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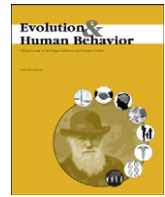
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Original Article

Evidence for quantity–quality trade-offs, sex-specific parental investment, and variance compensation in colonized Agta foragers undergoing demographic transition



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ABSTRACT

Evolutionary ecological models of human fertility predict that: (1) parents will bias investment toward the sex with the highest fitness prospects in a particular socio-ecological context; (2) fertility is subject to quantity–quality trade-offs; and (3) fertility decisions will be sensitive to both predictable and stochastic mortality risk and the relative fitness value of differently sized sib-sets (the variance compensation hypothesis). We test these predictions using demographic records from the Agta, an indigenous population from the Philippines, who, as a result of disruption by loggers, miners, and settlers, are undergoing a demographic and social/ecological transition from foragers to peasant laborers. Leveraging the spatial and temporal variation in the Agta Demographic Database, we conduct an analysis of Agta life-history traits across this transition. Specifically, we compare the Casiguran Agta (CA) with the more isolated peninsular San Ildefonso Agta (SIA) sub-population from before (phase 1) and after (phase 2) encroachment. We find: (1) evidence of a decline in overall survival from phase 1 to phase 2, coupled with increased parental investment in first-born daughters compared to first-born sons in the CA population, and increased parental investment in sons versus daughters in the SIA population; (2) evidence of a moderate quantity–quality trade-off in CA and SIA fertility in phase 1; and (3) support for predictions of the variance compensation hypothesis as a driver of the lowered relative fertility in the CA. Our customized methods, comparative framework, and simultaneous focus on fertility and mortality allow us to show how heterogeneity in mortality and fertility are linked to life history trade-offs and environmental context in a manner consistent with the predictions of evolutionary ecological models.

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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 & 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, Lawson, Makoli, & Goodman, 2013; Moorad, Promislow, Smith, & Wade, 2011; Zietsch, Kuja-Halkola, Walum, & Verweij, 2014; Lawson & Borgerhoff Mulder, 2016). Following their lead, we make use of the Agta Demographic Database (ADD, see Howell,

2011) produced by Headland, Headland, and Uehara (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 period that the 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 & Hurtado, 1996).

We begin by introducing the Agta data set and the ethnographic context. We then discuss key concepts in human life-history theory

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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. By considering both mortality and fertility changes in a unified framework, we are able to provide quantitative evidence in support of the adaptive transition to reduced fertility predicted by the variance compensation hypothesis (Leslie & Winterhalder, 2002; Winterhalder & Leslie, 2002).

1.1. The Agta Demographic Database

Headland et al. (2011) published records containing the complete demographic history of the San Ildefonso Agta over more than a half-century, drawing on Thomas and Janet Headland’s prolonged residency and ethnographic observations among them, from 1962 to 2010. The remarkable time depth and completeness of these demographic records make 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 (Gurven & Kaplan, 2007; Walker, Gurven, Burger, & Hamilton, 2008; Walker et al., 2006). Likewise, 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 spatial and temporal clustering. Each of these features is common in ethnographic data; each renders problematic analysis using the traditional statistical techniques of anthropological demography. The multi-level Bayesian approach adopted here allows us to circumvent these problems, by allowing us to account for uncertainty introduced by missing and censored data, while still characterizing the relationship between socio-ecological variation and human reproductive decision-making.

1.2. 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 lives on the

San Ildefonso Peninsula (Headland et al., 2011); see Fig. 1(a) for the locations of the CA and SIA.

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 led 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 increase 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 shifted from living as 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 term: *phase 1* to refer to the CA and SIA populations pre-1965, during their forager phase. Likewise, we use the term: *phase 2* to refer to the CA and SIA populations post-1965, during their peasantry phase. 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 (by authors JH and TH) and exploratory data analysis, we are confident that the dichotomous approach also captures the major modal adjustment in Agta livelihood and demography.

Agta livelihood changes from phase 1 to phase 2 are cross-cut by geographical differences and the interaction of phase and location; see Fig. 1(b). The mainland CA have traditionally lived in closer contact

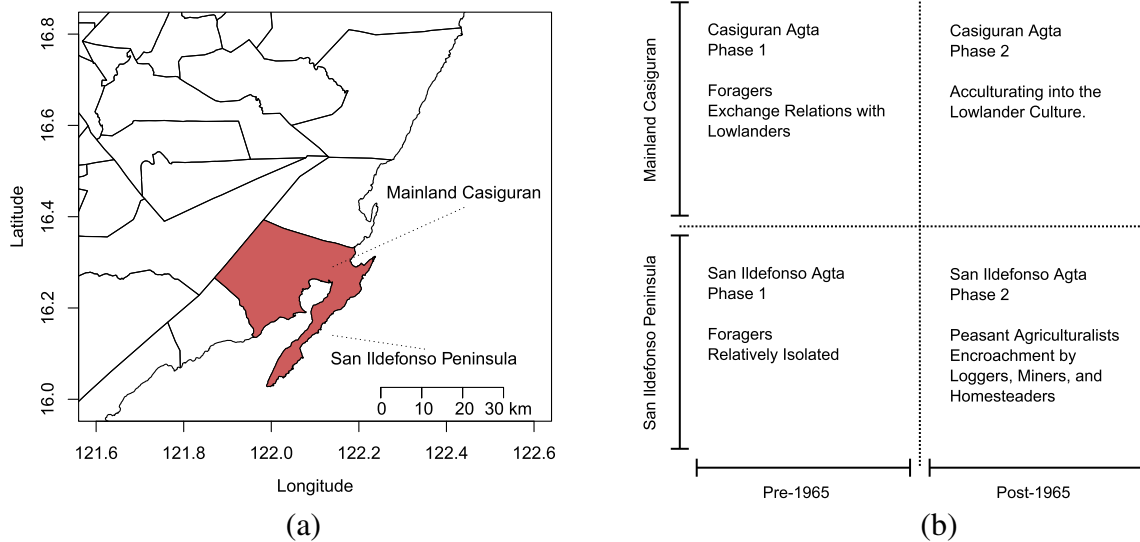


Fig. 1. Location of the Agta and the structuring of Agta data: Frame 1(a) location of the Casiguran municipality and the San Ildefonso Peninsula. Frame 1(b) the main contrasts in our analytic structure and data. We compare the life histories and demography of Agta in geographically separated subpopulations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

with the lowlanders than have the peninsular SIA, and have benefited from greater access to health care and other resources. 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 & DeVore, 1989](#)) or the Aka and Ngandu ([Hewlett, 1993](#)).

