

Bayesian Analysis of Agta Demography Through the Transition from Foraging to Landless Peasantry (Eastern Luzon, Philippines)

[REDACTED]^a, [REDACTED]^{a,b,c}, [REDACTED]^{a,b}, [REDACTED]^e,
[REDACTED]^d, [REDACTED]^d
^a [REDACTED]
^b [REDACTED]
^c [REDACTED]
^d [REDACTED]
^e [REDACTED]

Abstract

Drawing on the Agta Demographic Database, we conduct a Bayesian analysis of life-history traits, focused on sex-biased parental investment, birth-order effects, quantity-quality trade-offs, and adaptive fertility modulation in the Agta, a population undergoing a demographic and social/ecological transition from foragers to peasant laborers. We compare and contrast two geographic sub-divisions of the Agta population, a relatively isolated peninsular population and an acculturating mainland population, over two time periods. We find evidence of reliable demographic changes in: 1) offspring survival/parental investment by sex and birth-order, 2) maternal fertility, and 3) quantity-quality trade-offs, across these spatial and temporal categories. We interpret these responses to the transition from foraging to peasant agricultural labor from an evolutionary perspective. Additionally, we find partial quantitative evidence for adaptive, risk-sensitive fertility reduction. The multi-level Bayesian models used in our analysis allow us to integrate over uncertainty introduced by censored and missing data, and to partially pool information across clusters in the data. These models and their problem-specific derivations should be of broad interest to evolutionary anthropologists and demographers analyzing data sets with missing or censored information.

© 2014 Published by Elsevier Ltd.

Keywords: Human life-history, Quantity-Quality Trade-Offs, Birth-Order Effects, Sex-Biased Investment, Variance Compensation Hypothesis, Demographic Transition, Agta

Word Count (Paper Body): 7,762 words

Word Count (Figure Captions): 943 words

*Corresponding Author: [REDACTED]

1. Introduction

Human behavioral ecological (HBE) models give us predictions about evolutionary relationships between the socio-environmental context of a population and a variety of life-history traits (Winterhalder and Smith, 2000). In recent years, numerous studies have appeared testing specific predictions from the literature, but there is increasing recognition that such tests require the integration of multiple variables in the assessment of various suites of life-history trade-offs (see for example, Moorad et al., 2011; Lawson et al., 2013; Zietsch et al., 2014). Following their lead, we make use of the Agta Demographic Database (ADD, see Howell, 2011) produced by Headland et al. (2011) to conduct a Bayesian analysis of sex-biased parental investment, birth-order effects, quantity-quality trade-offs, and adaptive fertility modulation in the Agta population of eastern Luzon, Philippines. We investigate how life-history trade-offs change during the transition of the Agta subsistence system from foraging to peasant agricultural labor by comparing two geographic sub-divisions of the Agta, a relatively isolated peninsular population (San Ildefonso Agta) and a more rapidly acculturating mainland population (Casiguran Agta) across two time periods. Because the Agta database includes demographic and life-history data over the half-century period that Agta livelihood was transitioning from foraging to landless peasantry, it provides a valuable window into the dynamic relationship between socio-ecological circumstances and human life-history evolution (Hill and Hurtado, 1996). However, like most datasets of interest to anthropologists, the ADD, although carefully compiled and extensive in its coverage, is characterized by missing and censored information as well as data clustering. Our second, ancillary, objective therefore is to develop and illustrate Bayesian statistical methods which allow for, and in some cases turn to use, these database shortcomings.

We begin by introducing the Agta data set and the ethnographic context. We then discuss key concepts in human life-history theory and adaptive demographic change. We describe our operationalized research questions and outline our statistical methodology. Finally, we present our results and conclusions. We find reliable evidence for changes in: 1) offspring survival/parental investment by sex and birth-order, 2) maternal fertility, and 3) quantity-quality trade-offs, across Agta subpopulations and temporal phases indicative of the transition from foraging to peasantry. Likewise, we find evidence in support of a key component of adaptive fertility adjustment predicted by the variance compensation hypothesis.

1.1. The Agta Demographic Database

Headland et al. (2011) published records containing the demographic history of the San Ildefonso Agta over a 60 year period, drawing on Thomas and Janet Headland's prolonged residency and ethnographic observations among the Agta (1962 to 2010). The remarkable time depth and completeness of these demographic records makes the ADD a rich resource for testing the predictions of life-history theory in a foraging population. Despite its careful documentation and comprehensiveness, there has been little use of the ADD in evolutionary anthropology, except for select inclusion of Agta samples in cross-cultural comparisons (Walker et al., 2006; Gurven and Kaplan, 2007; Walker et al., 2008). There have been no thorough analyses of the entire Agta data set since the mostly qualitative and descriptive publication by Early and Headland (1998). This neglect may in part be because the ADD, despite its extraordinary value, is complicated by data censoring, missing information and clustering. Each of these features is common in ethnographic data; each renders problematic analysis using the traditional statistical techniques of anthropological demography. The newly-developed, multi-level Bayesian approaches utilized herein circumvent these problems, allowing us to propagate uncertainty introduced by missing and censored data through all levels of analysis, while still characterizing the relationship between socio-ecological variation and human reproductive decision-making.

We therefore propose two ancillary goals for this paper—1) the first systematic analysis of the ADD, and 2) a demonstration of how multi-level Bayesian modeling can fully leverage the value of rich anthropological and demographic data.

1.1.1. Ethnographic Background of the Agta

The subpopulations of Agta represented in the ADD include the Casiguran Agta (CA) who live on the mainland, and the San Ildefonso Agta (SIA), a geographically separate subpopulation that live on the San Ildefonso Peninsula (Headland et al., 2011).

In the period of their first detailed ethnographic description (1960s–70s) the Agta were foragers. They subsisted through hunting and gathering as well as through reciprocal exchange relations with Filipino lowlanders, especially in the case of the mainland CA. There were only limited encounters between the Agta and outsiders until the 1960s, when

large-scale logging operations began to deforest areas used by the Agta for subsistence. At the same time, a growing number of non-Agta homesteaders began to seize control of and occupy Agta territories. Logging operations led to the collapse of forest prey populations; the use of stream beds as heavy equipment routes muddied waters and destroyed fresh-water fish and shrimp stocks. As a consequence of extensive ecological damage and the in-migration of farmers, foraging became unsustainable (Headland, 1984). This transformation left the minority Agta as a largely landless peasantry (Headland, 1988) subsisting on wage labor. Increased alcoholism, generalized poverty, new diseases, and cases of outright land-grabbing, murder, and kidnapping lead to high death rates and related population changes (Headland, 2002).

Early and Headland (1998) argue that this transition began around 1965 and was complete by about 1980. Damage to their traditional livelihood and the concomitant increases in the population density of lowlanders had a significant impact on the ability of the Agta to provide for themselves and their children. Through the late 1960s and 1970s they developed from largely independent and self-sufficient foragers to an exploited underclass dominated by extractive industries and non-Agta farmers (Headland, 2002). In our analysis, we use the terms *forager phase* and *phase 1* to refer to the CA and SIA populations pre-1965. Likewise, we use the terms *peasantry phase* and *phase 2* to refer to the CA and SIA populations post-1965. Our before-after treatment of temporal phase differs from Early and Headland (1998), who define 1965–1980 as a transitional phase and post-1980 as the peasantry phase. The three periods used by Early and Headland (1998) are more ethnographically nuanced than the two phases used here, but the three-fold comparison they entail would make the statistical modeling less tractable. From long-term fieldwork and exploratory data analysis, we are confident that the dichotomous approach also captures the major modal adjustment in Agta livelihood and demography. We note that an extension of our methods using Gaussian Random Field models (Abrahamsen, 1997) might be useful in modeling secular fertility change in a more gradual manner.

Agta livelihood changes from phase 1 to phase 2 are cross-cut by geographic differences and the interaction of phase and location (See Figure 1). The mainland CA have traditionally lived in closer contact with the lowlanders than the peninsular SIA. Over the period covered by the ADD, there has been a greater degree of acculturation of the CA into the non-Agta, lowlander Philippine culture. This acculturation often results from the intermarriage of Agta females and lowlander males, the offspring of which are typically raised in the lowlander cultural tradition. The majority of the acculturating Agta population described by Early and Headland (1998) are CA and their Agta-lowlander descendants. These inter-cultural dynamics are analogous to the more well-studied African cases of cultural interdependence, as with the Efe and Lese (Bailey and DeVore, 1989), or the Aka and Ngandu (Hewlett, 1993).

[Figure 1 about here.]

Before the 1965–1980 transition, the SIA were able to forage effectively for their own food, but after the transition they were increasingly forced to subsist as agricultural laborers on a small fraction of the agricultural production of lowlanders who treated Agta as second-class residents. The SIA did not have the same options for acculturation and integration by marriage, with its improved access to resources. We sharpen the geographic distinction between CA and SIA in the sections that follow. The shift in livelihood and subsistence strategy from phase 1 to phase 2, and the shifting cultural constraints imposed on the Agta as a function of geographic location, CA or SIA, have the potential to create differential selective pressures on Agta demography. We explore how the behavioral strategies that maximize fitness might vary along these selection gradients.

1.2. Life-history Trade-Offs in the Agta

We focus primarily on investigating: 1) how sex- and parity-specific offspring survival (a proxy for parental investment) changes as a function of geographic location (SIA versus CA) and temporal phase (forager [pre-1965] and peasant [1965 and later]), and 2) how fertility rates and quantity-quality trade-offs in offspring shift along the same gradients. We review 3) how fertility rates might be affected by varying levels of extrinsic mortality, and the possibility of asymmetry in the value function (Winterhalder and Leslie, 2002) linking a narrowly defined *reproductive success* to a more generally defined *fitness*. We begin by briefly reviewing the empirical literature on human life-history, focusing on issues of importance to HBE that we can explore directly with Agta data.

1.2.1. *Birth-Order Effects and Sex Biases in Parental Investment and Offspring Survival*

Parental investment decisions are structured by the local socio-ecological and cultural conditions that mediate the effects of investment on offspring recruitment (Kaplan, 1996), offspring reproductive success (Mace, 1996; Borgerhoff Mulder, 1998; Gillespie et al., 2008) and ultimately, the parents' long term fitness (Harpending and Rogers, 1990; Rogers, 1995; Boone and Kessler, 1999). Multiple economic and cultural factors shape these outcomes. For instance, Hrdy and Judge (1993) argue that birth-order and sex-biased investment may become more important when land is owned and divided at inheritance among offspring. Parents in North American farm homesteads preferentially invested in a single male heir, thereby ensuring the survival of their farm-based lineage over time. Male-biased unigeniture was dropped as the importance of landholdings decreased and progressive legal changes improved the resource-holding potential of female offspring. Similarly, one can posit that differential investment in first-born daughters may be advantageous in contexts where the relative payoff to investment in female reproductive value and access to land or other resources exceeds that of males. Marriage offers such opportunities, as shown for marginalized populations such as Hungarian gypsies (Bereczkei and Dunbar, 1997), Central African Efe foragers (Bailey, 1988), and Kenyan Mukogodo transitional forager-pastoralists (Cronk, 1989, 1991).

There have been differences in the adaptive challenges faced by the SIA and CA. The SIA in the early phase were able to depend on foraged resources, while sometimes trading wild meat, forest products (such as rattan, wild honey, or copal), and medicinal plants for starch-based foods. Mortality was high compared to other groups in the Philippines, but families typically had relatively equal access to resources (Early and Headland, 1998). As the SIA subpopulation shifted from reliance on foraging to work as peasant laborers, access to resources, specifically land, became a key constraint in the production of the food needed to support a family and engage in trade. Indeed it appears that mortality in the SIA increased during this period (Early and Headland, 1998).

Conditions for the CA were rather different due to the possibility of intermarriage into the lowlander population and the challenge of integration in their culture. In almost all cases of inter-ethnic marriage between the Agta and lowlanders, it is an Agta woman who marries a lowlander male (Early and Headland, 1998). Thus, in the acculturating population, increased investment in daughters (especially in first-borns, since parents might not survive long enough to produce and care for later-borns) may have become important in securing their recruitment into the socially dominant population. Marriage of daughters to lowlander males may better secure access to farming land, and thus long-term lineage survival (Rogers, 1995; Boone and Kessler, 1999; Trivers and Willard, 1973), as has been observed in other foraging populations, such as the Efe (Bailey and DeVore, 1989) and Aka (Hewlett, 1993) during transition to a new mode of subsistence. Inter-ethnic marriage between an Agta male and a landowning lowlander female has remained untenable, making investment in male offspring less likely to result in increased reproductive success or access to land.

