birth weight, birth length, mother alcohol use while pregnant, mother's intended methods of child feeding, urban and rural, gross worth, and household value were used as independent variables to predict growth outcomes in focal children. Regression analysis (table 5) indicated household wealth in the form of home value, a long-term indicator of wealth, to be the best predictor of sex-specific childhood growth outcomes. Specifically, home value held statistical significance as an interaction term with child gender. While home value did not have significant predictive value on HAZ and WAZ scores of boys and girls, it did have a statistically significant effect on childhood ZBMI scores ($p = .024$). Infant weight and length also had statistically significant effects on childhood ZBMI scores ($p < .000$; $p < .000$). This model included a few outlying cases so another model was constructed which accounted only for home values under 100,000 pesos. Outliers are shown in figure 1. The significance did not change from model to model, indicating the outlying home value cases were not significantly affecting the model. Results of this second regression analysis are shown in table 6.

Table 5: Regression coefficients on ZBMI

	Unstandardized Coefficients		Standardized Coefficients		
Model	B	Std. Error	Beta	t	Sig.
(constant ZBMI)	-.144	.628		-.181	.856
Child Gender	.015	.022	.016	.677	.499
Infant Weight (grams)	.001	.000	.346	9.410	.000
Infant Length (cm)	-.056	.016	-.134	-3.610	.000
Alcohol Use Y/N	-.023	.049	-.011	-.462	.644
Breast Feeding Y/N	.014	.054	.006	.253	.800
Urban or Rural	.041	.047	.021	.859	.390
House Value	1.143E-006	.000	.024	.976	.329
House Value x Gender	-2.579E-006	.000	-.055	-2.259	.024

Figure 1: Histogram of house value

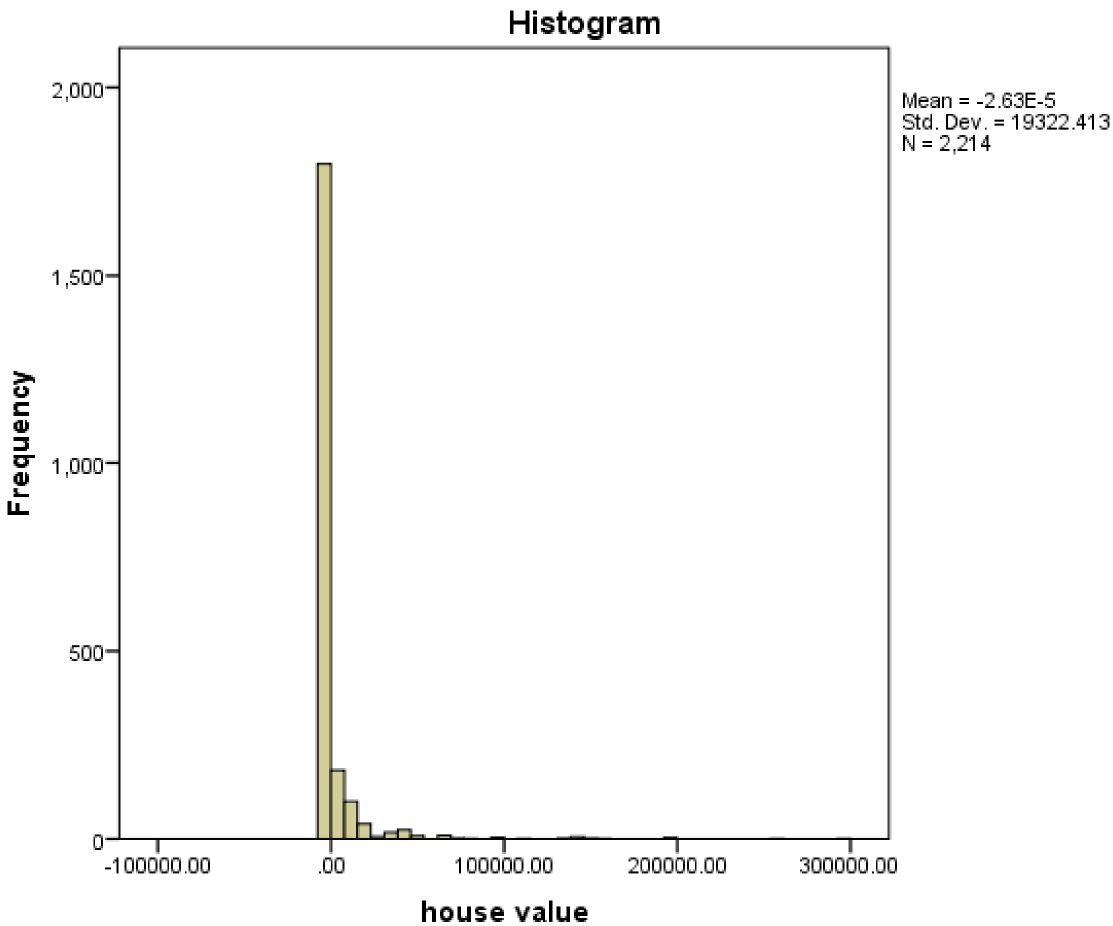


Table 6: Regression coefficients home value < 100,000 on ZBMI

	Unstandardized Coefficients		Standardized Coefficients		
Model	B	Std. Error	Beta	t	Sig.
(Constant ZBMI)	.166	.627		.265	.791
Child Gender	.010	.022	.012	.472	.637
Infant Weight (grams)	.001	.000	.358	9.768	.000
Infant Length (cm)	-.063	.016	-.151	-4.066	.000
Alcohol Use Y/N	-.027	.049	-.014	-.559	.576
Breast Feeding Y/N	-.002	.054	-.001	-.031	.976
Urban or Rural	.045	.047	.025	1.011	.312
House Value	2.977E-006	.000	.040	1.575	.115
House Value x Gender	-4.250E-006	.000	-.057	-2.318	.021

Scatter plots of both regression models were constructed and similarly reflect greater sensitivity among males than among females to home value as a marker of long-term wealth. These scatter plots are shown in figs 2 and 3. Reduced sensitivity of girls to long-term wealth as measured by home value are supportive evidence of female growth buffering.