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 them as second-class residents. The phase 2 SIA did not have the same options for acculturation and integration by marriage as the phase 2 CA. 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 selective pressures on Agta demography. We explore how the behavioral strategies that maximize fitness might vary along these selection gradients.

1.3. Life-history trade-offs in the Agta

We focus 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 then review: (3) how fertility rates might be affected by varying levels of stochastic mortality, and the possibility of asymmetry in the value function ([Winterhalder & 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.

1.3.1. 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 ([Borgerhoff Mulder, 1998](#); [Gillespie, Russell, & Lummaa, 2008](#); [Mace, 1996](#)), and ultimately, the parents' long term fitness ([Boone & Kessler, 1999](#); [Harpending & Rogers, 1990](#); [Rogers, 1995](#)). 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 viewed as impartible. Initially, 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, however, 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 & 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 & 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 & 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 interethnic marriage between the CA and lowlanders, it is an Agta woman who marries a lowlander male ([Early & 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 ([Boone & Kessler, 1999](#); [Rogers, 1995](#); [Trivers & Willard, 1973](#)), as has been observed in other foraging populations, such as the Efe ([Bailey & DeVore, 1989](#)) and Aka ([Hewlett, 1993](#)) during transition to a new mode of subsistence. Interethnic marriage between a CA male and a landowning lowlander female has remained socially 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 predict increased investment in early-born females relative to males in the acculturating CA population, where hypergyny could be 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. Our analysis relies on the assumption that investment decisions can at least partially be inferred on the basis of offspring survival; ideally, our analyses would be supplemented by other measurable indicators of investment, but such measures are not available in our data set.

1.3.2. Fertility and the quantity–quality trade-off

Variation in life-history traits among populations is believed to result from overall budget constraints and from differential allocations of limited energy among: (1) growth and reproduction (e.g., [Hill & Hurtado, 1996](#)), (2) reproduction and survival (e.g., [Penn & Smith, 2007](#)), and (3) 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 are often hypothesized to offer a greater availability of food and permit larger contributions of children to food production ([Bentley, Goldberg, & Jasieńska, 1993](#); [Kramer & Boone, 2002](#); [Sellen & Mace, 1997](#)). Despite a large overlap in values, farming populations typically have higher fertility than foraging populations ([Campbell & Wood, 1988](#); [Gurven et al., 2010](#)).

Fertility can also be affected by trade-offs between the number and quality of offspring produced ([Kaplan, 1996](#); [Kramer & Ellison, 2010](#); [Lack, 1947](#)). 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 ultimately 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 & Gillespie, 2002](#)) and Ghana ([Meij et al., 2009](#)). In other contexts, for instance in Kenyan agropastoralists ([Borgerhoff Mulder, 1998](#)) and Paraguayan foragers ([Hill & 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 & Bird, 2014) and tend to vary by social strata (Borgerhoff Mulder, 2000; Gillespie et al., 2008).

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 & 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 & 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 mortality is low and, among national subsamples where maternal somatic (height) and extrasomatic (education) capital is high (Lawson, Alvergne, & Gibson, 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 in the SIA because of their limited resources as foragers, whereas following Lawson et al. (2012) we would predict less sharp trade-offs in the SIA, insofar as mortality is more likely to be extrinsic. To make these comparisons, we estimate fertility rates and the extent of the quantity–quality trade-off in offspring using multi-level Gamma–Poisson regression models, which integrate over uncertainty due to censored observations and produce unique estimates of fertility rate and quantity–quality trade-offs in each Agta subpopulation in each temporal phase.

1.3.3. The variance compensation hypothesis

Risk sensitive fertility models incorporate the uncertainty of stochastically losing offspring into the estimate of optimal fertility. By linking geometric mean fitness effects to reproductive decisions, one finds 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. This is because risk-sensitive optimization requires compensation for both the mean effects of stochastic mortality, as well as compensation for the variance in stochastic mortality as affected by 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: (1) the outcome distribution of recruited offspring as a function of fertility; and (2) 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 from fertility). 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 on number of recruited offspring. 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 conceived 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 linking maternal births to mean recruited offspring, would be consistent with the predictions of the VCH model. Finally, we explicitly integrate the results of the survival analysis and quantity–quality trade-off models in order to numerically estimate the extent of variance compensation in each subpopulation in each phase.

1.4. 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 budgetary constraints. Assuming higher budgets in the CA relative to the SIA in phase 1, we would predict increased fertility in the CA. Assuming decreased budgets in phase 2 for both CA and SIA (relative to their respective phase 1 values), we would predict decreased phase 2 fertility in both populations relative to their phase 1 values.
 - 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.

- c. Assuming the quantity–quality trade-off is driving demographic transition, we predict decreased fertility in the subpopulations and phases with increased quantity–quality trade-offs.
- (3) VCH predictions
- a. We predict that reduced stochastic variance in reproductive outcomes will be associated with lower fertility.
 - b. We predict a decrease in fertility in response to an elevation of the lower portion of the fitness value function linking maternal pregnancies to mean recruited offspring.
 - c. We predict numerically elevated levels of variance compensation in the SIA relative to the CA in both phases.