With this background in mind, we expect to see that sex- and birth-order biases in Agta mortality are affected by geographic location and temporal phase. Specifically, we expect increased investment in early-born females relative to males in the acculturating CA population as hypergyny becomes an important adaptive strategy. We utilize a multi-level Bayesian survival analysis model to investigate the structuring of mortality by sex and birth-order in both space and time.

1.3. *Fertility and the Quantity-Quality Trade-Off*

Variation in life-history traits among populations are believed to result from overall budget constraints and from differential allocations of limited energy between: (a) growth and reproduction (e.g. Hill and Hurtado, 1996), (b) reproduction and survival (e.g. Penn and Smith, 2007), and (c) the quantity and quality of offspring (e.g. Meij et al., 2009).

Anthropologists typically attribute the higher fertility of intensive agriculturalists relative to foragers to lessened overall budgetary constraints. Well-established agricultural production systems typically offer a greater availability of food and permit larger contributions of children to food production (Bentley et al., 1993; Sellen and Mace, 1997; Kramer and Boone, 2002). Despite a large overlap in values, farming populations typically have higher fertility than foraging populations (Gurven et al., 2010; Campbell and Wood, 1988).

Fertility is also affected by trade-offs between the number and quality of offspring produced (Lack, 1947; Kaplan, 1996; Kramer and Ellison, 2010). Life-history models addressing this typically assume that resources are limited, that investment per offspring decreases as a function of the number of offspring conceived, that offspring reproductive

value increases as a function of maternal investment, and that maternal fitness is determined by the number and reproductive value of offspring recruited into the breeding population (e.g. Gillespie et al., 2008). Most empirical studies of the quantity-quality trade-off have focused on child survival. In some contexts, high fertility is associated with low survival, for example in small-scale farming populations in Mali (Strassmann and Gillespie, 2002) and Ghana (Meij et al., 2009). In other contexts, for instance in Kenyan agropastoralists (Borgerhoff Mulder, 1998) and Paraguayan foragers (Hill and Hurtado, 1996), there are no effects of increasing maternal fertility on child survival. When measures of quality extend from offspring survival to recruitment into the breeding population and subsequent fitness, the diminishing returns of increased parity can sometimes be much more apparent (e.g. in 19th century Utah residents, Jones and Bird, 2014), and tend to vary by social strata (Gillespie et al., 2008; Borgerhoff Mulder, 2000).

Some of the variability in whether sibling number affects child survival can be explained as a function of the local production system. Siblings may compete with one another over the inheritance of material resources, or they may have opportunities to help their parents and one another with childcare and food production. Accordingly, the negative effects of sibling number on child survival are typically stronger among farmers and herders, who rely heavily on inherited material resources (Borgerhoff Mulder et al., 2009), than among foragers (Lawson and Mace, 2011). Extrinsic mortality may also play a role. The sharpness of the trade-off between the number of offspring a mother can produce and the number she can keep alive may reflect the extent to which child mortality is extrinsic, or unresponsive to parental investment (Pennington and Harpending, 1988; Quinlan, 2007). The logic here is not that multiple offspring fail to deplete maternal resources, but that mortality cannot easily be averted by deploying these resources. A large analysis of child survival in relation to family size across sub-Saharan Africa suggests that the costs of a large sib set on child survival are highest where the local risk of extrinsic mortality is low and, among national subsamples where maternal somatic (height) and extrasomatic (education) capital is high (Lawson et al., 2012). Conversely, population-specific studies in 18th and 19th century Finland (Gillespie et al., 2008) and among Kenyan agropastoralists (Borgerhoff Mulder, 2000) suggest that the trade-off is more apparent in resource-limited sectors of the population. These latter studies suggest that it is budgetary constraints rather than features of the mortality regime that affect the extent to which offspring quantity trades off against quality.

Here we assess whether the subsistence shift from forager to peasant laborer has an effect on fertility, and we analyze the direction of the effect of changes in extrinsic mortality on the quantity-quality trade-off. Following Gillespie et al. (2008), we would predict sharper trade-offs and larger effects in the SIA because of their limited resources as foragers, whereas following Lawson et al. (2012), we would predict smaller effects in the SIA, insofar as mortality is more likely to be extrinsic. The first prediction only holds insofar as the Agta had smaller energy budgets as foragers than as peasant laborers, and the latter insofar as mortality is more likely to be intrinsic in the CA than in the SIA. The second assumption seems appropriate given the effects of acculturation, whereas the first may be unrealistic given the disrupted resource access of Agta peasant laborers. To make these comparisons, we estimate fertility rates and the extent of the quantity-quality trade-off in offspring using a multi-level Bayesian Gamma-Poisson regression model, which integrates over uncertainty due to censored observations and produces unique estimates of the quantity-quality trade-off in each Agta subpopulation in each temporal phase.

1.4. *The Variance Compensation Hypothesis*

Risk sensitive fertility models incorporate the uncertainty of losing an offspring into the estimate of optimal fertility. Linking geometric mean fitness effects to reproductive decisions indicates that the trade-off between offspring quantity and quality is dependent on the nature of mortality risks. Boone and Kessler (1999) and (Rogers, 1995) show that inter-generational wealth transmission, coupled with a strong effect of wealth on survival and even moderate levels of catastrophic population dynamics can create ecological conditions where selection favors reduced family size in response to large-scale stochastic shocks. Leslie and Winterhalder (2002), however, argue that elevated levels of stochastic forms of mortality unrelated to maternal investment, may cause selective pressures leading to the overproduction of children, since risk-sensitive optimization requires compensation for both the mean effects of stochastic mortality, as well as for the associated variance and asymmetries in the value to parents of surviving sibships of differing sizes.

The Variance Compensation Hypothesis (VCH), introduced by Winterhalder and Leslie (2002) and Leslie and Winterhalder (2002), entails the following logic. If survival from birth to adulthood is probabilistic and parents, aware of this fact, are making reproductive decisions with an eye to their completed fertility in terms of recruited adult offspring, then analysis of their fertility decisions requires a risk-sensitive approach. Modeling those decisions requires

that we estimate the product of two functions: (i) the outcome distribution of recruited offspring as a function of fertility; and (ii) the fitness value to the parents of each outcome. In this analysis, we focus on the first of these functions, as it is directly estimable from the data (i.e. we implicitly assume that the fitness value of fertility decisions is directly proportional to the recruited offspring outcome function). In the discussion, we outline theoretical and empirical reasons why we believe that as the Agta population is approaching a possible cultural extinction, the fitness value of a smaller number of offspring with increased investment is actually elevated relative to higher fertility behavior. For these reasons, our assumption of proportionality between the outcome function of recruited offspring from fertility and the fitness value function from recruited offspring is conservative in our test of the VCH.

We test if fertility rates shift according to two major predictions of the VCH. Leslie and Winterhalder (2002) argue that (1) reduced stochastic outcome variance (variance in recruited offspring, holding constant the effects of maternal parity) will lead to reduction in fertility. To test this prediction, we estimate the residual difference between the estimated value function linking maternal births to recruited offspring in each location-phase pairing and the observed data. A decrease in age-specific fertility in response to a decrease in the dispersion of these residuals would be consistent with the predictions of the VCH model for demographic transition to lowered fertility. Additionally, Leslie and Winterhalder (2002) argue that (2) an increase in the value of a small number of surviving offspring will drive a reduction in fertility. To test this prediction, we estimate and compare the mean value (in terms of recruited offspring) of lowered fertility across Agta subpopulations. A decrease in age-specific fertility in response to an increased value of low fertility behavior, detected as an elevation of the lower portion of the value function, would be consistent with the predictions of the VCH model.

1.5. *Research Questions and Predictions*

1) Structuring of Mortality

a. Since opportunities for hypergyny into a wealthier population favor female-biased investment in offspring, we predict increased investment (and, thus, decreased mortality) in daughters—particularly first born daughters—relative to sons in the CA across phases.

2) Structuring of Fertility

a. Age-specific fertility will vary across the SIA and mainland CA populations during the forager and peasantry phases as a consequence of changing budget constraints. Assuming decreased budgetary constraints in phase 2 in both the SIA and CA, we would expect to see increased phase two fertility in both locations.

b. The extent of the quantity/quality trade-off will vary across the SIA and mainland CA populations during the forager and peasantry phases of Agta society as a result of variation in the costs of raising children and/or the impact of extrinsic mortality. Following Gillespie et al. (2008), we would predict more extreme quantity-quality trade-offs in the SIA because of their limited resources as foragers. On the other hand, following Lawson et al. (2012), we would predict smaller trade-offs in the SIA, insofar as mortality is more likely to be extrinsic.

3) VCH Predictions

a. We predict that reduced stochastic outcome variance will be associated with lower fertility.

b. We predict that elevation of the lower portion of the value function will be associated with lower fertility.

2. **Methods**

2.1. *Data Source: Agta Demographic Database*

The data used in this study come from the female fertility reports in the Microsoft Access © database hosted on the Summer Institute of Linguistics servers (Headland et al., 2011). We selected reports for both the SIA and CA (non-SIA) subpopulations.

Survival analysis was conducted using only the offspring of Agta women. The quantity-quality trade-off was modeled using the reproductive outcomes of Agta women who have had at least a single birth or miscarriage. We set exposure to risk of pregnancy equal to Age minus 15 years; it is capped at 40 years, implying that pregnancy after age

55 has zero probability. As noted earlier, the year 1965 marks the switch point between phase 1 and 2. In the survival analysis model, anyone born on or after 1965 was considered as part of phase 2. In the quantity-quality trade-off and fertility models, any woman who began her reproductive career (reached the age of 15) in the year 1965 or later was considered as part of phase 2. An offspring is considered recruited if he or she survives to an age of 15 years. In the text, we use the phrase *reported pregnancies* to refer to the number of reported births, still births, and miscarriages attributed to each woman in the Agta database. The sample sizes (N) of observed, censored, and missing data in each class of interactions used in our analyses is included in the Supplementary Materials.

2.2. Hierarchical Bayesian Statistical Modeling

Testing life-history predictions using human demographic data on foraging populations is challenging. Historical demographic data sets rarely include hunter-gatherer populations, and contemporary data sets are frequently incomplete and plagued by censored information. The data used in this analysis are highly detailed and very complete across approximately 4–7 generations. However, a large portion of the data are censored, meaning that women's reproductive careers were still unfolding, and hence incomplete at the time of data collection. We wish to avoid typical approaches to dealing with censored data, such as removing censored cases, treating the age of censoring as an observation, *ad hoc* weighting schemes, and selection of data sets based on completeness instead of relevance to theoretical questions. Because Bayesian approaches allow for propagation of uncertainty due to missing, partially known, and censored data (Gelman et al., 2013; Stan Development Team, 2013b), we use hierarchical full Bayesian models to address our predictions. This form of data analysis allows us to make the most of the information content in the Agta database. The hierarchical model structure allows for spatially and temporally clustered data to be used to infer location- and time-specific effects (Mace, 2013).

To estimate unknown parameters in our models, we use Hamiltonian Markov Chain Monte Carlo simulation (Hoffman and Gelman, 2014). Our Markov chains are coded in templated C++ using the Stan 2.2.0 C++ library (Stan Development Team, 2013a). They were run for at least 2,000 warm-up iterations and 8,000 sampling iterations. In the Supplementary Materials sections 1.3–1.5, we address model fit, Markov chain convergence diagnostics, and effective posterior sample sizes for each model.