Figure 2:Scatter plot ZBMI by home value by gender

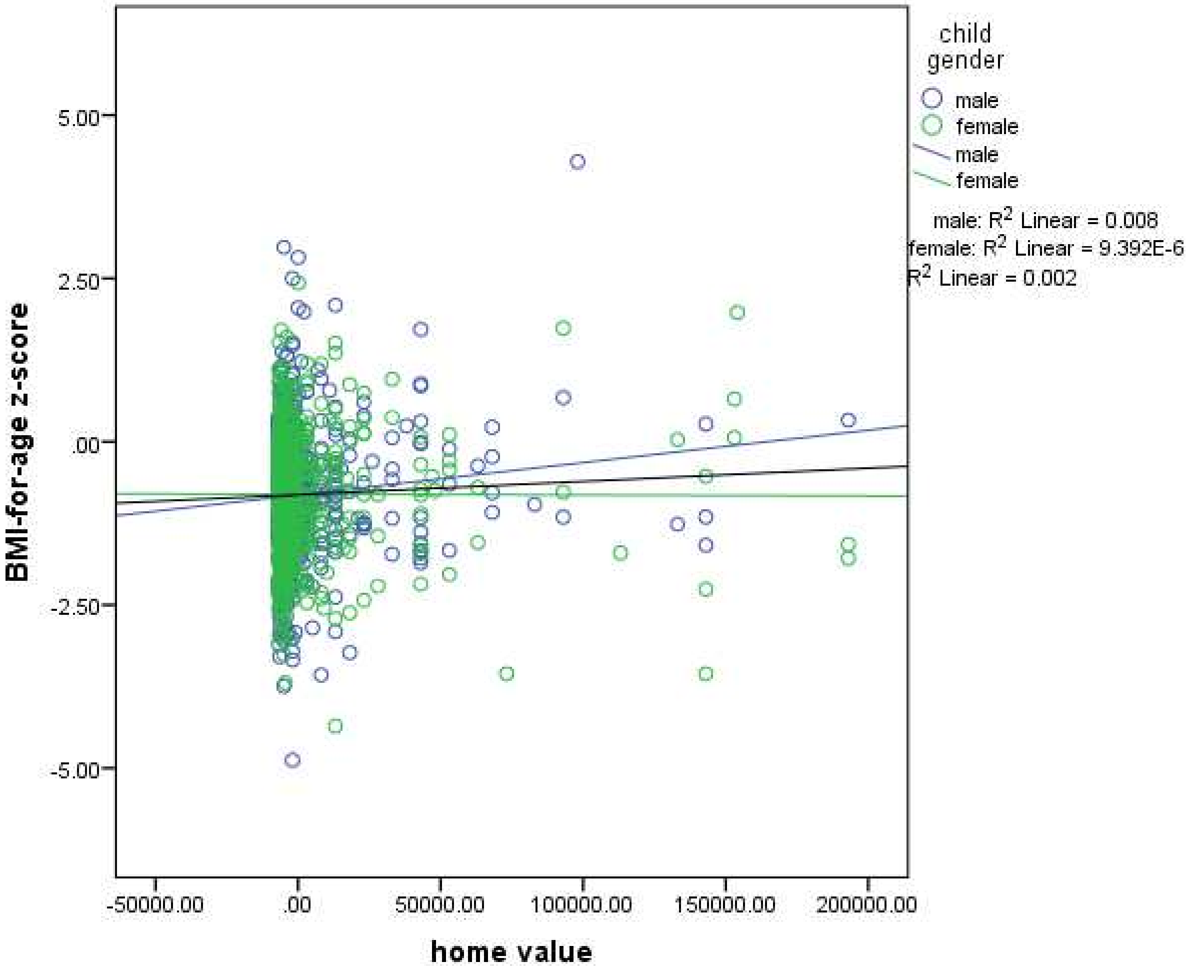
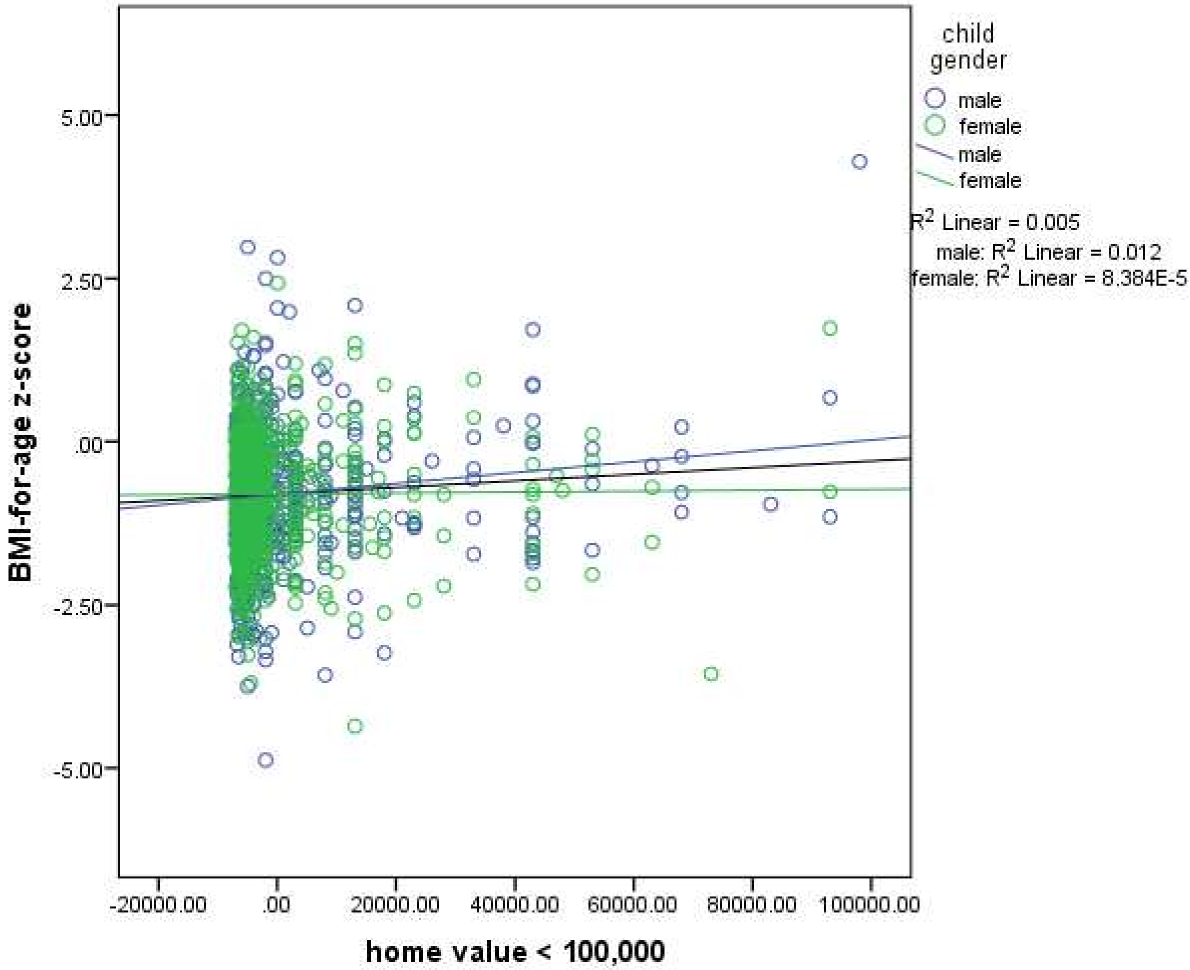