2. Methods

2.1. Data source: the 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 the ages of death or censoring for all individuals in the data-set with a known year of birth by an Agta woman. Fertility and quantity–quality trade-off outcomes were modeled using the data from all 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 phases 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. While it is often more common to analyze only live births, given the thoroughness of the data and our interest in the dynamics leading parents to conceive new offspring, we decided to classify all reported pregnancies as fertility decisions. This methodological choice also allows for the mortality patterns apparent as stochastic outcome variance in our quantity–quality trade-off model to be interpreted in conjunction with the results of our survival analysis model, since they are based on the same set of survival outcomes. Additionally, we were worried that cases of infanticide could have been described as still births, and information on sex-specific parental investment would be lost by excluding such cases. The sample sizes of observed, censored, and missing data in each class of interactions used in our analyses are included in the Supplementary Materials, Section 1.9.

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 ADD data used in this analysis are highly detailed and very complete across approximately 4–7 generations. However: 1) 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, 2) the sex of many offspring who died early in life is unknown, 3) there is variation in the accuracy of age data, and 4) there is multi-level structuring in the data. To address these data issues, we designed custom statistical models which can accommodate these shortcomings. Specifically, we define models which: 1) deal with censored outcomes, 2) integrate over uncertainty in the effects of sex for offspring which have missing sex data, 3) model measurement error

in age, and 4) use a hierarchical structure to infer location- and phase-specific effects (Mace, 2013).

To estimate unknown parameters in our models, we use Hamiltonian Markov Chain Monte Carlo simulation (Hoffman & Gelman, 2014). Our Markov chains are coded in C++ using the Stan 2.2.0 library (Stan Development Team, 2013a), and implemented through the RStan interface. 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 & Smith, 1993; Ibrahim, Chen, & Sinha, 2005; Peltola, Havulinna, Salomaa, & Vehtari, 2014). 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:

$$AOD_{[i]} \sim \text{Weibull} \left(\phi_{[l_{[i]}, p_{[i]}]}, \exp \left(- \frac{\psi_{[l_{[i]}, p_{[i]}, s_{[i]}, b_{[i]}]}}{\phi_{[l_{[i]}, p_{[i]}]}} \right) \right) \quad (1)$$

and, following the parameterization suggested in example Stan models provided by Peltola et al. (2014), we model individuals with an observed age of censoring, $AOC_{[i]}$, as:

$$AOC_{[i]} \sim \text{Weibull}_{\text{CCDF}} \left(\phi_{[l_{[i]}, p_{[i]}]}, \exp \left(- \frac{\psi_{[l_{[i]}, p_{[i]}, s_{[i]}, b_{[i]}]}}{\phi_{[l_{[i]}, p_{[i]}]}} \right) \right) \quad (2)$$

where the symbol $\text{Weibull}_{\text{CCDF}}$ is the complimentary cumulative distribution – or survival – function. The symbols $l_{[i]}$, $p_{[i]}$, $s_{[i]}$, and $b_{[i]} \in \{1, 2\}$ 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:

$$\psi_{[l, p, s, b]} \sim \text{Normal}(\mu_{\psi}, \sigma_{\psi}) \quad (3)$$

Some individuals in the Agta data set are not classified as male or female, normally due to death during the infancy period. 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 $\xi_{[l, p]}$ 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:

$$\xi_1_{[l_{[i]}, p_{[i]}]} \psi_{[l_{[i]}, p_{[i]}, s=1, b_{[i]}]} + \xi_2_{[l_{[i]}, p_{[i]}]} \psi_{[l_{[i]}, p_{[i]}, s=2, b_{[i]}]} \quad (4)$$

The shape parameter of the Weibull distribution, ϕ , determines how the hazard changes over the life course. A value of one indicates a constant hazard and a value less than one indicates a decreasing hazard over time. A ϕ 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 ϕ coefficients for each combination of temporal phase and location using partial pooling:

$$\log(\phi_{[l, p]}) \sim \text{Normal}(\mu_{\phi}, \sigma_{\phi}) \quad (5)$$

All hyperparameters are given weakly regularizing priors, which concentrate prior probability in the realm of empirically plausible parameter values (see Chapter 6.3, McElreath, 2015):

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

$$\mu_\phi \sim \text{Normal}(0, 10) \tag{7}$$

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

$$\sigma_\phi \sim \text{Cauchy}(0, 2.5)T[0, \infty] \tag{9}$$

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:

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

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:

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

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

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

where $\mu_{AOC_{[i]}}$ is the estimated 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 $(0, Z)$:

$$Pr(D_Z|l, p, s, b) = \int_0^Z \text{Weibull}_{\text{CDF}}\left(\phi_{[l,p]}, \exp\left[-\frac{\psi_{[l,p,s,b]}}{\phi_{[l,p]}}\right]\right) \tag{13}$$

Conditional probabilities of death (e.g., the probability of dying before age 15 conditional on having survived to age 1) can then be understood as a difference of integrals over the CDF.

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 multi-level Bayesian Gamma–Poisson (a.k.a. Negative Binomial, Spencer, 1980; Wood, 1994) regression models to estimate age-specific fertility and 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 quantity–quality trade-offs across locations and temporal phases 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:

$$Y_{[i]} \sim \text{Poisson}(\lambda_{[i]}) \tag{14}$$

and:

$$\lambda_{[i]} \sim \text{Gamma}(A_{[i]}, B_{[i],P_{[i]}}) \tag{15}$$

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 :

$$\log\left(\frac{A_{[i]}}{B_{[i],P_{[i]}}}\right) = \theta_1_{[i],P_{[i]}} + \theta_2_{[i],P_{[i]}} \log(P_{[i]}) \tag{16}$$

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:

$$\log(B_{[l,p]}) \sim \text{Normal}(\mu_B, \sigma_B) \tag{17}$$

with regularizing priors on the hyperparameters:

$$\mu_B \sim \text{Normal}(0, 1) \tag{18}$$

$$\sigma_B \sim \text{Normal}(0, 1)T[0, \infty] \tag{19}$$

The $\theta_{[l,p]}$ 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:

$$\theta_{[l,p]} \sim \text{Multivariate Normal}(\mu_\theta, \Sigma_\theta) \tag{20}$$