2.2.1. A Hierarchical Bayesian Survival Analysis Model

To estimate the survival profiles of the Agta subpopulations in each phase and location, we utilize a multi-level Bayesian Weibull regression model, a standard approach to parametric survival analysis (Dellaportas and Smith, 1993; Ibrahim et al., 2005). We estimate subpopulation and phase-specific effects of the interaction of sex and birth-order (first-born vs. later-born). We account for censoring by modeling individuals with an observed age of death, $AOD_{[i]}$, as:

$$AOD_{[i]} \sim \text{Weibull}(r_{[Loc_{[i]}, Phase_{[i]}]}, e^{-\left(\frac{\psi_{[Loc_{[i]}, Phase_{[i]}, Sex_{[i]}, BO_{[i]}]}{r_{[Loc_{[i]}, Phase_{[i]}]}}\right)}) \quad (1)$$

and, following the Stan reparameterization of the *Mice* example model from the BUGS software environment, we model individuals with an observed age of censoring, $AOC_{[i]}$, as:

$$\varphi_{[i]} \sim \text{Weibull}(r_{[Loc_{[i]}, Phase_{[i]}]}, \frac{e^{-\left(\frac{\psi_{[Loc_{[i]}, Phase_{[i]}, Sex_{[i]}, BO_{[i]}]}{r_{[Loc_{[i]}, Phase_{[i]}]}}\right)}}{AOC_{[i]}}) \quad (2)$$

where $\varphi_{[i]} \in (1, 90)$ is a parameter with an explicit lower bound of 1, which through the model definition provides an implicit lower bound of $AOC_{[i]}$, allowing for the estimated time of death to be possibly greater than, but never less than the age of censoring. The symbols $Loc_{[i]}$, $Phase_{[i]}$, $Sex_{[i]}$, and $BO_{[i]} \in \{1, 2\}$ are indicators of the location, temporal phase, sex, and birth-order of individual i . The ψ parameters are defined as a $2 \times 2 \times 2 \times 2$ array, and are partially pooled in a multi-level framework:

$$\psi_{[Loc, Phase, Sex, BO]} \sim \text{Normal}(\mu_{\psi}, \sigma_{\psi}) \quad (3)$$

Some individuals in the Agta data set are not classified as male or female, normally due to death early in childhood. The distribution of individuals of unclassified sex is modeled as a mixture of males and females, with unknown mixing proportions unique to each location and phase. Let $\xi_{[Loc, Phase]}$ be a unit 2-simplex, so for all cases where the sex of the

individual is unknown, we integrate over uncertainty in sex by using a weighted sum of the sex-specific ψ parameters in the Weibull model:

$$\xi_1[Loc_{[i]}, Phase_{[i]}] \psi[Loc_{[i]}, Phase_{[i]}, Sex=1, BO_{[i]}] + \xi_2[Loc_{[i]}, Phase_{[i]}] \psi[Loc_{[i]}, Phase_{[i]}, Sex=2, BO_{[i]}] \quad (4)$$

The shape parameter of the Weibull distribution, r , determines how the hazard changes over the life course. A value of one indicates a constant hazard and a value less than one a decreasing hazard over time. An r value of less than one is typically indicative of infant mortality in population data. To estimate and control for infant mortality across subpopulations (SIA vs CA) and temporal phase, we estimate unique r coefficients for each combination of temporal phase and location using partial pooling:

$$\log(r_{[Loc, Phase]}) \sim \text{Normal}(\mu_r, \sigma_r) \quad (5)$$

All hyperparameters are given weakly regularizing priors:

$$\mu_\psi \sim \text{Normal}(0, 10) \quad (6)$$

$$\mu_r \sim \text{Normal}(0, 10) \quad (7)$$

$$\sigma_\psi \sim \text{Cauchy}(0, 2.5)T[0, \infty] \quad (8)$$

$$\sigma_r \sim \text{Cauchy}(0, 2.5)T[0, \infty] \quad (9)$$

Ages in the Agta database are not always known exactly. Both year of birth and year of death are characterized by uncertainty ranging from less than a month to more than nine years. To account for this uncertainty, we model age of death as a random variable for all deceased individuals using a standard Gaussian measurement error model:

$$AOD_{[i]} \sim \text{Normal}(\mu_{AOD_{[i]}}, \sigma_{AOD_{[i]}}) \quad (10)$$

where $\mu_{AOD_{[i]}}$ is the estimated of age of death provided in the Agta database. To obtain $\sigma_{AOD_{[i]}}$, a standard deviation, we assume that errors in age are Gaussian, such that an error range can be described by 6 standard deviations, covering approximately 99.7% of observations. For deceased individuals we assume that errors in year of birth and year of death are independent. Error on age of death, $\sigma_{AOD_{[i]}}$, then can be described from the errors on year of birth, $\sigma_{YOB_{[i]}}$ and year of death, $\sigma_{YOD_{[i]}}$, as:

$$\sigma_{AOD_{[i]}} = \sqrt{\sigma_{YOB_{[i]}}^2 + \sigma_{YOD_{[i]}}^2} \quad (11)$$

Likewise, we model age of censoring as a random variable for all censored individuals using a standard measurement error model:

$$AOC_{[i]} \sim \text{Normal}(\mu_{AOC_{[i]}}, \sigma_{AOC_{[i]}}) \quad (12)$$

where $\mu_{AOC_{[i]}}$ is the estimate of age of censoring provided in the Agta database and $\sigma_{AOC_{[i]}}$ is equal to $\sigma_{YOB_{[i]}}$.

To estimate the probability of death, $Pr(D_Z)$ before a given age Z , we integrate the Weibull cumulative distribution function (CDF) on the interval $(0, Z)$:

$$Pr(D_Z|Loc, Phase, Sex, BO) = \int_0^Z \text{Weibull_CDF}(r_{[Loc, Phase]}, e^{-\left(\frac{\psi_{[Loc, Phase, Sex, BO]}}{r_{[Loc, Phase]}}\right)}) \quad (13)$$

Conditional probabilities of death (e.g., the probability of dying before age 15 conditional on having survived to age 5) can then be understood as a difference of integrals over the CDF. The median age of death, M , is estimated as:

$$M_{[Loc, Phase, Sex, BO]} = (\log(2)e^{-\left(\frac{\psi_{[Loc, Phase, Sex, BO]}}{r_{[Loc, Phase]}}\right)})^{\frac{1}{r_{[Loc, Phase]}}} \quad (14)$$

2.2.2. Hierarchical Bayesian Fertility Model

To investigate the relationship between offspring quantity and quality in the Agta, we replicate analyses that have regressed recruited offspring on maternal fertility, as performed by Meij et al. (2009), Gillespie et al. (2008), and Strassmann and Gillespie (2002). However, in contrast to these studies, we utilize a multi-level Bayesian Poisson regression model to estimate age-specific fertility, and a multi-level Bayesian Gamma-Poisson regression model to estimate the number of offspring recruited to reproductive age as a function of reported pregnancies. The complete model allows us to characterize both age-specific fertility and the quality-quantity trade-off across location and temporal phase in a single unified framework that integrates over uncertainty introduced by data censoring and missing information.

The total recruited offspring, $Y_{[i]}$, of individual i , is modeled using a Gamma-Poisson model structure, where:

$$Y_{[i]} \sim \text{Poisson}(\lambda_{[i]}) \quad (15)$$

and:

$$\lambda_{[i]} \sim \text{Gamma}(A_{[i]}, B_{[Loc_{[i]}, Phase_{[i]}]}) \quad (16)$$

We use the Gamma-Poisson structure because these data show signs of over-dispersion relative to a pure Poisson distribution. The A parameter vector of the Gamma distribution is modeled as a function of the number of reported pregnancies, $P_{[i]}$, of individual i :

$$\log\left(\frac{A_{[i]}}{B_{[Loc_{[i]}, Phase_{[i]}]}}\right) = \theta_{1[Loc_{[i]}, Phase_{[i]}]} + \theta_{2[Loc_{[i]}, Phase_{[i]}]}\log(P_{[i]}) \quad (17)$$

which implies a linear model on the mean through a log link function, since the mean of a Gamma distribution can be written as $\mu = \frac{A}{B}$. The B parameter is modeled hierarchically as:

$$\log(B_{[Loc_{[i]}, Phase_{[i]}]}) \sim \text{Normal}(\mu_B, \sigma_B) \quad (18)$$

with regularizing priors on the hyperparameters:

$$\mu_B \sim \text{Normal}(0, 1) \quad (19)$$

$$\sigma_B \sim \text{Normal}(0, 1)T[0, \infty] \quad (20)$$

The $\theta_{[Loc, Phase]}$ parameter array allows each combination of location and temporal phase to have unique regression lines. These regression parameters are partially pooled in a hierarchical framework using a multivariate normal distribution:

$$\theta_{[Loc, Phase]} \sim \text{Multivariate Normal}(\mu_\theta, \Sigma_\theta) \quad (21)$$

where each cell of the mean hyperparameter vector has a weakly regularizing prior distribution:

$$\mu_\theta \sim \text{Normal}(0, 10) \quad (22)$$

A prior on the covariance matrix is specified using a Cholesky factor parameterization. This approach improves Markov Chain Monte Carlo efficiency when the posterior distributions of parameters are correlated (details in Supplementary Materials Subsection 1.7; Supplementary Stan Code).

Some women in this population have incomplete or censored reproductive careers; the number of their pregnancies and recruited offspring are known only to lower limits. There are three classes of mothers in the Agta database:

- 1) Women either dead or older than fifty-five years who have complete pregnancy and rearing records (all offspring are either dead or recruited, i.e., ≥ 15 years of age).
- 2) Women either dead or older than fifty-five years who have complete pregnancy records and incomplete or censored rearing records (some offspring are alive and not yet recruited).
- 3) Women alive and younger than fifty-five years who have incomplete pregnancy records and, therefore, incomplete or censored rearing records.

We model data from the first class of women using the statistical methodology presented above. Data from the other two classes must be modeled using a more complex variant of the above model. Censored outcome data can be modeled by analytically integrating over the area of the CDF falling above the lower censoring threshold, $min Y_{[i]}$, which is known by counting the total number of recruited offspring for woman i at the time of censoring, and below $max Y_{[i]}$, the maximum number of recruited offspring possible given the number of already recruited offspring and the remaining number of living and unrecruited offspring of woman i . See Supplementary Materials section 1.6 for details.

The number of reported pregnancies, $P_{[i]}$, of individual i is modeled as a function of the time each woman has spent at reproductive age, $E_{[i]}$, defined in this analysis as the number of years lived by each woman in the interval $\{15, 16, \dots, 55\}$ years of age, using a standard Poisson regression model:

$$P_{[i]} \sim \text{Poisson}(\Lambda_{[i]}) \quad (23)$$

where:

$$\log(\Lambda_{[i]}) = \phi_{1[Loc_{[i]}, Phase_{[i]}]} + \phi_{2[Loc_{[i]}, Phase_{[i]}]} \log(E_{[i]}) \quad (24)$$

and:

$$\phi_{[Loc, Phase]} \sim \text{Multivariate Normal}(\mu_\phi, \Omega) \quad (25)$$

$$\mu_\phi \sim \text{Normal}(0, 10) \quad (26)$$

3. Results

3.1. The Structuring of Survival by Location, Phase, Sex, and Birth-Order

There is substantial variation in the survival profiles of Agta as a function of the interaction of location, phase, sex, and birth-order. Table 1 displays the cumulative probabilities of death for each category of Agta on the intervals: 0–1 year, 0–5 years, and 0–15 years, as well as the estimated median age of death. Figure 2 plots these data. The full posterior estimates from the survival analysis model for the four variables, as well as the empirical survivorship curves are included in the Supplementary Materials section 1.1.

[Figure 2 about here.]

These patterns are evident: 1) Across phases, the CA have longer expected lifespans than the SIA; 2) Survival outcomes for the SIA were better in phase 1 when they were foragers, before the territorial encroachment of loggers, miners, and homesteaders; 3) The survival outcomes of younger CA were better in phase 1 than phase 2, however, the survival outcomes of adult CA are better during phase 2; 4) Survival of first-borns declines drastically in the SIA from phase 1 to phase 2, while it remains roughly constant across the phase 2 transition for later-borns; 5) There is evidence of an emerging male survival bias in the SIA phase 2; and, 6) in phase 2 of the CA, the survival of first-born males is significantly reduced relative to other classes.

Infant mortality appears to be highest in the SIA phase 2, $r = 0.33$ (PCI95: 0.31, 0.46), and lowest in the CA phase 1, $r = 1.38$ (PCI95: 1.24, 1.52), with intermediate levels in the SIA phase 1, $r = 0.51$ (PCI95: 0.47, 0.56), and the CA phase 2, $r = 0.51$ (PCI95: 0.47, 0.56).