Figure 3:Scatter plot ZBMI by home value < 100,000 by gender



5.2. *Drosophila melanogaster*

Results *Drosophila* portion of this research also revealed differences in male and female growth outcomes. In total, 1,661 males and 2,658 females developed into 3rd instar larvae. Descriptive statistics of mean *Drosophila* growth outcomes are shown in table 8. There were no statistically significant differences in weight between males (.212 mg) and females (.207 mg) (p=.435) as shown by a one-way ANOVA (table 9). However, a one-way ANOVA (table 10) indicated statistically significant differences in mean weight across diets (p<.000) and genotypes (p<.000), suggesting there to be complex interactions between diet, sex, and genotype on phenotypic outcomes. Tukey post hoc tests for this one-way ANOVA are shown in tables 11 and 12. Weight differences were illustrated in figs 4 and 5 using error bar charts to show mean male and female weights by diet and genotype by diet at a 95% confidence interval. A one-way ANOVA (table 13) indicated no significant difference in male and female protein storage ($p=.941$), but did show significant differences in triglyceride storage ($p<.000$). This indicated that females were storing adipose tissue in differing amounts than males. These tests only show that differences exist and do not control for diet and genotype as significant contributors to phenotypic outcomes.

Table 7: Drosophila melanogaster mean physical attributes

Genotype GH30								
Sex	Male n=961 (50%)				Female n=966 (50%)			
Diet	Normal	Low Protein	Low Calorie	Low Carb	Normal	Low Protein	Low Calorie	Low Carb
Weight	.719	.127	.084	.719	.992	.176	.109	.992
Triglyceride	.0560698	.0187161	.0150584	.0460207	.0570645	.0171952	.0117667	.0413046
Protein	.008398	.0001916	.0016891	.0086752	.0104586	.0002722	.0000000	.0104702
Genotype GH06								
Sex	Male n=409 (29%)				Female n=990 (71%)			
Diet	Normal	Low Protein	Low Calorie	Low Carb	Normal	Low Protein	Low Calorie	Low Carb
Weight	.772	.134	.009	.621	.896	.166	.121	.632
Triglyceride	.0582907	.0194235	.0155688	.0420252	.0445907	.0157231	.0087443	.0372807
Protein	.0087728	.0005769	.0003994	.0056021	.0095382	.0002434	.0001144	.0058331
Genotype GH74								
Sex	Male n=291 (29%)				Female n=702 (71%)			
Diet	Normal	Low Protein	Low Calorie	Low Carb	Normal	Low Protein	Low Calorie	Low Carb
Weight	.886	.09	.021	.758	.783	.157	.078	.759
Triglyceride	.0658643	.0216087	.0043886	.0445571	.0441658	.0178236	.0093138	.0243961
Protein	.0083299	.0009458	.0013632	.0093471	.0098743	.0003093	.0014757	.0087981

Table 8: One-way ANOVA of male and female weight

	Sum of Squares	df	Mean Square	F	Sig.
Weight	-3.835	1	.010	.610	.435
Between Groups					

Table 9: One-way ANOVA of diet and genotype on mean weights

	Sum of Squares	df	Mean Square	F	Sig.
Diet	18.527	3	6.176	1510.364	.000
Between Groups					
Genotype	.498	2	.249	15.794	.000
Between Groups					

Table 10: Tukey multiple comparisons post hoc test genotype and weight

(I) Genotype	(J) Genotype	Mean Difference	Std. Error	Sig
GH 30	GH 74	.00898	.00815	.513
	GH 06	.04074	.00739	.000
GH 74	GH 30	-.00898	.00815	.513
	GH 06	.00867	.00867	.001
GH 06	GH 30	-.04074	.00739	.000
	GH 74	-.03175	.00867	.001