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

$$\mu_\theta \sim \text{Normal}(0, 10) \tag{21}$$

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 Section 1.8; 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 1.7 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 Gamma–Poisson regression model:

$$P_{[i]} \sim \text{Poisson}(\Lambda_{[i]}) \tag{22}$$

where:

$$\Lambda_{[i]} \sim \text{Gamma}(Q_{[i]}, V_{[l_{[i]}, p_{[i]}]}) \tag{23}$$

$$\log\left(\frac{Q_{[i]}}{V_{[l_{[i]}, p_{[i]}]}}\right) = \zeta_{1[l_{[i]}, p_{[i]}]} + \zeta_{2[l_{[i]}, p_{[i]}]} \log(E_{[i]}) \tag{24}$$

and:

$$\zeta_{[l,p]} \sim \text{Multivariate Normal}(\mu_{\zeta}, \Omega) \tag{25}$$

$$\log(V_{[l,p]}) \sim \text{Normal}(\mu_V, \sigma_V) \tag{26}$$

with priors:

$$\mu_{\zeta} \sim \text{Normal}(0, 10) \tag{27}$$

$$\mu_V \sim \text{Normal}(0, 1) \tag{28}$$

$$\sigma_V \sim \text{Normal}(0, 1)T[0, \infty] \tag{29}$$

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, 0–15 years, and 0–45 years, as well as on the interval 1–15 years. Fig. 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.

Table 1
Mortality in the Agta: estimates of the cumulative probability of death, CDP, in the time periods from birth to 1, 15, and 45 years, and the CPD to age 15 conditional on surviving to age 1 (CPD15|S1), as plotted in Fig. 2.

Loc	P	Sex	BO	CPD1	CPD15	CPD45	CPD15 S1
SIA	1	F	FB	0.11 (0.08, 0.15)	0.37 (0.29, 0.45)	0.56 (0.46, 0.66)	0.26 (0.21, 0.31)
SIA	1	F	LB	0.12 (0.1, 0.15)	0.41 (0.36, 0.46)	0.61 (0.55, 0.66)	0.29 (0.26, 0.32)
SIA	1	M	FB	0.18 (0.14, 0.23)	0.54 (0.47, 0.62)	0.75 (0.67, 0.82)	0.37 (0.32, 0.41)
SIA	1	M	LB	0.2 (0.16, 0.24)	0.6 (0.55, 0.64)	0.8 (0.76, 0.83)	0.39 (0.36, 0.42)
SIA	2	F	FB	0.41 (0.3, 0.51)	0.59 (0.46, 0.71)	0.67 (0.53, 0.78)	0.18 (0.15, 0.2)
SIA	2	F	LB	0.3 (0.24, 0.34)	0.45 (0.37, 0.5)	0.52 (0.44, 0.58)	0.15 (0.13, 0.17)
SIA	2	M	FB	0.33 (0.24, 0.44)	0.49 (0.37, 0.62)	0.57 (0.43, 0.7)	0.16 (0.12, 0.19)
SIA	2	M	LB	0.29 (0.25, 0.34)	0.43 (0.38, 0.5)	0.5 (0.44, 0.57)	0.15 (0.13, 0.17)
CA	1	F	FB	<0.01 (0, 0.01)	0.14 (0.11, 0.19)	0.51 (0.42, 0.59)	0.14 (0.11, 0.18)
CA	1	F	LB	<0.01 (0, 0.01)	0.17 (0.14, 0.21)	0.58 (0.52, 0.64)	0.17 (0.14, 0.2)
CA	1	M	FB	<0.01 (0, 0.01)	0.15 (0.11, 0.21)	0.53 (0.44, 0.62)	0.15 (0.11, 0.2)
CA	1	M	LB	<0.01 (0, 0.01)	0.17 (0.13, 0.2)	0.56 (0.5, 0.62)	0.16 (0.13, 0.2)
CA	2	F	FB	0.09 (0.05, 0.15)	0.16 (0.09, 0.26)	0.21 (0.12, 0.33)	0.08 (0.04, 0.12)
CA	2	F	LB	0.11 (0.07, 0.15)	0.2 (0.15, 0.26)	0.25 (0.19, 0.33)	0.09 (0.07, 0.12)
CA	2	M	FB	0.23 (0.16, 0.32)	0.4 (0.3, 0.52)	0.49 (0.37, 0.62)	0.17 (0.13, 0.22)
CA	2	M	LB	0.16 (0.12, 0.2)	0.29 (0.23, 0.35)	0.36 (0.3, 0.44)	0.13 (0.1, 0.16)

Each row presents estimates for the specified subpopulation/location (SIA or CA); phase, P, (1 or 2); sex (male or female); and, birth-order, BO, (first-born or later-born). The estimates are posterior medians, with posterior PCI95s in parentheses. Note that the estimated infant mortality in CA phase 1 is suspiciously low and might reflect dropout from the sample that could not be accounted for in the model. See Supplementary Materials Section 1.1 for plots of the empirical survival functions and the model's posterior predictions of these functions.

These patterns are evident: (1) across phases, the CA have reduced pre-recruitment mortality relative to the SIA; (2) survival outcomes for young CA and SIA were better in phase 1, before the encroachment of loggers, miners, and homesteaders; (3) conditional on surviving to age 1, risk of death before recruitment is greatest in the SIA phase 1 (especially for males); (4) there is evidence of an emerging male survival bias in the SIA from phase 1 to phase 2; and, (5) there is evidence of an emerging female survival bias in the CA phase 2.

Infant mortality appears to be highest in the SIA phase 2, $\phi = 0.19$ (PCI95: 0.17, 0.21), and lowest in the CA phase 1, $\phi = 1.38$ (PCI95: 1.25, 1.51), with intermediate levels in the SIA phase 1, $\phi = 0.52$ (PCI95: 0.47, 0.57), and the CA phase 2, $\phi = 0.25$ (PCI95: 0.23, 0.31). Note that the symbol PCI95 indicates the equal-tail ninety-five percent posterior credibility interval.

3.2. The structuring of age-specific fertility by location and phase

In Fig. 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 superimpose 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 remains 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).