We comment more extensively in the discussion on the mortality patterns uncovered by our survival analysis.

[Table 1 about here.]

3.2. The Structuring of Age-Specific Fertility by Location and Phase

In Figure 3, we present predictions from the regression model of reported pregnancies on years at risk for pregnancy for each geographic subpopulation of Agta in each phase; we hyper-impose the model predictions on the observed data. Fertility in the CA is reduced relative to fertility in the SIA. Fertility slightly increases in the SIA from phase 1 to phase 2, while it has remained low in the CA across phases. Table 2 displays the parameter estimates and ninety-five percent posterior credibility intervals (PCI95s) of our model.

Mean completed fertility (fertility at 40 years post-menarche) in the SIA phase 1 is 5.95 (PCI95: 5.55, 6.36); it is only 3.94 (PCI95: 3.63, 4.23) in the CA during phase 1. Fertility increases in the SIA during phase 2 to reach 7.11 (PCI95: 6.49, 7.75), while it remains approximately constant in the CA during phase 2 at 4.13 (PCI95: 3.62, 4.70).

[Figure 3 about here.]

[Table 2 about here.]

3.3. The Structuring of the Quantity-Quality Trade-Off by Location and Phase

In Figure 4, we plot the predictions of the regression model of recruited offspring on number of reported pregnancies for each subpopulation of Agta in each phase; we hyper-impose the model predictions, the distribution of censored observations, and the raw data. There is evidence of a quantity-quality trade-off in both the SIA and CA in phase 1, as indicated by the exposure parameters falling reliably short of proportionality. There is less evidence of such a trade-off in phase 2, as indicated by the confidence intervals including 1.0, the value of proportionality. Evidence of a quantity-quality trade-off is, however, stronger in the SIA in phase 1, where the exposure parameter equals 0.80 (PCI95: 0.68, 0.91), than in the CA in phase 1, where the exposure parameter equals 0.84 (PCI95: 0.72, 0.96). Table 3 displays the parameter estimates and credibility intervals of our model.

[Figure 4 about here.]

[Table 3 about here.]

3.4. The Variance Compensation Hypothesis

To investigate if fertility change in the Agta follows the predictions of the VCH model, we utilize information from the quantity-quality trade-off and age-specific fertility models. We estimate the extent of stochastic outcome variance—variance in pre-recruitment death of offspring, controlling for the effects of maternal parity—by calculating the maximum *a posteriori* residuals for all observed and censored data. Residuals for censored data were calculated using $\max Y_{[i]} - \min Y_{[i]}$ as a data point. We present kernel density estimates of these residuals in each location phase pair in Figure 5(a). An increasing width of dispersion in these residuals indicates an increasing amount of stochastic pre-recruitment death in offspring, controlling for the mean effects of maternal parity. In ecological contexts with lowered levels of stochastic outcome variance, the VCH predicts lowered fertility, since mothers will need to engage in less bet hedging to ensure recruitment of the desired number of offspring. In phase 1, the variance of the residuals was 1.73 and 0.89 in the SIA and CA respectively; this is a ratio of 1.94 (PCI95, F-test: 1.46, 2.58), which is strong evidence of increased stochastic outcome variance in the SIA. In phase 2, the variance of the residuals was 1.47 and 0.98 in the SIA and CA respectively; this is a ratio of 1.50 (PCI95, F-test: 1.06, 2.11), which is also strong evidence of increased stochastic outcome variance in the SIA.

In Figure 5(b), we present the results of an analysis illustrating the influence of the shape of the value function on fertility. Across both phases, the value function is significantly elevated in the CA relative to the SIA. We illustrate the expected effect of this difference in the value function on fertility by showing the number of pregnancies needed to reach a target number of recruited offspring in each subpopulation. For example, if the target number of recruited offspring were 4, then in phase 1 an SIA mother would need 7.0 (PCI95: 6.2, 7.9) pregnancies on average to yield such an outcome, while 5.2 (PCI95: 4.6, 5.8) pregnancies would suffice for a mother in the CA. A similar pattern holds true in phase 2, where an SIA mother would need 10.0 (PCI95: 8.0, 14.0) pregnancies to reach a target of 4 recruited offspring on average, while only 6.7 (PCI95: 5.0, 9.1) pregnancies would be needed by a CA mother on average.

[Figure 5 about here.]

4. Discussion

In one of the classic papers of evolutionary biology, Levins (1966) argued that multiple simple models would be needed to address any complex adaptive phenomenon. Similarly, recent studies (e.g. Moorad et al., 2011; Lawson et al., 2013; Zietsch et al., 2014) have argued for the integration of multiple variables into the assessment of life-history trade-offs. We acknowledge both perspectives by investigating, within the framework of human behavioral ecology and life-history theory, predictions of several models concerning heterogeneity in mortality and fertility. We examine how these demographic characteristics are structured by sex and parity across the socio-economic changes

represented in the two locations and time periods captured in the Agta Demographic Database. Of equal importance, we illustrate key methodological advances by deriving problem-specific Bayesian models that incorporate and control for the multi-level structuring of data and integrate over uncertainty due to data estimation, censoring, and missing information.

4.1. *Effects of Birth-Order and Sex on Survival*

There is substantial heterogeneity in Agta survival outcomes by temporal phase and location.

1) Across phases, the elevated SIA mortality relative to that in the CA generally is consistent with studies showing elevated mortality among foragers (e.g. Hill and Hurtado, 1996). The SIA experience relatively high mortality during both infancy and post-infancy, a result somewhat different from that of Sellen and Mace (1997), who found that the elevated mortality of foragers is normally reflected only in mortality after infancy.

2) Elevated mortality in the SIA phase 2 relative to phase 1 is unexpected on the basis of production system changes (Sellen and Mace, 1997). It is, however, understandable in light of ecological damage and displacement, and the abuse of the SIA by settlers, loggers, and miners (Early and Headland, 1998; Headland, 2002, 2004). Although the SIA appear to be shifting away from foraging, their socio-economic subjugation as landless peasants obviates any potential mortality reduction. More generally, the Agta case illustrates that care must be taken when using contemporary data to inform demographic transitions in prehistory. Although agriculture has replaced foraging as the predominant subsistence mode in the Casiguran region, subsistence is not the most important factor in the Agta demographic experience there.

3) Decreased mortality in the CA during phase 2 is expected on the basis of acculturation and hypergenous marriage patterns (Headland and Headland, 1998; Early and Headland, 1998). This change may be driven by economic status, specifically the increased access of the acculturating Agta to the resources held by lowlander families, as well as the associated cultural capital (Early and Headland, 1998) and western medical facilities (Headland, 2004).

4) In the SIA, the transition from foraging to peasant labor is marked by a significant decrease in median survival, especially for first-borns. This may be related to dynamics described by Borgerhoff Mulder and Beheim (2011) and Kembo and Van Ginneken (2009), where elevated mortality in first-borns is seen as the result of the immature reproductive systems of young mothers producing underweight babies (Rutstein, 1984). We hypothesize that the decreased availability of resources in the SIA population in phase 2 may be increasing the hazard of death in first-borns.

5) There is evidence for increasing parental favoritism directed toward male offspring in the SIA in phase 2, perhaps a result of the increased value of males as agricultural laborers (Burton and White, 1984; Boserup, 2007). Alternatively, if Agta women played an important role in foraging, they may have suffered a decline in status as foraged foods became replaced in the SIA economy by male-oriented labor and exchange.

6) In the CA, however, the transition to phase 2 has been marked by a significant decrease in survival for first-born males, but increased survival for females and later-born males. This pattern may be related to what Bereczkei and Dunbar (1997) found in Hungarian Gypsy populations and Cronk (1989) found in the Mukogodo; opportunities for hypergyny into a wealthier population favor female-biased investment in offspring. In the present phase 2 circumstances of the CA, marriage into a lowlander family is one of the surest ways of securing long-term lineage survival. In the face of pressures from loggers, miners, homesteaders, and international socio-political struggles, the population levels of the Agta have been declining in both relative and absolute terms. The Agta were ~10% of the Philippine population during the Spanish colonial period, but are only 0.05% currently; the CA and SIA numbered ~1,000 individuals in 1936, but number less than 600 individuals today (Headland et al., 2011). Given such dramatic population decline, intermarriage and acculturation may be the only way in which lineage survival can be insured (Headland and Headland, 1998). We hypothesize that the external disruption of their livelihood has placed intense pressure on CA adults to invest primarily in daughters, as a means of seeing that their offspring are recruited into the lowlander cultural group.

4.2. *Fertility Change and the Quantity-Quality Trade-Off*

4.2.1. *Fertility Change*

With respect to fertility change in the Agta, we find: 1) strong evidence of reduced age-specific fertility in the CA relative to the SIA, possibly reflecting an early onset of demographic transition, and 2) we find a small increase in

age-specific fertility in the SIA between phase 1 and phase 2. This increase (2) is unlikely to reflect relaxed budgetary constraints, insofar as SIA phase 2 is characterized by considerable disturbance to the major resource base. Rather it may reflect elevated levels of extrinsic mortality, increasing the need of parents to overproduce offspring in order to have a viable sibship at offspring adulthood (Lawson et al., 2012; Leslie and Winterhalder, 2002).

4.2.2. *The Quantity-Quality Trade-Off*

We find evidence of the quantity-quality trade-off, but the absolute magnitude of the effect is moderate (as in Lawson et al., 2012). It predominately occurs during phase 1, and is unlikely to be the principle factor affecting fertility or, indeed, fertility decline. The quantity-quality trade-off during phase 1 is stronger in the SIA than in the CA, suggesting that the costs associated with raising children under a limited budget, harsher environmental context and lack of medicine are important factors in driving mortality as maternal parity increases.

Our analysis of the quantity-quality trade-off is potentially compromised by phenotypic correlation (Hill and Hurtado, 1996). Phenotypic correlation, or correlation between increased maternal quality and increased offspring recruitment, has the potential to obscure the quantity-quality trade-off. Fortunately, we can test for the quantity-quality trade-off while controlling for maternal quality, operationalized as maternal height, weight, or weight-for-height, variables included in the ADD. We fit several basic maximum likelihood Poisson regression models to a subset of the Agta data for which we have complete fertility records and anthropometric data (Supplementary Materials section 1.2). Formal model comparison with AIC indicates that the base model, with no controls for maternal state, is preferred to other models. This indicates that our main findings are not confounded by maternal embodied capital, at least as measured by these proxy variables. Our results parallel those of Sear (2007), who found that controlling for maternal condition in Gambia did not affect her findings concerning quantity-quality trade-offs.

Results presented in Supplementary Materials section 1.2 also show that repeated reproduction is associated with lessened maternal condition and greater child mortality. In the second ranked model, the parameter modulating the effect of weight-for-height on number of recruited offspring indicates a strong negative association between maternal embodied capital and number of recruited offspring. Put differently, there is a trade-off between maternal investment in her own body mass and the survival of her offspring. This suggests that over the short term women with elevated weight-to-height ratios could invest body mass in increased reproduction. However, long-term considerations might make it non-adaptive to do so. These results parallel some of the findings on ‘maternal depletion syndrome’ reviewed by Dewey and Cohen (2007), and are congruent with classic studies in the non-human animal literature; for example, the negative effects of large clutch size in songbirds often do not show up until subsequent breeding seasons (e.g. Williams, 1966).

4.3. *Variance Compensation*

We tested two hypotheses that spring from the idea that no parent can be sure whether or not their child will survive to recruitment age—in other words, that target reproductive outcomes are affected by stochastic variance (Winterhalder and Leslie, 2002; Leslie and Winterhalder, 2002). Other factors being equal, lower fertility is predicted in contexts where stochastic outcome variance is reduced, and where the value function linking pregnancies to recruited offspring approaches proportionality. Both predictions are supported.

Controlling for the mean effects of maternal parity, reduced stochastic outcome variance in recruited offspring is associated with lower fertility. Stochastic outcome variance is significantly lower in the CA than the SIA. Likewise, we observe an elevation of the lower portion of the value function—the expected number of recruited offspring given a small number of pregnancies, e.g., 1–5 pregnancies—in the CA relative to the SIA.