Table 11: Tukey multiple comparisons post hoc test diet and weight

(I) Diet	(J) Diet	Mean Difference	Std. Error	Sig.
Normal	Low Carb	.2648	.00393	.000
	Low Protein	.24005	.00471	.000
	Low Cal	.25662	.00523	.000
Low Carb	Normal	-.02648	.00393	.000
	Low Protein	.21357	.00472	.000
	Low Cal	.23014	.00524	.000
Low Protein	Normal	-.24005	.00471	.000
	Low Carb	-.21357	.00472	.000
	Low Cal	.01657	.00585	.024
Low Cal	Normal	-.25662	.00523	.000
	Low Carb	-.23014	.00524	.000
	Low Protein	-.01657	.00585	.024

Table 12: One-way ANOVA of triglyceride storage between males and females

	Sum of Squares	df	Mean Square	F	Sig.
Triglyceride storage Between Groups	.013	1	.013	22.531	.000
Protein storage Between Groups	.000	1	.000	.005	.941

Figure 4: Diet by sex by weight error bar chart

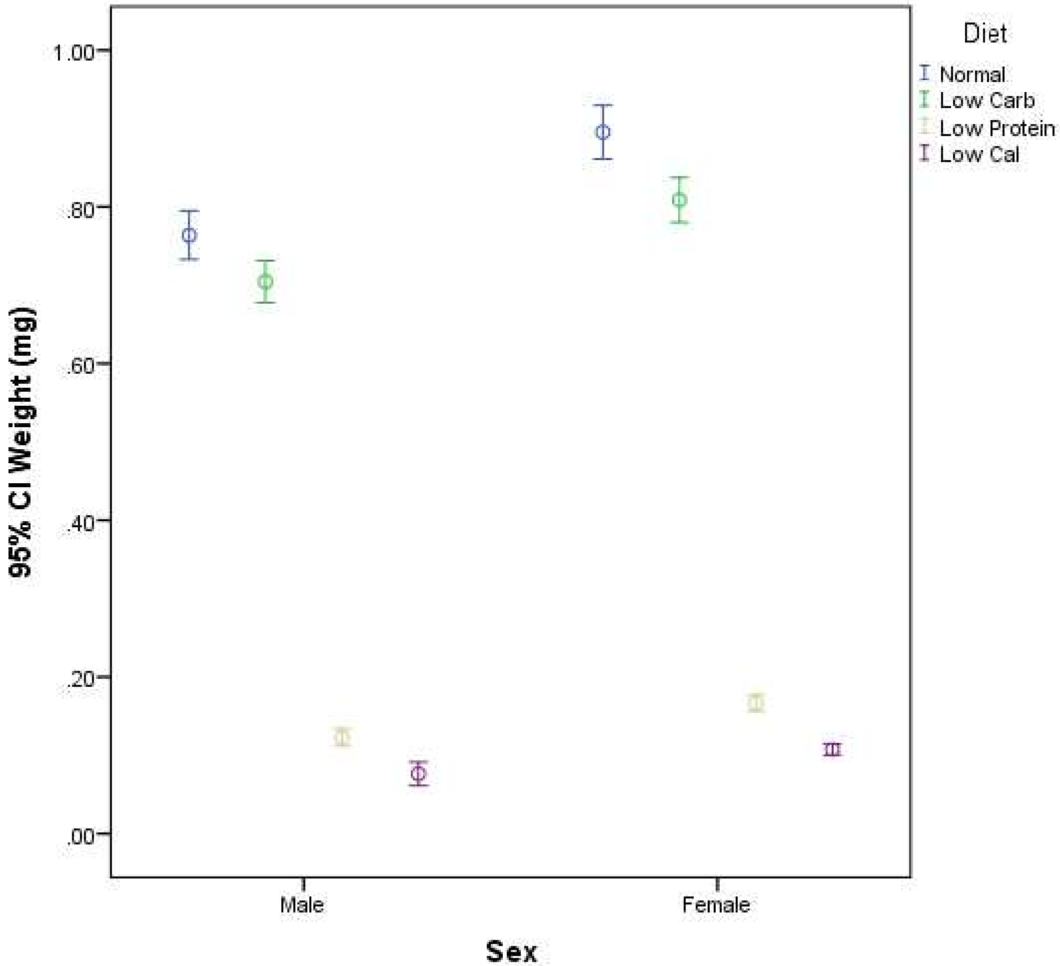
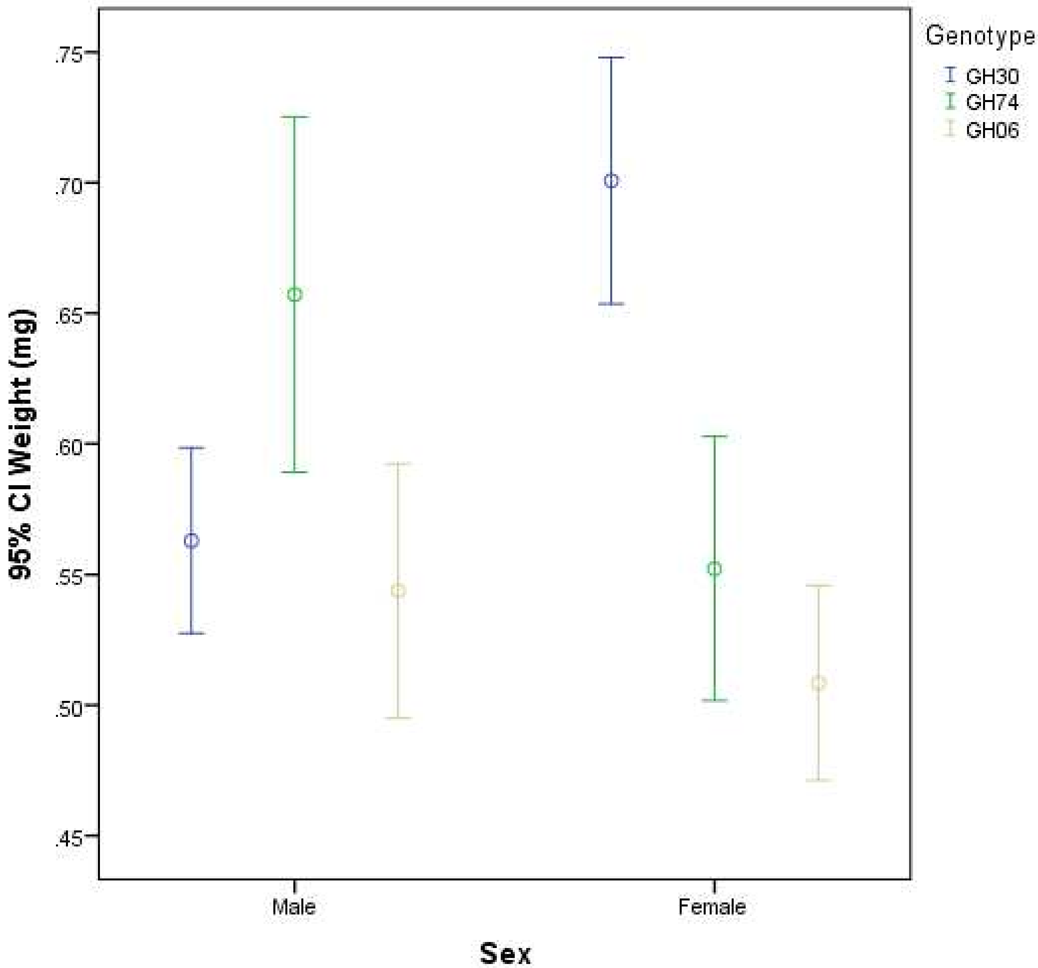