3.3. The structuring of the quantity–quality trade-off by location and phase

In Fig. 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 superimpose 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 parameter, θ_2 , falling reliably short of proportionality. If there were no quantity–quality trade-off, we would expect recruitment to increase linearly ($\theta_2 = 1$) with reported pregnancies. The substantially concave fit ($\theta_2 < 1$) provides evidence for the existence of a quantity–quality trade-off. There is less evidence of such a trade-off in phase 2, as indicated by the credibility intervals on θ_2 including 1, the value of

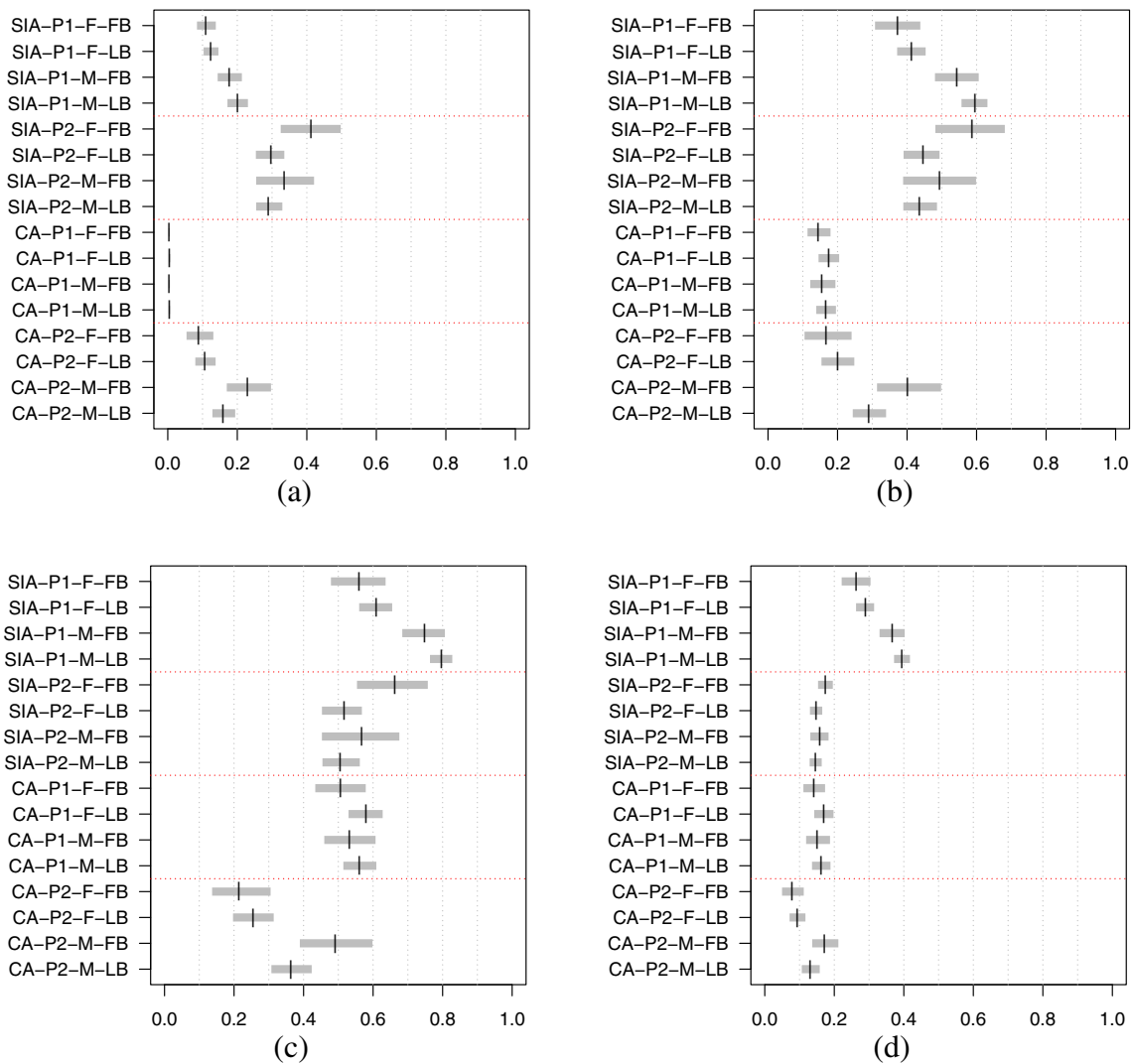


Fig. 2. Mortality in the Agta: Frame 2(a) cumulative probability of death in age interval (0, 1). Frame 2(b) cumulative probability of death in age interval (0, 15). Frame 2(c) cumulative probability of death in age interval (0, 45). Frame 2(d) probability of death in age interval (1, 15). These plots depict the mortality estimates provided in Table 1. SIA and CA indicate the geographic subpopulation. P1 and P2 indicate temporal phase. F and M indicate female and male. FB and LB indicate first-born and later-born, respectively. We note that infant mortality in the phase 1 CA is likely to be underestimated.

proportionality. Evidence of a quantity–quality trade-off is, however, slightly stronger in the SIA in phase 1, where θ_2 equals 0.80 (PCI95: 0.68, 0.91), than in the CA in phase 1, where θ_2 equals 0.84 (PCI95: 0.72, 0.96). Table 3 displays the parameter estimates and credibility intervals of our model.

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 survival, age-specific fertility, and quantity–quality trade-off models.

We first note from the fertility model that completed fertility is reduced in the CA relative to the SIA in both phases. From the survival analysis, we note that the CA show significantly reduced rates of pre-recruitment offspring mortality in both phases relative to the SIA. While these results are consistent with the VCH, the model has the merit of offering a more specific set of predictions. Accordingly, 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 Fig. 5(a) and (b). 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 anticipatory compensation 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. As before, these results are consistent with what would be expected under the VCH model of fertility decline.