The value of a smaller number of offspring may be elevated in the CA relative to the SIA in ways not reducible strictly to offspring recruitment. While many researchers of non-human animal behavior measure the value of reproductive decisions by assessing the number of recruited offspring or grand-offspring per fertility decision, it is likely that the value function in humans is more complex. Potentially it is a result of offspring number, embodied capital, and socio-relational and material wealth (Rogers, 1995; Boone and Kessler, 1999; Kaplan, 1996; Winterhalder and Leslie, 2002; Smith et al., 2010; Gurven et al., 2010; Borgerhoff Mulder et al., 2009; Snopkowski and Kaplan, 2014). By intermarrying with the Filipino lowlanders and reducing fertility, the acculturating CA could be building more economic and social/relational security (Headland and Headland, 1998), and thus increasing the likelihood of long-term lineage survival. Confirmation of this possibility would require more in-depth ethno-demographic study of

acculturating CA. We note that such a context would serve to increase the value of lowered fertility to a greater extent than that assumed in our analysis. Our results are grounded on what we believe is a more conservative assumption that the value function is based only on offspring recruitment, and we still find evidence in support of the VCH.

4.4. Fertility Change, Variance Compensation, and the Agta Demographic Transition

The general situation of the Agta—rife with exploitation and dispossession of traditional resources—suggests that lowered fertility in the CA may be adaptive in the way argued by Rogers (1995) and Boone and Kessler (1999). As lineage survival becomes best ensured by producing high-quality daughters who can marry hypergynously, selection can favor lowered total reproduction (Winterhalder and Leslie, 2002; Leslie and Winterhalder, 2002), especially in contexts where population dynamics are marked by severe shocks and increased investment per offspring can help to shift a lineage out of an ecological context that would lead to extirpation (Boone and Kessler, 1999). Our successful empirical tests of the VCH as an explanation for demographic transition of course does not exclude the possibility that other adaptive (Kaplan, 1996; Kaplan et al., 1995) and non-adaptive (Richerson and Boyd, 2008; Pérusse, 1993; Goodman et al., 2012; Collier et al., 2014) theories for the demographic transition might also be consistent with the data.

Our discussion has focused on exploring specific HBE models that may explain variability in Agta demographic outcomes, but we cannot conclude without acknowledging a more fundamental result evident in our analyses of Agta demography in the late 20th century: the incursion of settlers and extractive industries into Agta territory, and the ensuing expropriation of Agta homeland and natural resources has been disastrous for demographic measures of the welfare of the Agta people (Headland et al., 2011).

4.5. The Value of Bayesian Methods in Twenty-First Century Anthropology

Finally, as a secondary goal of this paper, we have demonstrated how full Bayesian model specification allows researchers to create custom statistical tools that rigorously account for uncertainty in measurement of covariates and outcomes, missing data, and censored variables like recruited offspring. Our analytical tools, detailed in the Supplemental Materials, give us access to the full information content of imperfect data without the need to restrict analysis to small subsets or complete cases. Demographic and anthropological data on foraging and other subsistence populations, like data on archaeological sites (Winterhalder et al., 2010), are often limited in sample size, highly localized and potentially unique, and difficult and costly to gather. As is evident in the ADD, collection of such data requires years or even decades of detailed anthropological fieldwork. Statistical tools like Stan (Stan Development Team, 2013b) are both user friendly and have the computational power to allow us to make complete use of this painstakingly collected information despite its imperfections.

5. Acknowledgments

We would like to thank [REDACTED] and [REDACTED] for guidance through all phases of research design, analysis, and statistical modeling. We thank [REDACTED] for help with final editing. [REDACTED] designed and conducted the statistical analysis; [REDACTED], [REDACTED] and [REDACTED] conceptualized and wrote the paper; [REDACTED] and [REDACTED] collected ADD data and provided ethnographic expertise; [REDACTED] constructed the ADD.

References

- Abrahamsen, P. (1997). *A review of Gaussian random fields and correlation functions*. Norsk Regnesentral/Norwegian Computing Center.
- Bailey, R. C. (1988). The significance of hypergyny for understanding subsistence behavior among contemporary hunters and gatherers. *Diet and Subsistence: Current Archaeological Perspectives*, pages 57–65.
- Bailey, R. C. and DeVore, I. (1989). Research on the efe and lese populations of the ituri forest, zaire. *American Journal of Physical Anthropology*, 78(4):459–471.
- Bentley, G. R., Goldberg, T., and Jasieńska, G. z. y. (1993). The fertility of agricultural and non-agricultural traditional societies. *Population Studies*, 47(2):269–281.
- Berezkei, T. and Dunbar, R. I. (1997). Female-biased reproductive strategies in a hungarian gypsy population. *Proceedings of the Royal Society Series B: Biological Sciences*, 264(1378):17–22.
- Boone, J. L. and Kessler, K. L. (1999). More status or more children? social status, fertility reduction, and long-term fitness. *Evolution and Human Behavior*, 20(4):257–277.

- Borgerhoff Mulder, M. (1998). Brothers and sisters: How sibling interactions affect optimal parental allocations. *Human Nature*, 9(2):119–161.
- Borgerhoff Mulder, M. (2000). Optimizing offspring: the quantity–quality tradeoff in agropastoral kipsigis. *Evolution and Human Behavior*, 21(6):391–410.
- Borgerhoff Mulder, M. and Beheim, B. A. (2011). Understanding the nature of wealth and its effects on human fitness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1563):344–356.
- Borgerhoff Mulder, M., Bowles, S., Hertz, T., Bell, A., Beise, J., Clark, G., Fazzio, I., Gurven, M., Hill, K., Hooper, P. L., et al. (2009). Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science*, 326(5953):682–688.
- Boserup, E. (2007). *Woman's role in economic development*. Earthscan.
- Burton, M. L. and White, D. R. (1984). Sexual division of labor in agriculture. *American Anthropologist*, 86(3):568–583.
- Campbell, K. L. and Wood, J. W. (1988). Fertility in traditional societies. *Natural Human Fertility: Social and Biological Determinants*, pages 39–69.
- Colleran, H., Jasienska, G., Nenko, I., Galbarczyk, A., and Mace, R. (2014). Community-level education accelerates the cultural evolution of fertility decline. *Proceedings of the Royal Society B: Biological Sciences*, 281(1779):20132732.
- Cronk, L. (1989). Low socioeconomic status and female-biased parental investment: The mukogodo example. *American Anthropologist*, 91(2):414–429.
- Cronk, L. (1991). Preferential parental investment in daughters over sons. *Human Nature*, 2(4):387–417.
- Dellaportas, P. and Smith, A. F. (1993). Bayesian inference for generalized linear and proportional hazards models via gibbs sampling. *Applied Statistics*, 42:443–443.
- Dewey, K. G. and Cohen, R. J. (2007). Does birth spacing affect maternal or child nutritional status? a systematic literature review. *Maternal & Child Nutrition*, 3(3):151–173.
- Early, J. D. and Headland, T. N. (1998). *Population dynamics of a Philippine rain forest people: The San Ildefonso Agta*. University Press of Florida.
- Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., and Rubin, D. B. (2013). *Bayesian data analysis*. CRC press.
- Gillespie, D. O., Russell, A. F., and Lummaa, V. (2008). When fecundity does not equal fitness: evidence of an offspring quantity versus quality trade-off in pre-industrial humans. *Proceedings of the Royal Society Series B: Biological Sciences*, 275(1635):713–722.
- Goodman, A., Koupil, I., and Lawson, D. W. (2012). Low fertility increases descendant socioeconomic position but reduces long-term fitness in a modern post-industrial society. *Proceedings of the Royal Society B: Biological Sciences*, 279(1746):4342–4351.
- Gurven, M., Borgerhoff Mulder, M., Hooper, P. L., Kaplan, H., Quinlan, R., Sear, R., Schniter, E., Von Rueden, C., Bowles, S., Hertz, T., et al. (2010). Domestication alone does not lead to inequality. *Current Anthropology*, 51(1):49–64.
- Gurven, M. and Kaplan, H. (2007). Longevity among hunter-gatherers: A cross-cultural examination. *Population and Development Review*, 33(2):321–365.
- Harpending, H. and Rogers, A. (1990). Fitness in stratified societies. *Ethology and Sociobiology*, 11(6):497–509.
- Headland, T., Headland, J., and Uehara, R. (2011). Agta demographic database: Chronicle of a hunter-gatherer community in transition.
- Headland, T. N. (1984). Agta negritos of the philippines. *Cultural Survival Quarterly*, 8(3):29–33.
- Headland, T. N. (1988). Ecosystemic change in a philippine tropical rainforest and its effect on a negrito foraging society. *Tropical Ecology*, 29(2):121–135.
- Headland, T. N. (2002). *Why southeast Asian Negritos are a disappearing people: A case study of the Agta of eastern Luzon, Philippines*, pages 25–40. SIL International and International Museum of Cultures, Dallas, TX.
- Headland, T. N. (2004). Basketballs for bows & arrows: Deforestation and agta culture. *Cultural Survival Quarterly*, 28(2):41–45.
- Headland, T. N. and Headland, J. D. (1998). Hypergyny: The outmarriages of agta women and the future of philippine negrito post-foraging populations. In *97th Annual Meeting of the American Anthropological Association*, pages 2–6.
- Hewlett, B. S. (1993). *Intimate fathers: The nature and context of Aka Pygmy paternal infant care*. University of Michigan Press.
- Hill, K. R. and Hurtado, A. M. (1996). *Ache life history: The ecology and demography of a foraging people*. Transaction Publishers.
- Hoffman, M. D. and Gelman, A. (2014). The no-u-turn sampler: Adaptively setting path lengths in hamiltonian monte carlo. *Journal of Machine Learning Research*, 15:1351–1381.
- Howell, N. (2011). Review of thomas n. headland, janet d. headland, and ray t. uehara's agta demographic database: Chronicle of a hunter-gatherer community in transition (dallas: Sil international, 2011). *Human Nature*, 22(4):444–446.
- Hrdy, S. B. and Judge, D. S. (1993). Darwin and the puzzle of primogeniture. *Human Nature*, 4(1):1–45.
- Ibrahim, J. G., Chen, M.-H., and Sinha, D. (2005). *Bayesian survival analysis*. Wiley Online Library.
- Jones, J. H. and Bird, R. B. (2014). The marginal valuation of fertility. *Evolution and Human Behavior*, 35(1):65–71.
- Kaplan, H. (1996). A theory of fertility and parental investment in traditional and modern human societies. *American journal of Physical Anthropology*, 101(S23):91–135.
- Kaplan, H. S., Lancaster, J. B., Johnson, S. E., and Bock, J. A. (1995). Does observed fertility maximize fitness among new mexican men? *Human Nature*, 6(4):325–360.
- Kembo, J. and Van Ginneken, J. K. (2009). Determinants of infant and child mortality in zimbabwe: Results of multivariate hazard analysis. *Demographic Research*, 21(13):367–384.
- Kramer, K. and Boone, J. (2002). Why intensive agriculturalists have higher fertility: A household energy budget approach. *Current Anthropology*, 43(3):511–517.
- Kramer, K. L. and Ellison, P. T. (2010). Pooled energy budgets: Resituating human energy-allocation trade-offs. *Evolutionary Anthropology: Issues, News, and Reviews*, 19(4):136–147.
- Lack, D. (1947). The significance of clutch-size. *Ibis*, 89(2):302–352.
- Lawson, D. W., Alvergne, A., and Gibson, M. A. (2012). The life-history trade-off between fertility and child survival. *Proceedings of the Royal Society B: Biological Sciences*, 279(1748):4755–4764.
- Lawson, D. W. and Mace, R. (2011). Parental investment and the optimization of human family size. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1563):333–343.