Figure 5: Genotype by sex by weight error bar chart



A linear regression analysis was performed to test the effects of diet and genotype on differential phenotypic outcomes of males and females. First, sex, low carbohydrate diet, low protein diet, low calorie diet, genotype GH30, and genotype GH74, sex by diet interactions, and sex by genotype interactions were used as independent variables to predict weight as the dependent outcome variable. Results of this regression (table 14) indicate sex (p<.000), low protein diet (p<.000), low calorie diet (p<.000), genotype GH30 (p<.000), and genotype GH74 (p<.000), sex by diet (p<.000), and sex by genotype (p<.000) to all be significant predictors of weight. The low protein and low calorie diets were both significantly different from the normal diet. The low carbohydrate diet (p=.345) was not significantly different from the normal diet. A second linear regression analysis (table 15) used the same independent variables with protein storage as the dependent outcomes. This analysis showed sex (p=.006), the low carb diet (p=.003), the low protein diet (p<.000), the low calorie diet (p<.000), genotype GH30 (p<.000) and GH74 (p<.000), and sex by diet (p=.004) to be significant predictors of protein storage with the low carb diet, low protein diet, and low calorie diets all being significantly different from the normal diet. Sex by genotype was not significant in this model (p=.443). The regression analysis was run again on triglyceride storage as the dependent outcomes and results are presented in table 16. This model indicated sex (p=.028), low carbohydrate diet (p<.000), low protein diet (p<.000), low calorie diet (p<.000), and sex by diet (p=.006) to all be significant predictors of triglyceride storage. Genotypes GH30 (p=.089), GH74 (p=.652), and sex by genotype (p=.103) did not hold significance in this model.

Table 13: Linear regression coefficients table for weight

	Unstandardized Coefficients		Standardized Coefficients		
Model	B	Std. Error	Beta	t	Sig.
(Constant)	.255	.011		23.028	.000
Sex	.107	.010	.411	10.886	.000
Low carb diet	-.006	.006	-.022	-.945	.345
Low protein diet	-.195	.011	-.594	-17.278	.000
Low calorie diet	-.188	.017	-.505	-10.9.5	.000
Line GH30	-.048	.012	-.190	-3.887	.000
Line GH74	-.030	.008	-.101	-4.010	.000
Sex*Diet	-.015	.003	-.249	-4.525	.000
Sex*Genotype	-.024	.004	-.352	-6.568	.000

Table 14: Linear regression coefficients table for protein storage

	Unstandardized Coefficients		Standardized Coefficients		
Model	B	Std. Error	Beta	t	Sig.
(Constant)	.005	.001		3.259	.001
Sex	.003	.001	.233	2.736	.006
Low carb diet	-.001	.000	-.090	-2.957	.003
Low protein diet	-.009	.000	-.705	-23.308	.000
Low calorie diet	-.008	.000	-.643	-21.324	.000
Line GH30	.001	.000	.100	3.498	.000
Line GH74	.001	.000	.102	3.560	.000
Sex * Diet	.000	.000	-.176	-2.890	.004
Sex * Genotype	.000	.000	-.050	-.767	.443

Table 15: Linear regression coefficients table for triglyceride storage

	Unstandardized Coefficients		Standardized Coefficients		
Model	B	Std. Error	Beta	t	Sig.
(Constant)	.068	.007		9.952	.000
Sex	-.010	.004	-.201	-2.204	.028
Low Carb Diet	-.015	.002	-.271	-8.356	.000
Low Protein Diet	-.036	.002	-.641	-19.775	.000
Low Calorie Diet	-.043	.002	-.736	-22.806	.000
GH 30	.003	.002	-.052	1.706	.089
GH 74	-.001	.002	-.014	-.452	.652
Sex*Diet	.002	.001	.180	2.755	.006
Sex*Genotype	-.001	.001	-.114	-1.632	.103