In Fig. 5(c) and (d), we present the results of an analysis illustrating the influence of the shape and level of the value function on fertility. Across both phases, the value function linking pregnancies to expected recruited offspring is significantly elevated in the CA relative to the SIA. We illustrate the effect of this change 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

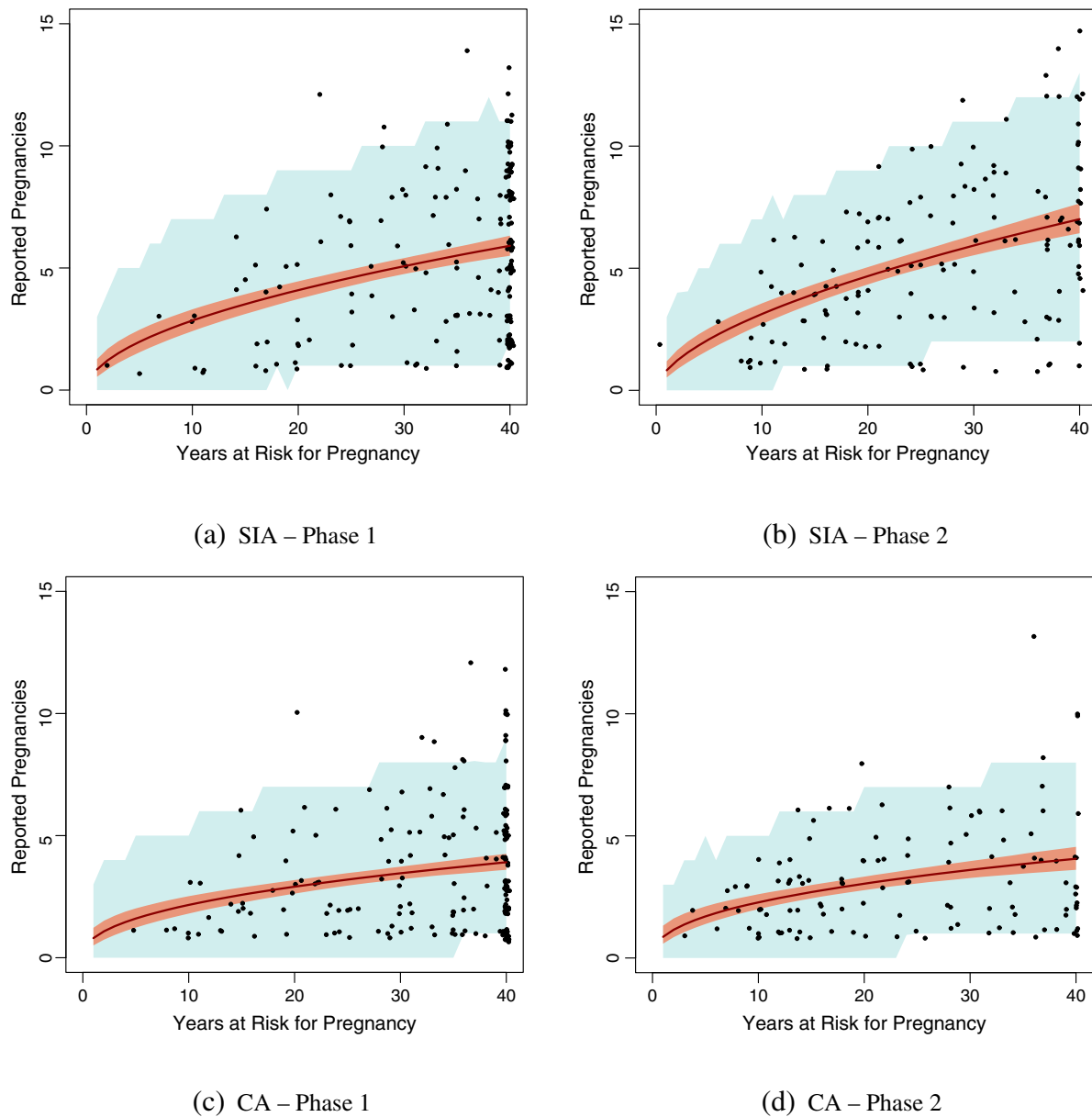


Fig. 3. Age-specific fertility in the Agta: Results of Gamma–Poisson regression modeling of reported pregnancies on years at risk for pregnancy, by location and phase, using the parameters from Table 2. Frame 3(a) phase 1 fertility in the SIA. Frame 3(b) phase 2 fertility in the SIA. Frames 3(c) and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

Table 2

Age-specific fertility regression estimates: key parameter estimates from the age-specific fertility model plotted in Fig. 3.

Loc	Phase	Parameter	Variable	Mean	SE	2.5 PCI	97.5 PCI
SIA	1	ζ_1	Intercept	−0.36	0.24	−0.84	0.10
SIA	1	ζ_2	Exposure	0.58	0.07	0.45	0.72
SIA	2	ζ_1	Intercept	−0.36	0.22	−0.82	0.06
SIA	2	ζ_2	Exposure	0.63	0.07	0.5	0.77
CA	1	ζ_1	Intercept	−0.39	0.25	−0.93	0.09
CA	1	ζ_2	Exposure	0.48	0.07	0.34	0.63
CA	2	ζ_1	Intercept	−0.28	0.24	−0.74	0.22
CA	2	ζ_2	Exposure	0.46	0.08	0.3	0.61

The value of the parameter labeled ζ_2 across locations and phases is indicative of fertility as a function of years at risk for pregnancy (a.k.a. exposure). 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 remains roughly constant in the CA across phases.

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: 8.3, 13.0) pregnancies to reach a target of 4 recruited offspring on average, while only 6.7 (PCI95: 5.3, 8.5) pregnancies would be needed by a CA mother on average. As such, assuming a target fertility of 4 recruited offspring, this analysis predicts about 2 fewer offspring in the CA relative to the SIA in phase 1, and 3 fewer offspring in the CA relative to the SIA in phase 2, estimates which correspond almost exactly with the empirical differences in completed fertility in each phase.