- 581 Lawson, D. W., Makoli, A., and Goodman, A. (2013). Sibling configuration predicts individual and descendant socioeconomic success in a modern
582 post-industrial society. *PLoS ONE*, 8(9):e73698.
- 583 Leslie, P. and Winterhalder, B. (2002). Demographic consequences of unpredictability in fertility outcomes. *American Journal of Human Biology*,
584 14(2):168–183.
- 585 Levins, R. (1966). The strategy of model building in population biology. *American scientist*, pages 421–431.
- 586 Mace, R. (1996). Biased parental investment and reproductive success in gabbra pastoralists. *Behavioral Ecology and Sociobiology*, 38(2):75–81.
- 587 Mace, R. (2013). Social science: The cost of children. *Nature*, 499(7456):32–33.
- 588 Meij, J., Van Bodegom, D., Ziem, J., Amankwa, J., Polderman, A., Kirkwood, T., De Craen, A., Zwaan, B., and Westendorp, R. (2009). Quality–
589 quantity trade-off of human offspring under adverse environmental conditions. *Journal of Evolutionary Biology*, 22(5):1014–1023.
- 590 Moorad, J. A., Promislow, D. E., Smith, K. R., and Wade, M. J. (2011). Mating system change reduces the strength of sexual selection in an
591 american frontier population of the 19th century. *Evolution and Human Behavior*, 32(2):147–155.
- 592 Penn, D. J. and Smith, K. R. (2007). Differential fitness costs of reproduction between the sexes. *Proceedings of the National Academy of Sciences*,
593 104(2):553–558.
- 594 Pennington, R. and Harpending, H. (1988). Fitness and fertility among kalahari! kung. *American Journal of Physical Anthropology*, 77(3):303–319.
- 595 Pérusse, D. (1993). Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels. *Behav-
596 ioral and Brain Sciences*, 16(02):267–283.
- 597 Quinlan, R. J. (2007). Human parental effort and environmental risk. *Proceedings of the Royal Society B: Biological Sciences*, 274(1606):121–125.
- 598 Richerson, P. J. and Boyd, R. (2008). *Not by genes alone: How culture transformed human evolution*. University of Chicago Press.
- 599 Rogers, A. R. (1995). For love or money: the evolution of reproductive and material motivations. In Dunbar, R. I., editor, *Human Reproductive
600 Decisions*, pages 76–95.
- 601 Rutstein, S. O. (1984). Infant and child mortality: levels trends and demographic differentials.
- 602 Sear, R. (2007). The impact of reproduction on gambian women: does controlling for phenotypic quality reveal costs of reproduction? *American
603 Journal of Physical Anthropology*, 132(4):632–641.
- 604 Sellen, D. W. and Mace, R. (1997). Fertility and mode of subsistence: A phylogenetic analysis. *Current Anthropology*, 38(5):878–889.
- 605 Smith, E. A., Hill, K., Marlowe, F., Nolin, D., Wiessner, P., Gurven, M., Bowles, S., Borgerhoff Mulder, M., Hertz, T., and Bell, A. (2010). Wealth
606 transmission and inequality among hunter-gatherers. *Current Anthropology*, 51(1):19.
- 607 Snopkowski, K. and Kaplan, H. (2014). A synthetic biosocial model of fertility transition: testing the relative contribution of embodied capital
608 theory, changing cultural norms, and women’s labor force participation. *American journal of physical anthropology*, 154(3):322–333.
- 609 Stan Development Team (2013a). Stan: A c++ library for probability and sampling, version 2.0.
- 610 Stan Development Team (2013b). *Stan Modeling Language User’s Guide and Reference Manual, Version 2.0*.
- 611 Strassmann, B. I. and Gillespie, B. (2002). Life–history theory, fertility and reproductive success in humans. *Proceedings of the Royal Society
612 Series B: Biological Sciences*, 269(1491):553–562.
- 613 Trivers, R. L. and Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068):90–92.
- 614 Walker, R., Gurven, M., Hill, K., Migliano, A., Chagnon, N., De Souza, R., Djurovic, G., Hames, R., Hurtado, A., Kaplan, H., et al. (2006). Growth
615 rates and life histories in twenty-two small-scale societies. *American Journal of Human Biology*, 18(3):295.
- 616 Walker, R. S., Gurven, M., Burger, O., and Hamilton, M. J. (2008). The trade-off between number and size of offspring in humans and other
617 primates. *Proceedings of the Royal Society Series B: Biological Sciences*, 275(1636):827–834.
- 618 Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of lack’s principle. *American Naturalist*, pages 687–690.
- 619 Winterhalder, B., Kennett, D. J., Grote, M. N., and Bartruff, J. (2010). Ideal free settlement of california’s northern channel islands. *Journal of
620 Anthropological Archaeology*, 29(4):469–490.
- 621 Winterhalder, B. and Leslie, P. (2002). Risk-sensitive fertility: the variance compensation hypothesis. *Evolution and Human Behavior*, 23(1):59–82.
- 622 Winterhalder, B. and Smith, E. A. (2000). Analyzing adaptive strategies: Human behavioral ecology at twenty-five. *Evolutionary Anthropology
623 Issues News and Reviews*, 9(2):51–72.
- 624 Zietsch, B. P., Kuja-Halkola, R., Walum, H., and Verweij, K. J. (2014). Perfect genetic correlation between number of offspring and grandoffspring
625 in an industrialized human population. *Proceedings of the National Academy of Sciences*, 111(3):1032–1036.

List of Figures

- 1 **Location of the Agta:** Frame (a) plots the location of the Casiguran municipality and the San Ildefonso Peninsula. Frame (b) plots the main contrasts in our analytic structure and data. We compare the life histories and demography of Agta in geographically separated subpopulations (vertical axis), clustered by temporal phase (horizontal axis). Subsistence strategies and socio-ecological context vary across these geographic and temporal clusters. 18
- 2 **Mortality in the Agta:** Frame (a) cumulative probability of death in age interval (0,1). Frame (b) cumulative probability of death in age interval (0,5). Frame (c) cumulative probability of death in age interval (0,15). Frame (d) median age of death. Frames (a)–(d) depict the mortality estimates provided in Table 1. SIA and CA indicate the geographic subpopulation; T1 and T2 indicate temporal phase; F and M indicate female and male; and FB and LB indicate first-born and later-born, respectively. . . . 19
- 3 **Age-Specific Fertility in the Agta:** Results of Poisson regression modeling of reported pregnancies on years at risk for pregnancy, by location and phase, using the parameters from Table 2. Frame (a) phase 1 fertility in the SIA (left plot) and CA (right plot). Frame (b) phase 2 fertility in the SIA (left plot) and CA (right plot). The black points are (jittered) observed data; the dark red line is the maximum *a posteriori* estimate of the regression line. The light blue shaded area is the central ninety-five percent posterior prediction interval; the shaded red area is the central ninety-five percent posterior confidence interval of the model of the mean. 20
- 4 **The Quantity-Quality Trade-Off in the Agta:** Results of Gamma-Poisson regression modeling of recruited offspring on number of reported pregnancies by location and phase, using the parameter estimates contained in Table 3. Frame (a) phase 1 quantity-quality trade-offs in SIA (left plot) and CA (right plot). Frame (b) phase 2 quantity-quality trade-offs in SIA (left plot) and CA (right plot). The diagonal black lines represent direct one-to-one proportionality of recruited offspring and reported pregnancies (no offspring mortality before recruitment); the black points are (jittered) observed data. The vertical grey bars are (jittered) censored data. The dark red line is the maximum *a posteriori* estimate of the regression line, the light blue shaded area is the central ninety-five percent posterior prediction interval, and the shaded red area is the central ninety-five percent posterior confidence interval of the model of the mean. 21
- 5 **Variance Compensation and Demographic Transition in the Agta:** Frame (a) kernel density estimates of stochastic outcome variance in the SIA (green) and CA (orange), phase 1 (left plot), phase 2 (right plot). The area of the central ninety-five percent of each distribution is delineated by vertical confidence bars. There is reduced stochastic outcome variance in the CA compared to the SIA, regardless of phase. Frame (b) the left plot presents the estimated value functions (and ninety-five percent PCIs) linking pregnancies to recruited offspring in the SIA (green) and CA (orange) in phase 1; the right plot presents the corresponding results in phase 2. The diagonal black line represents direct proportionality between pregnancies and recruited offspring. The horizontal black line represents a possible target number of recruited offspring ($= 4$). To calculate the number of pregnancies needed to reach this target on average, we move down vertically from the intersection of the value function and the target outcome. The solid vertical bars represent the estimated number of pregnancies needed to reach target fertility (see discussion in text), and the dashed vertical bars are PCI95s. 22

Figure 1. **Location of the Agta:** Frame (a) plots the location of the Casiguran municipality and the San Ildefonso Peninsula. Frame (b) plots the main contrasts in our analytic structure and data. We compare the life histories and demography of Agta in geographically separated subpopulations (vertical axis), clustered by temporal phase (horizontal axis). Subsistence strategies and socio-ecological context vary across these geographic and temporal clusters.

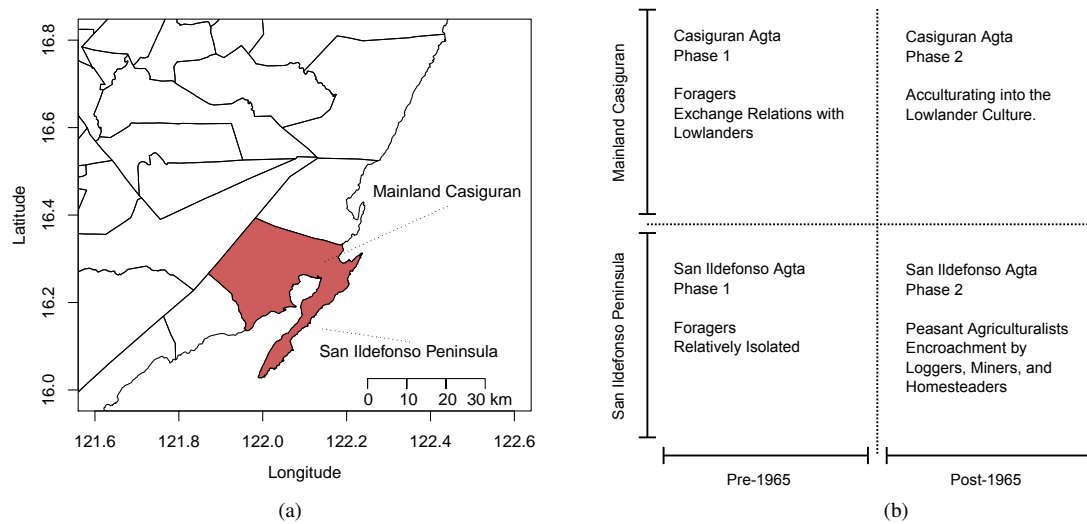


Figure 2. **Mortality in the Agta:** Frame (a) cumulative probability of death in age interval (0,1). Frame (b) cumulative probability of death in age interval (0,5). Frame (c) cumulative probability of death in age interval (0,15). Frame (d) median age of death. Frames (a)–(d) depict the mortality estimates provided in Table 1. SIA and CA indicate the geographic subpopulation; T1 and T2 indicate temporal phase; F and M indicate female and male; and FB and LB indicate first-born and later-born, respectively.