CHAPTER 6

DISCUSSION

Secondary data analysis of the Cebu Longitudinal Health and Nutrition Survey revealed a population experiencing severe nutritional stress as shown by stunting and wasting prevalence and indicated sex-specific growth outcomes. Specifically, it showed that Filipino females appeared to show growth closer to the reference standard than their male counterparts similar to findings by Adair and Guilkey (1997). Females showed higher WAZ and HAZ scores in addition to greater mean arm circumference and mean skinfold measurements. This suggested that females appeared to be faring better than males despite being subjected to similar conditions of prolonged nutritional stress as shown by stunting and wasting prevalence. Similarly, females showed less sensitivity to changes in long-term indicators of wealth in the form of home value. These results, coupled with cultural evidence of non-preferential gender investment in the Philippines, support the hypothesis that females are buffered against environmental perturbations. It should be noted that despite there being significant differences in male and female HAZ and WAZ scores, long-term wealth did not reliably contribute to these growth measures as it did for ZBMI; thus, complicating the model. The importance of the mother in the Filipino family unit and her value in society and lack of son preference indicates these differences are probably not due to preferential gender treatment and are possibly outcomes due to some underlying biological mechanism. Evidence of female canalization may be a more recent trend, however, as women have been historically marginalized in Filipino society and may have appeared to be more sensitive to environmental perturbations than males in the past. The Spanish occupation and catholicization which took place in the 16th-19th centuries enforced a male-dominated hierarchy where men had access to better jobs and more prestigious roles in society. Additionally, men were the primary income-earners during this time and may have had privileged access to nutritive resources. In modernity, these trends are changing as Filipino women have better access to jobs in the technology, education, and healthcare sectors, as well as work abroad, and are becoming primary income earners. The shift in societal roles for Filipino women, presumably from influential Western ideologies in education and culture throughout the 20th century, may have led to conditions where reduced female phenotypic variation is more apparent. Though complete societal egalitarianism could not be accounted for in this analysis, if conditions for women are improving then perhaps the effects of marginalization are also lessening. If this is the case then perhaps any perceived difference in growth and development patterns among boys and girls is not due to societal marginalization and are instead the result of underlying biological mechanisms. This is purely speculative as data prior to the 1984 baseline survey was not analyzed for this research and limits the ability to examine sex-specific growth and development outcomes throughout historical changes Filipino society. This highlights the importance of investigating local cultural and socioeconomic conditions that may be producing such differential effects. This is also suggestive of the possibility there are multiple, complex interactions taking place that cannot be controlled for in human populations, such as gene-by-environment interactions.

The *Drosophila* portion of this research showed there are in fact complex interactions between sex, diet, and genotype. These results show that while sex, diet, and genotype are all significant predictors of weight, the same does not hold true for protein and triglyceride storage. While protein storage was affected by sex, diet, genotype, and sex by diet in the regression analysis, it was not affected by sex interacting with genotype. In the triglyceride storage regression model, genotype did not play a significant role as it did in other models. This indicates sex by diet and sex by genotype interactions to have significant value in contributing to weight outcomes while different homogenous genotypes affect certain types of tissue storage. Genotype and diet significantly affected protein storage while sex and diet played a larger role in triglyceride storage. While sex, genotype, and diet were demonstrated to have significant effects on phenotypic outcomes, the degree to which *Drosophila* showed evidence of canalization was difficult to determine in this analysis. This was due to observed cases of reduced phenotypic variation among females being present in some circumstances but not in others and was not universal across all experimental conditions. Overall, this analysis showed that females and males store protein and triglycerides in varying amounts across diets and genotypes and provided evidence that sex, diet, and genotype form complex interactions with respect to differing phenotypic outcomes.

This research supported the first hypothesis that girls would have greater HAZ, WAZ, and scores than boys at age eight, however, girls did not have significantly greater ZBMI scores than boys. The second hypothesis stating there would be a significant interaction between adversity and sex-specific childhood growth outcomes was also supported. A significant interaction was found for home value as an indicator of long-term wealth but not gross net worth. The third hypothesis stating that girls experiencing household economic adversity will have greater markers of growth than boys experiencing household economic adversity was rejected in an interesting way. As home value went up, so too did boy ZBMI scores. However, under the same conditions, the ZBMI of girls did not increase but instead maintained a steady baseline. This is supportive evidence of the proposed female canalization model where girls maintain optimum baseline conditions despite environmental perturbations. Additionally, this supports the fourth hypothesis that girls at age eight will exhibit reduced sensitivity to economic adversity in the form of growth markers. This would suggest that under certain conditions, selective pressures reinforce the dampening of phenotypic expression regardless of whether conditions improve or decline. The fifth hypothesis stating that female *Drosophila* will show greater diet-specific phenotypic measures than males across all diets was not supported. This ties into the sixth hypothesis positing there will be sex, diet, and genotype interactions that contribute to sex-specific phenotypic outcomes. Results indicated there to differences in the way males and females respond to nutritional change depending on specific genotype by diet by environment interactions. In turn, this supported the sixth hypothesis, to a degree, as sex by genotype by diet interactions proved to be significant contributors to differential growth outcomes. However, these outcomes were not consistent across diets and genotypes and suggests these interactions to be highly dependent on a number of factors. Lastly, the final hypothesis that female *Drosophila* will show evidence of canalization in the form of reduced phenotypic expression across environmental changes was not proven conclusively. As female growth buffering was more apparent in the human database analysis, the picture was more complicated in the *Drosophila* model. The lack of clear buffering effects in female *Drosophila* may be due complicated interactions between genotype and diet that are not fully understood in this analysis.