Finally in Fig. 6(a) and (b), we use code developed in Winterhalder, Puleston, and Ross (2015) to explicitly integrate the results of both the survival analysis and the quantity–quality trade-off model in order to generate numerical predictions (see Table 4) that allow us to decompose excess

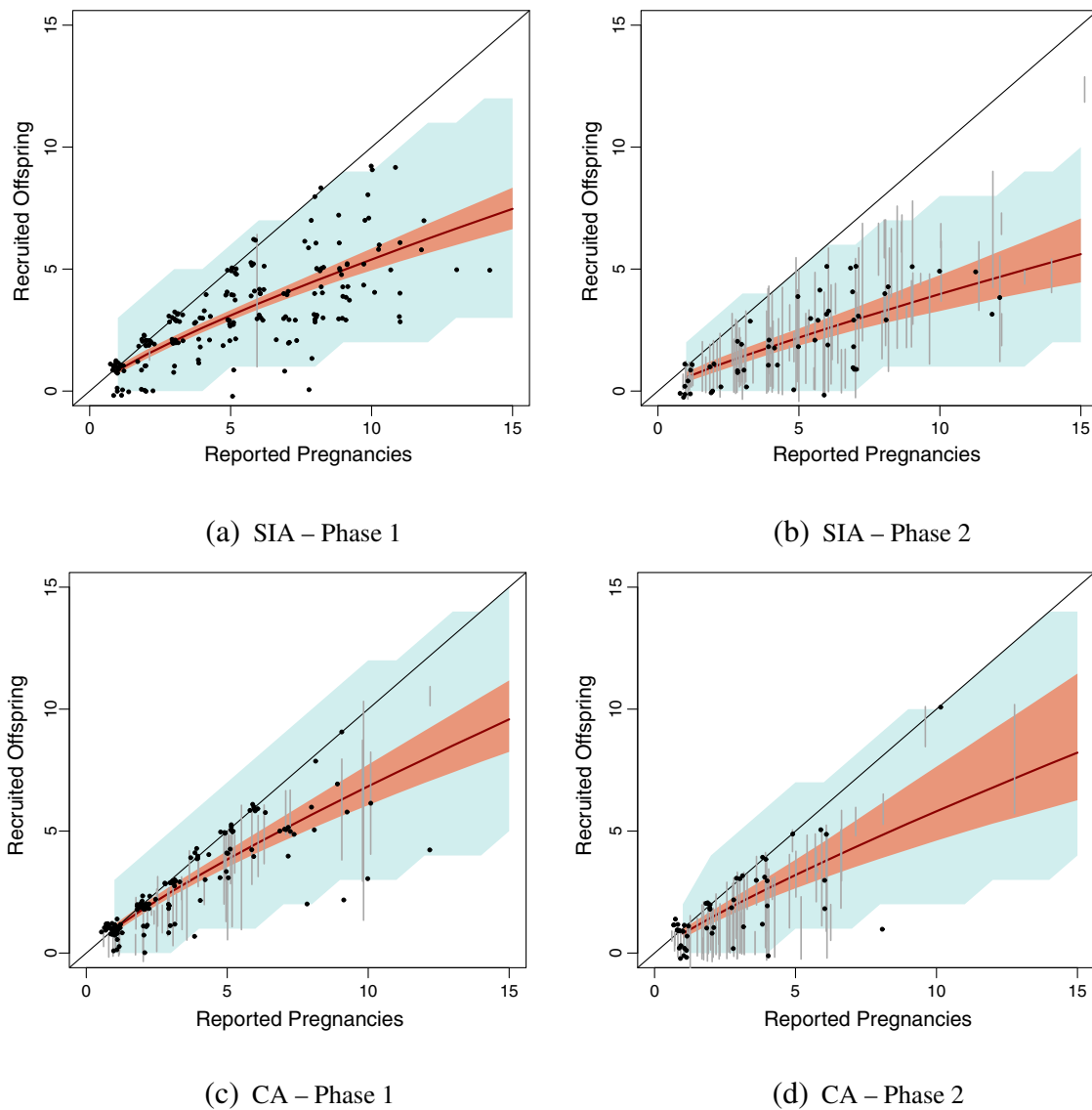


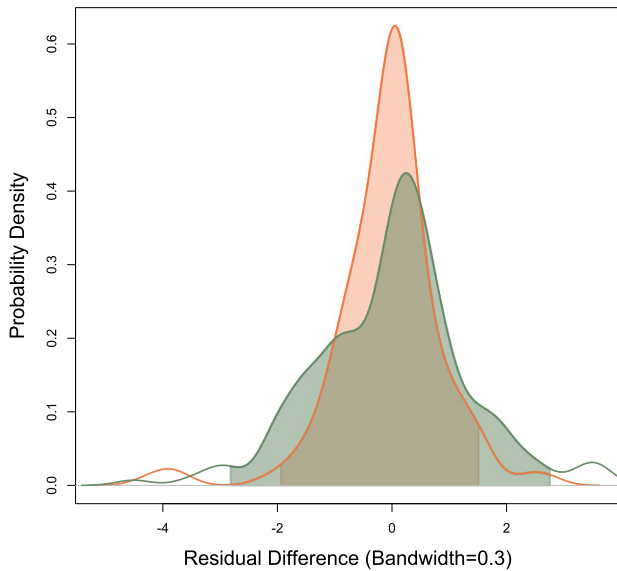
Fig. 4. The quantity–quality trade-off in the Agta: Results of Gamma–Poisson regression modeling of recruited offspring on number of reported pregnancies by location and phase, using the parameter estimates contained in Table 3. Frame 4(a) phase 1 quantity–quality trade-offs in the SIA. Frame 4(b) phase 2 quantity–quality trade-offs in the SIA. Frames 4(c) and 4(d) are the corresponding plots for the CA. 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 gray bars are (jittered) censored data. The dark red line is the maximum *a posteriori* estimate of the regression line, the shaded red area is the central ninety-five percent posterior credibility interval of the model of the mean, and the light blue shaded area is the central ninety-five percent posterior prediction interval.

Table 3
Quantity–quality trade-off regression estimates: key parameter estimates of the quantity–quality trade-off model plotted in Fig. 4.