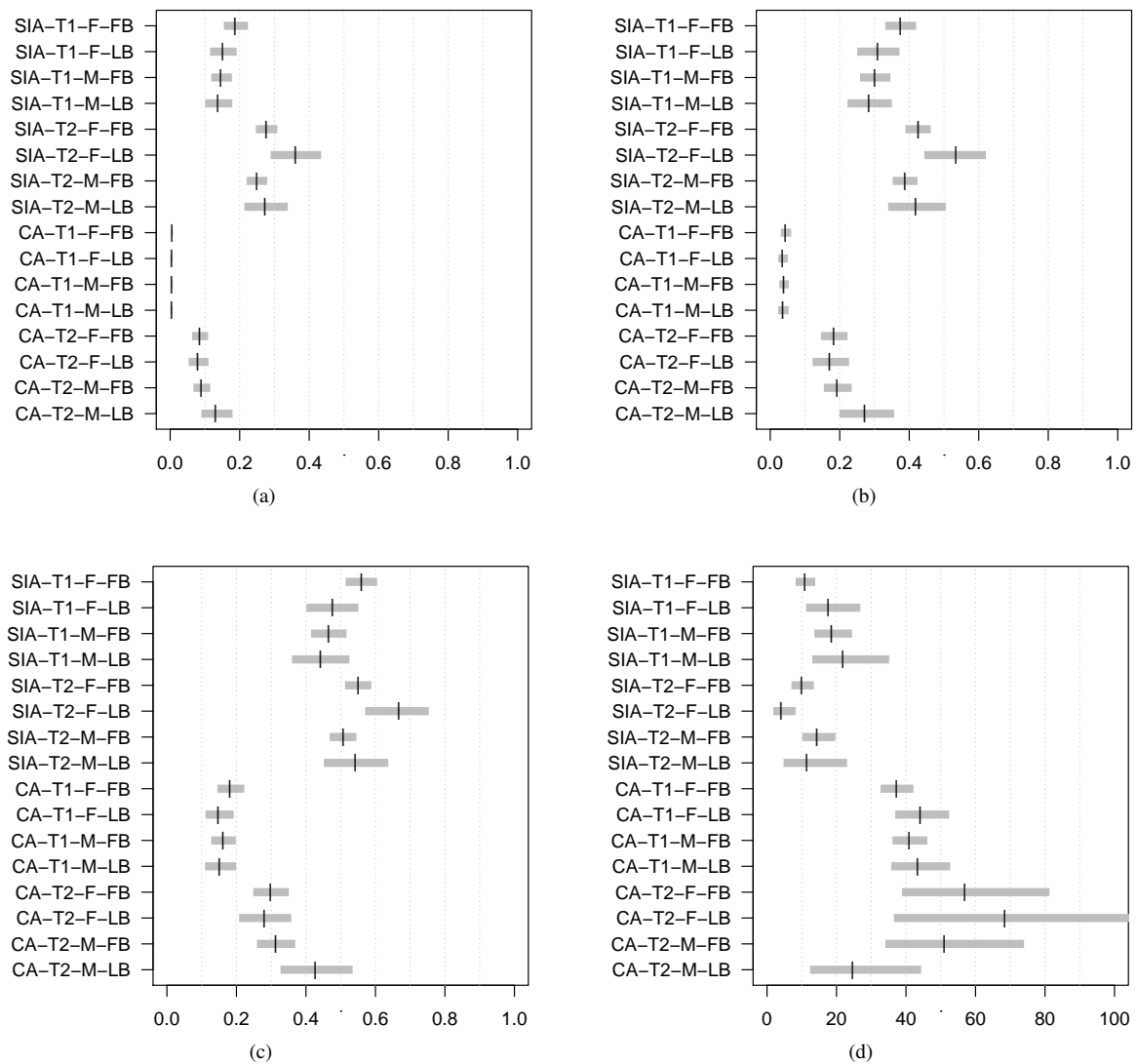


Figure 3. **Age-Specific Fertility in the Agta:** Results of Poisson regression modeling of reported pregnancies on years at risk for pregnancy, by location and phase, using the parameters from Table 2. Frame (a) phase 1 fertility in the SIA (left plot) and CA (right plot). Frame (b) phase 2 fertility in the SIA (left plot) and CA (right plot). The black points are (jittered) observed data; the dark red line is the maximum *a posteriori* estimate of the regression line. The light blue shaded area is the central ninety-five percent posterior prediction interval; the shaded red area is the central ninety-five percent posterior confidence interval of the model of the mean.

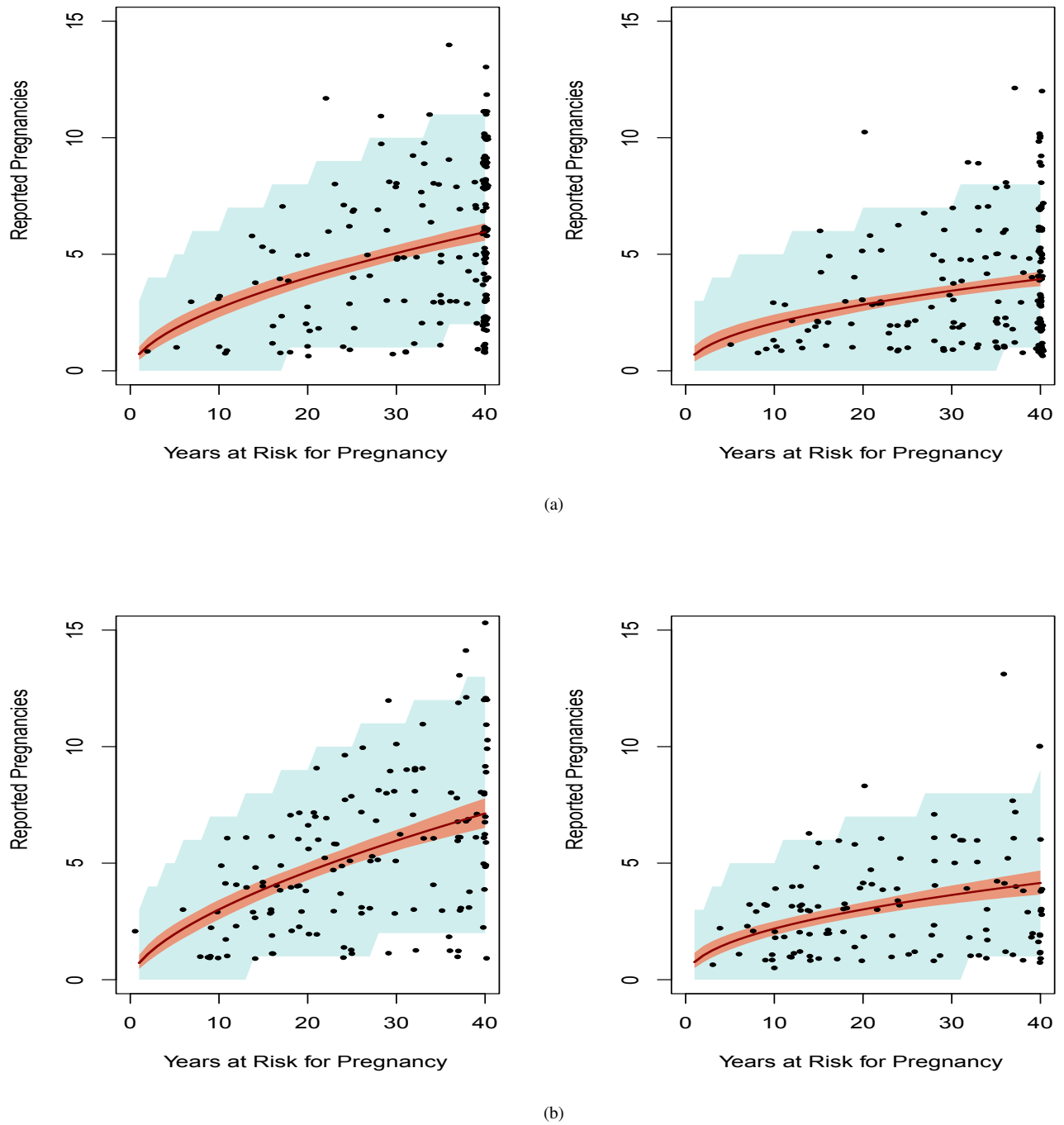
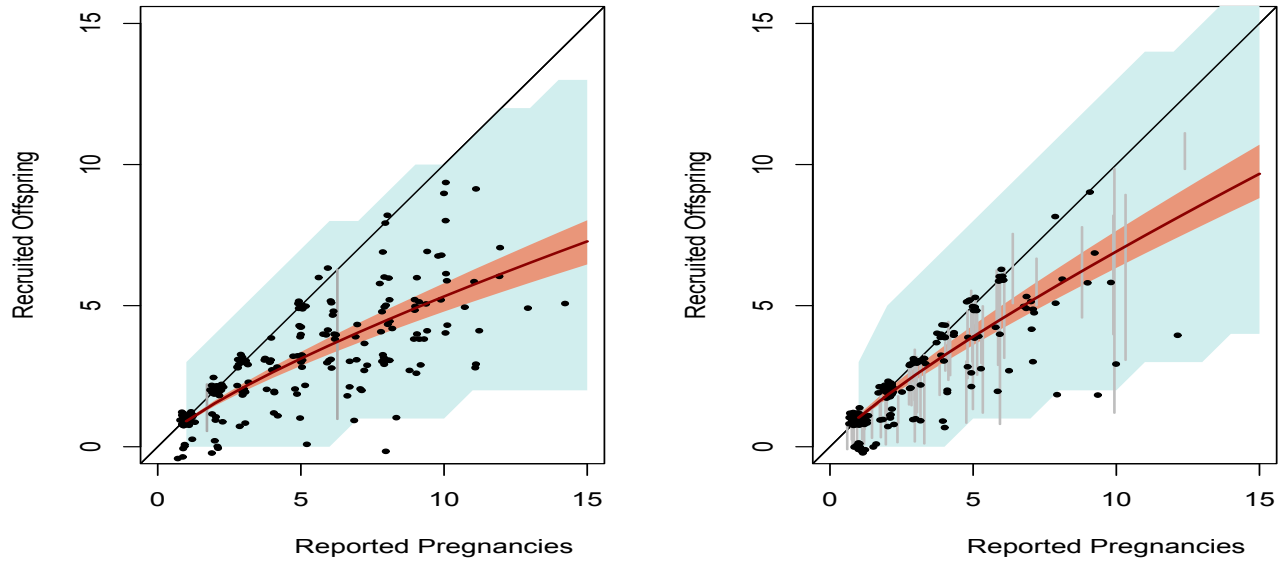
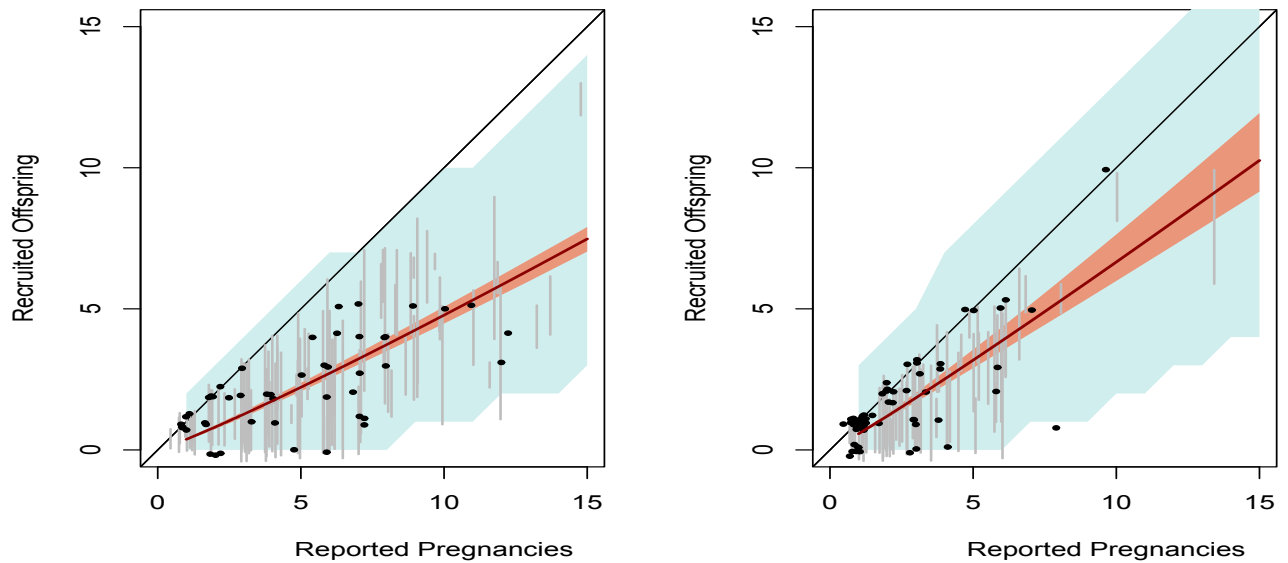


Figure 4. **The Quantity-Quality Trade-Off in the Agta:** Results of Gamma-Poisson regression modeling of recruited offspring on number of reported pregnancies by location and phase, using the parameter estimates contained in Table 3. Frame (a) phase 1 quantity-quality trade-offs in SIA (left plot) and CA (right plot). Frame (b) phase 2 quantity-quality trade-offs in SIA (left plot) and CA (right plot). The diagonal black lines represent direct one-to-one proportionality of recruited offspring and reported pregnancies (no offspring mortality before recruitment); the black points are (jittered) observed data. The vertical grey bars are (jittered) censored data. The dark red line is the maximum *a posteriori* estimate of the regression line, the light blue shaded area is the central ninety-five percent posterior prediction interval, and the shaded red area is the central ninety-five percent posterior confidence interval of the model of the mean.