CHAPTER 7

LIMITATIONS

One limitation of my research was the partial capacity by which I was able to examine cultural influences on growth and development outcomes of children in the Cebu Metro area of the Philippines. Short of travelling to the Philippines, a historical and ethnographic literature review was the only means available to study Filipino culture and the extent to which culture intersect with gender. The data contained in the Cebu Longitudinal Health and Nutrition Survey was limited in the amount of cultural context it provided as much of the data focused on anthropometrics and socioeconomic data reflective of biosocial interactions. The economic data proved useful but more cultural data would be preferred when trying to frame my research in a broader cultural context. Another limitation of my research was that it did not account for the nutritional status of children in the Philippines. Reconstruction of diet would have enabled for a more robust analysis and would have provided additional insight into the way diet interacts with differential growth outcomes in humans. Without nutrition composition tables, anthropometric z-scores were the only way to provide indirect evidence of a population experiencing nutritional stress. Additionally, the control and experimental diets used in the *Drosophila melanogaster* portion of this research are not representative of overall variation in nutrition present in the human diet. Sexual dimorphism also limited the inferences that could be made by my research as, converse to humans, *Drosophila* females are larger than males and produce many more offspring as they are an R-selected species. Lastly, my research did not conduct a cross-cultural analysis of female canalization to determine whether or not it is universal and the degree to which varying local conditions affect sex-specific growth outcomes.

CHAPTER 8

CONCLUSION

The canalization model presented here posits that evolutionary stabilizing selective pressures have increased beneficial trait frequencies in the female population to maintain optimal phenotypic baselines needed for costly future reproduction. In this manner, females will continue to express similar phenotypic outcomes regardless of changes in the environment. This research found results supportive of a female canalization model that creates a more robust concept of female buffering as buffering alone does not capture the effects of selective pressures. This research also showed that socioeconomic conditions can interact with sex to produce differential growth outcomes between males and females. Females were found to be less sensitive to economic adversity and maintained stable ZBMI scores as long-term wealth increased, further supporting the canalization hypothesis. Modern Filipino society also offers more economic and social opportunity for women than in the past, possibly creating a more reliable measure of female canalization as societal conditions for women start to more closely approximate those of men. Filipino egalitarian treatment of children and lack of son preference also suggest that observed differences should not be due to child-rearing preferences. This highlights the need for a careful consideration of culture before making interpretations of anthropometric outcomes. However, cultural complexities and genetic heterogeneity in human populations makes it difficult to differentiate between the underlying factors that contribute to female canalization. While evidence for female canalization was found in the human population, the level of canalization in *Drosophila* was hard to determine. This caused further impediment when asserting canalization as an ancestral evolutionary mechanism. The use of *Drosophila melanogaster* did, however, introduce the concept that genotype has an impact on growth and development outcomes. *Drosophila* also uncovered complexities we cannot see in humans by using controlled diets and homogenous genotypes that produced significant genetic and environmental effects on phenotypic outcomes. Cultural complexity in the human condition makes it impossible to control for gene by environment interactions. Although we cannot control for such conditions in humans, *Drosophila* suggests that similar interaction may be happening in human populations as well. This is valuable because it helps raise complications and questions regarding the interpretation of human data. While we know what is happening in human populations, we don't know how human genotype and nutrition are interacting to produce what we observe. *Drosophila* as a lab model provides insight into these questions and complicates the human picture in a useful way by forcing us to think critically about conclusions. The lab model also tells us that what is happening in humans is not universal and that local conditions are important. This research demonstrates that local conditions and culture are important to the extent that environmental stimuli contribute to the possibility of canalization – lending further complexity to the human condition.

REFERENCES

Adair, L. S., & Guilkey, D. K. (1997). Age-specific determinants of stunting in Filipino children. *The Journal of Nutrition*, *127*(2), 314–320.

Adair, L. S., & Popkin, B. (2001). The Cebu longitudinal health and nutrition survey: History and major contributions of the project. *Philippine Quarterly of Culture and Society*, *29*(1/2), 5–37.

Ashburner, M. (1989). *Drosophila: a laboratory handbook*. New York, NY: Cold Spring Harbor Laboratory Pr.

Aston, B., Hill, K., Piazza, A., & Zeitz, R. (1984). Famine in China, 1958-1961. *Population and Development Review*, *10*(4), 613-645.

Attané, I. (2005). Chinese population challenges: fewer girls, more old people. *Population & Societies*, (416), 1.

Bautista, M. L. (1988). Historical influences on gender preference in the Philippines. *Journal of Comparative Family Studies*, *19*(1), 143–153.

Bellen, H. J., Tong, C., & Tsuda, H. (2010). 100 years of Drosophila research and its impact on vertebrate neuroscience: a history lesson for the future. *Nature Reviews Neuroscience*, *11*(7), 514–522.

Chandler, J. (Ed.). (2017). *The colonial and postcolonial experience in East and Southeast Asia*. New York, NY: Britannica Educational Publishing in association with Rosen Educational Services.

Cunningham, A.S. (1995). Breastfeeding: adaptive behavior for child health and longevity. In *Breastfeeding: Biocultural Perspectives,* 243-264.

Constable, N. (2007). *Maid to order in Hong Kong: Stories of migrant workers*. Ithaca: Cornell University Press.

Eviota, Elizabeth. *The political economy of gender: Women and the sexual division of labour in the Philippines*. London: Zed Books, 1992.

Foster, Z., Byron, E., Reyes-García, V., Huanca, T., Vadez, V., Apaza, L., & Leonard, W. R. (2005). Physical growth and nutritional status of Tsimane' Amerindian children of lowland Bolivia: Growth of Tsimane' children. *American Journal of Physical Anthropology*, *126*(3), 343–351.

Frisancho, A.R., Guire, K., Babler, W., Borkan, G., & Way, A. (1980) Nutritional influence on childhood development and genetic control of adolescent growth of Quechua and Mestizos from the Peruvian lowlands. *American Journal of Physical Anthropology, 52*, 367-375.

Graham, M.J., Larsen, U., & Xu, X. (1998). Son preference in Anhui province, China. *International Family Planning Perspectives 24*(2), 72-77.

Goetz, P. W. (Ed.). (1987). *The new encyclopedia britannica: Knowledge in depth* (Vol. 25). Chicago: Encyclopedia Britannica.

Haas, J.D., Frongillo, E.A., Stepick, C.D., Beard, J.L., and Hurtado, G.L. (1980). Altitude, ethnic and sex difference in birth weight and length in Bolivia. *Human Biology*, *52*, 459-477.

Institute for Medicine (U.S.) Subcommittee on Nutrition During Lactation (1991). *Nutrition during lactation*. Washington, D.C.: National Academy Press.

Jennings, B. H. (2011). Drosophila–a versatile model in biology & medicine. *Materials Today*, *14*(5), 190–195.

Kavishe, F. P. (1995). Investing in nutrition at the national level: an African perspective. *Proceedings of the Nutrition Society*, *54*(2), 367–378.

Lan, P. (2006). *Global cinderellas: Migrant domestics and newly rich employers in Taiwan*. Durham, NC: Duke University Press.

Leonard, W. R., Snodgrass, J. J., & Robertson, M. L. (2009). Evolutionary perspectives on fat ingestion and metabolism in humans. In *Fat Detection: Taste, Texture, and Post Ingestive Effects,* (pp. 3-18). CRC Press, Boca Raton, FL.

Li, J. (2004). Gender inequality, family planning, and maternal and child care in a rural Chinese county. *Social Science and Medicine, 59*(4), 695-708.

Martorell, R., & Habicht, J. P. (1986). Growth in early childhood in developing countries. In *Human Growth Vol. 3. Methodology, Ecological, Genetic, and Nutrition Effects on Growth, 2nd ed.* New York, N.Y.: Plenum, 241-262.

Mendez, P. P., & Jocano, F. L. (1979). *The Filipino adolescent in a rural and an urban setting: a study in culture and education*. Manila, Philippines: Mendiola.

Mendez, S., Watanabe, L., Hill, R., Owens, M., Moraczewski, J., Rowe, G.C., Riddle, N., Reed, L. K. (2016). The TreadWheel: A novel apparatus to measure genetic variation in response to gently induced exercise for Drosophila. *PLOS ONE*, *11*(10), e0164706.

McGarvey, S. T. (1994). The thrifty gene concept and adiposity studies in biological anthropology. *The Journal of the Polynesian Society*, *103*(1), 29–42.

Myers, J. H. (1978). Sex ratio adjustment under food stress: maximization of quality or numbers of offspring? *American Naturalist*, 381–388.

Neel, J. V. (1962). Diabetes mellitus: A "thrifty" genotype rendered detrimental by "progress"? *American Journal of Human Genetics*, *14*(4), 353–362.

Paz, D. (1974). An application of the coombs preference scales for family size and sex composition. *Philippine Sociological Review*, *23*(1), 118-126.

Pebley, A. R., & Goldman, N. (1995). Social inequality and children's growth in Guatemala. *Health Transition Review*, 1–20.

Peng, X. (1987). Demographic consequences of the great leap forward in China's provinces. *Population and Development Review*, *13*(4), 639.

Reiter, L. T. (2001). A systematic analysis of human disease-associated gene sequences in Drosophila melanogaster. *Genome Research*, *11*(6), 1114–1125.

Rodell, P. A. (2002). *Culture and customs of the Philippines*. Westport, CT: Greenwood Press.

Scharping, T. (2003). *Birth control in China 1949-2000: Population, policy, and demographic development*. New York, NY: Routledge.

Skorupa, D. A., Dervisefendic, A., Zwiener, J., & Pletcher, S. D. (2008). Dietary composition specifies consumption, obesity, and lifespan in *Drosophila melanogaster*. *Aging Cell*, *7*(4), 478–490.

Song, S. (2012). Does famine influence sex ratio at birth? Evidence from the 1959-1961 great leap forward famine in China. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1739), 1-8.

Song, S., & Burgard, S. A. (2008). Does son preference influence children's growth in height? A comparative study of Chinese and Filipino children. *Population Studies*, *62*(3), 305–320.

Stinson (1985). Sex differences in environmental sensitivity during growth and development. *American Journal of Physical Anthropology, 28*(6), 123–147.

Stinson (2012). Growth variations: Biological and cultural factors. In S. Stinson, B. Bogin, & D.O'Rourke (Eds.), *Human Biology: An Evolutionary and Biocultural Perspective, Second Edition* (pp. 587-635). Hoboken, New Jersey: John Wiley & Sons, Inc.

Stocker, H., & Gallant, P. (2008). Getting started. In C. Dahmann (Ed.), *Drosophila: Methods and protocols* (pp. 27–44). Totowa, NJ: Humana Press.

Sudha, S., & Rajan, S.I. (1999). Female demographic disadvantage in India 1981-1991: Sex selective abortions and female infanticide. *Development and Change*, *30*, 585-618.

Symington, M. M. (1987). Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behavioral Ecology and Sociobiology*, *20*(6), 421–425.

Trivers, R. L., & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, *179*(4068), 90–92.

VanDerslice, J., Popkin, B., & Briscoe, J. (1994). Drinking-water quality, sanitation, and breast-feeding: their interactive effects on infant health. *Bulletin of the World Health Organization*, *72*(4), 589.

Waddington, C.H. (1957). *The strategies of genes*. New York, NY: MacMillan Co.

Wagner, G. P., Booth, G., & Bagheri-Chaichian, H. (1997). A population genetic theory of canalization. *Evolution*, *51*(2), 329–347.

Woods, D. L. (2006). *Philippines: A global studies handbook*. Santa Barbara, California: ABC-CLIO.

Yang, C., Sangthong, R., Chongsuvivatwong, V., McNeil, E., & Lu, L. (2009). Effect of village income and household income on sanitation facilities, hygiene behaviours and child undernutrition during rapid economic growth in a rural cross-border area, Yunnan, China. *Journal of Epidemiology & Community Health*, *63*(5), 403–407.