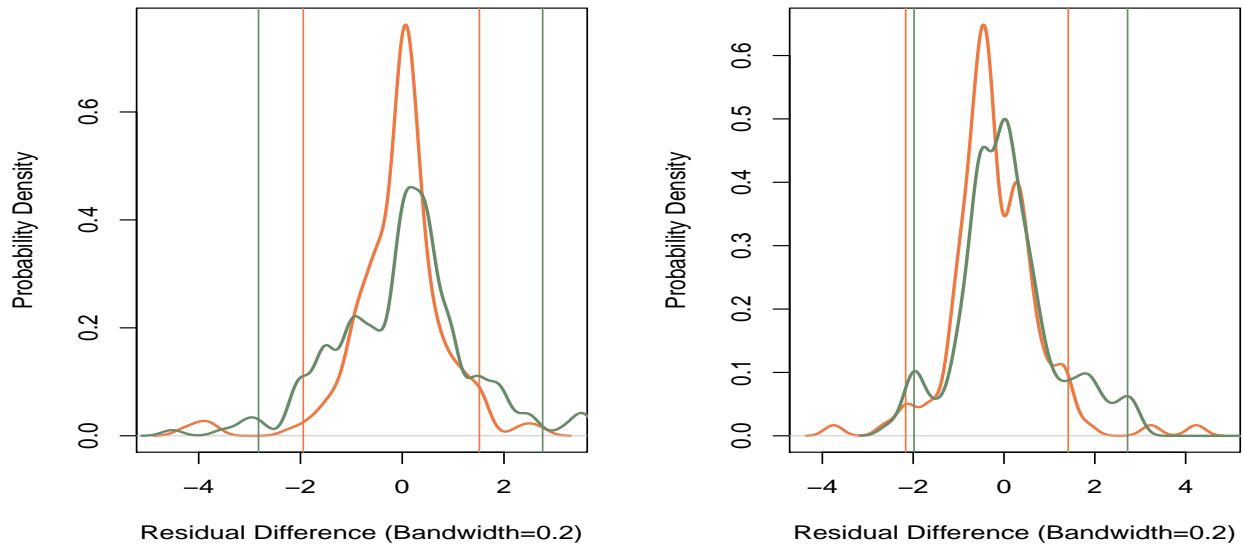


(a)

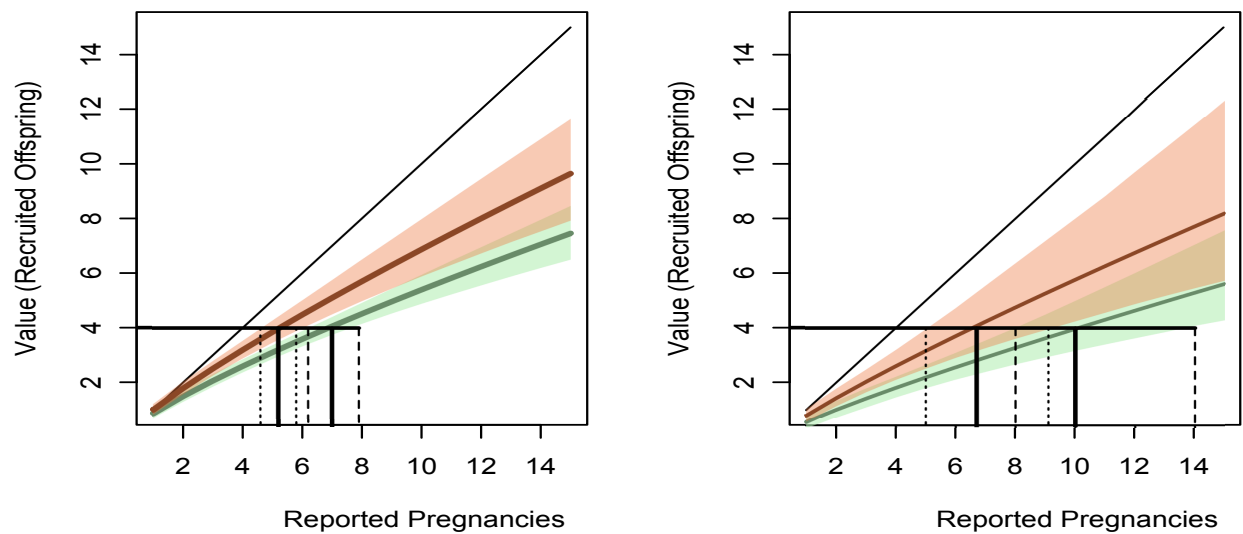


(b)

Figure 5. **Variance Compensation and Demographic Transition in the Agta:** Frame (a) kernel density estimates of stochastic outcome variance in the SIA (green) and CA (orange), phase 1 (left plot), phase 2 (right plot). The area of the central ninety-five percent of each distribution is delineated by vertical confidence bars. There is reduced stochastic outcome variance in the CA compared to the SIA, regardless of phase. Frame (b) the left plot presents the estimated value functions (and ninety-five percent PCIs) linking pregnancies to recruited offspring in the SIA (green) and CA (orange) in phase 1; the right plot presents the corresponding results in phase 2. The diagonal black line represents direct proportionality between pregnancies and recruited offspring. The horizontal black line represents a possible target number of recruited offspring ($= 4$). To calculate the number of pregnancies needed to reach this target on average, we move down vertically from the intersection of the value function and the target outcome. The solid vertical bars represent the estimated number of pregnancies needed to reach target fertility (see discussion in text), and the dashed vertical bars are PCI95s.



(a)



(b)

List of Tables

1	Mortality in the Agta: Estimates of median age of death, M , and the cumulative probability of death, CPD , in the time periods from birth to 1, 5, and 15 years, as plotted in Figure 2. Each row presents estimates for the specified subpopulation/location: Loc , (SIA or CA); phase, P , (1 or 2); Sex , (male or female); and, birth-order, BO , (first-born or later-born). The symbol SE refers to the standard error of the estimates in the preceding column. It should be noted that the estimated median age of death for females in the CA in phase 2 is likely to be an over-estimate, and is highly uncertain (note the inflated standard error). This model behavior arises because an abnormally high fraction (relative to the rest of the data) of females in the CA phase 2 survived to the time of censoring, and the model is highly uncertain about the predicted time of death for these individuals. See Supplementary Materials section 1.1 for plots of the empirical survival functions and the model's posterior predictions of these functions.	24
2	Age-Specific Fertility Regression Estimates: Key parameter estimates from the age-specific fertility model plotted in Figure 3. The value of the parameter labeled <i>Exposure</i> across locations and phases is indicative of fertility as a function of years at risk for pregnancy. We note elevated fertility in the SIA relative to the CA in both phases. Further, we note a slight increase in SIA fertility from phase 1 to phase 2, while fertility has remained roughly constant in the CA across phases.	25
3	Quantity-Quality Trade-Off Regression Estimates: Key parameter estimates of the quantity-quality trade-off model plotted in Figure 4. The value of the parameter labeled <i>Exposure</i> across locations and phases is indicative of offspring recruitment as a function of offspring conceived and at risk of recruitment. We note evidence of the quantity-quality trade-off in the SIA and CA, during phase 1, as the <i>Exposure</i> parameter in these models falls significantly short of proportionality. We fail to find robust evidence of the quantity-quality trade-off in the SIA or CA during phase 2.	26

Table 1. **Mortality in the Agta:** Estimates of median age of death, M , and the cumulative probability of death, CPD , in the time periods from birth to 1, 5, and 15 years, as plotted in Figure 2. Each row presents estimates for the specified subpopulation/location: Loc , (SIA or CA); phase, P , (1 or 2); Sex , (male or female); and, birth-order, BO , (first-born or later-born). The symbol SE refers to the standard error of the estimates in the preceding column. It should be noted that the estimated median age of death for females in the CA in phase 2 is likely to be an over-estimate, and is highly uncertain (note the inflated standard error). This model behavior arises because an abnormally high fraction (relative to the rest of the data) of females in the CA phase 2 survived to the time of censoring, and the model is highly uncertain about the predicted time of death for these individuals. See Supplementary Materials section 1.1 for plots of the empirical survival functions and the model's posterior predictions of these functions.

Loc	P	Sex	BO	M	SE	CPD1	SE	CPD5	SE	CPD15	SE
SIA	1	Female	Later	10.84	1.41	0.19	0.02	0.37	0.02	0.56	0.02
SIA	1	Female	First	17.64	4.01	0.15	0.02	0.31	0.03	0.48	0.04
SIA	1	Male	Later	18.58	2.82	0.15	0.02	0.3	0.02	0.46	0.03
SIA	1	Male	First	21.84	5.76	0.14	0.02	0.28	0.03	0.44	0.04
SIA	2	Female	Later	9.91	1.65	0.28	0.02	0.43	0.02	0.55	0.02
SIA	2	Female	First	4.05	1.65	0.36	0.04	0.53	0.04	0.67	0.05
SIA	2	Male	Later	14.3	2.46	0.25	0.02	0.39	0.02	0.51	0.02
SIA	2	Male	First	11.42	4.8	0.27	0.03	0.42	0.04	0.54	0.05
CA	1	Female	Later	37.27	2.4	<0.01	<0.01	0.04	0.01	0.18	0.02
CA	1	Female	First	44.05	3.94	<0.01	<0.01	0.03	0.01	0.15	0.02
CA	1	Male	Later	40.87	2.57	<0.01	<0.01	0.04	0.01	0.16	0.02
CA	1	Male	First	43.33	4.4	<0.01	<0.01	0.04	0.01	0.15	0.02
CA	2	Female	Later	56.91	10.8	0.08	0.01	0.18	0.02	0.3	0.03
CA	2	Female	First	68.39	21.25	0.08	0.01	0.17	0.03	0.28	0.04
CA	2	Male	Later	50.98	10.27	0.09	0.01	0.19	0.02	0.31	0.03
CA	2	Male	First	24.6	8.37	0.13	0.02	0.27	0.04	0.43	0.05

Table 2. **Age-Specific Fertility Regression Estimates:** Key parameter estimates from the age-specific fertility model plotted in Figure 3. The value of the parameter labeled *Exposure* across locations and phases is indicative of fertility as a function of years at risk for pregnancy. We note elevated fertility in the SIA relative to the CA in both phases. Further, we note a slight increase in SIA fertility from phase 1 to phase 2, while fertility has remained roughly constant in the CA across phases.

Loc	Phase	Parameter	Mean	SE	2.5 PCI	97.5 PCI
SIA	1	Intercept	-0.36	0.24	-0.84	0.10
SIA	1	Exposure	0.58	0.07	0.45	0.72
CA	1	Intercept	-0.39	0.25	-0.93	0.09
CA	1	Exposure	0.48	0.07	0.34	0.63
SIA	2	Intercept	-0.36	0.22	-0.82	0.06
SIA	2	Exposure	0.63	0.07	0.5	0.77
CA	2	Intercept	-0.28	0.24	-0.74	0.22
CA	2	Exposure	0.46	0.08	0.3	0.61

Table 3. **Quantity-Quality Trade-Off Regression Estimates:** Key parameter estimates of the quantity-quality trade-off model plotted in Figure 4. The value of the parameter labeled *Exposure* across locations and phases is indicative of offspring recruitment as a function of offspring conceived and at risk of recruitment. We note evidence of the quantity-quality trade-off in the SIA and CA, during phase 1, as the *Exposure* parameter in these models falls significantly short of proportionality. We fail to find robust evidence of the quantity-quality trade-off in the SIA or CA during phase 2.

Loc	Phase	Parameter	Mean	SE	2.5 PCI	97.5 PCI
SIA	1	Intercept	-0.15	0.11	-0.36	0.08
SIA	1	Exposure	0.80	0.06	0.68	0.91
CA	1	Intercept	0.0	0.10	-0.19	0.20
CA	1	Exposure	0.84	0.06	0.72	0.96
SIA	2	Intercept	-0.59	0.22	-1.09	-0.2
SIA	2	Exposure	0.85	0.11	0.65	1.12
CA	2	Intercept	-0.24	0.16	-0.58	0.04
CA	2	Exposure	0.87	0.1	0.69	1.1