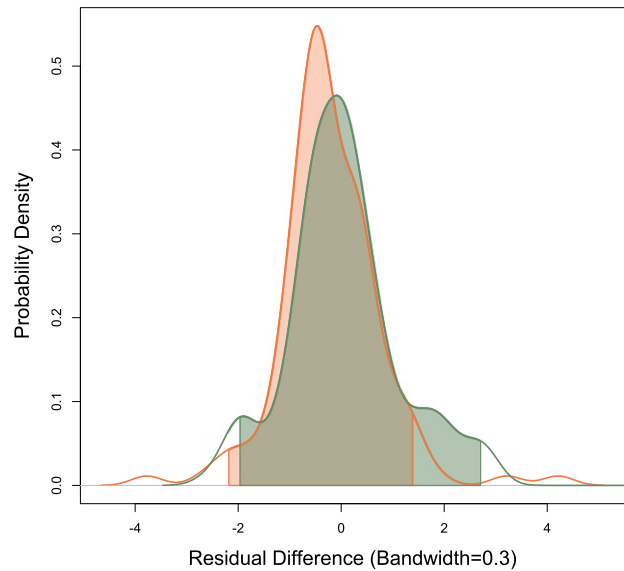
Loc	Phase	Parameter	Variable	Mean	SE	2.5 PCI	97.5 PCI
SIA	1	θ_1	Intercept	−0.15	0.11	−0.36	0.08
SIA	1	θ_2	Pregnancies	0.80	0.06	0.68	0.91
SIA	2	θ_1	Intercept	−0.59	0.22	−1.09	−0.2
SIA	2	θ_2	Pregnancies	0.85	0.11	0.65	1.12
CA	1	θ_1	Intercept	0.0	0.10	−0.19	0.20
CA	1	θ_2	Pregnancies	0.84	0.06	0.72	0.96
CA	2	θ_1	Intercept	−0.24	0.16	−0.58	0.04
CA	2	θ_2	Pregnancies	0.87	0.1	0.69	1.1

The value of the parameter labeled θ_2 across locations and phases is indicative of offspring recruitment as a function of reported pregnancies. We note evidence of the quantity–quality trade-off in the SIA and CA, during phase 1, as the θ_2 parameter in these models falls significantly short of 1, the value which indicates proportionality between reported pregnancies and recruited offspring. We fail to find robust evidence of the quantity–quality trade-off in the SIA or CA during phase 2.

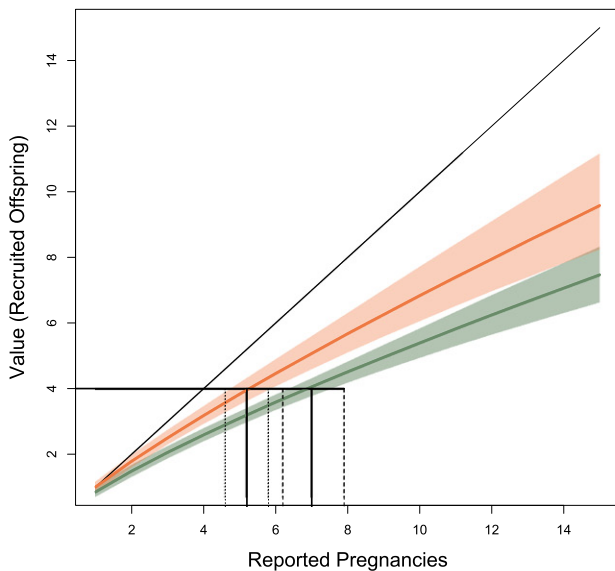
fertility relative to a target number of recruited offspring into mean compensation and variance compensation. In both phases, the empirical difference in completed fertility between the SIA and CA – about 2 pregnancies in phase 1 and 3 pregnancies in phase 2 – is numerically consistent with the relative levels of predicted mean and variance compensation arising from the differential fitness value of a given number of pregnancies in each sub-population and differences between the subpopulations in levels of stochastic mortality. Note that variance compensation is strongest in the SIA phase 1, where stochastic mortality is highest. In phase 2, we do not observe as much evidence of variance compensation under the coarse assumptions of the model, but we still see high levels of mean compensation due to the elevated predictable mortality in the SIA in phase 2 lowering the value function. The joint model correctly predicts both that fertility should be elevated in the SIA relative to the CA in both phases – even under the assumption that both populations have similar targets for number of recruited offspring – and that SIA fertility should increase by about 1 birth over phases, which it does.



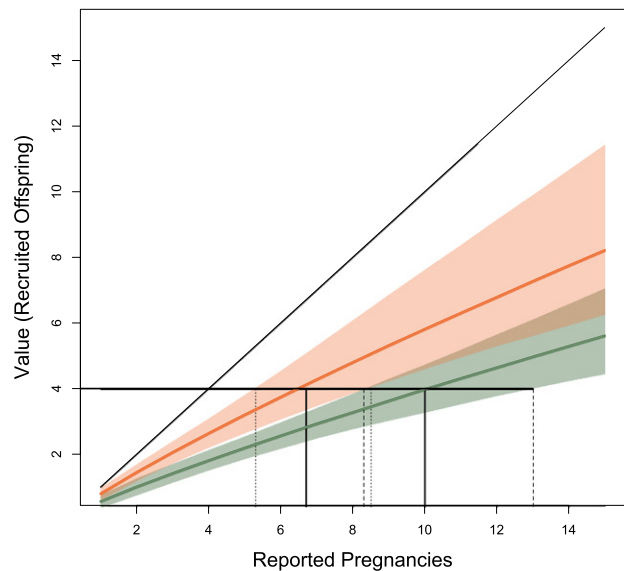
(a) Kernel density estimates of the variance of the residuals from the quantity–quality trade-off model in the SIA (green) and CA (orange), phase 1.



(b) Kernel density estimates of the variance of the residuals from the quantity–quality trade-off model in the SIA (green) and CA (orange), phase 2.



(c) Estimated value functions (and ninety-five percent PCIs) linking pregnancies to recruited offspring in the SIA (green) and CA (orange), phase 1.



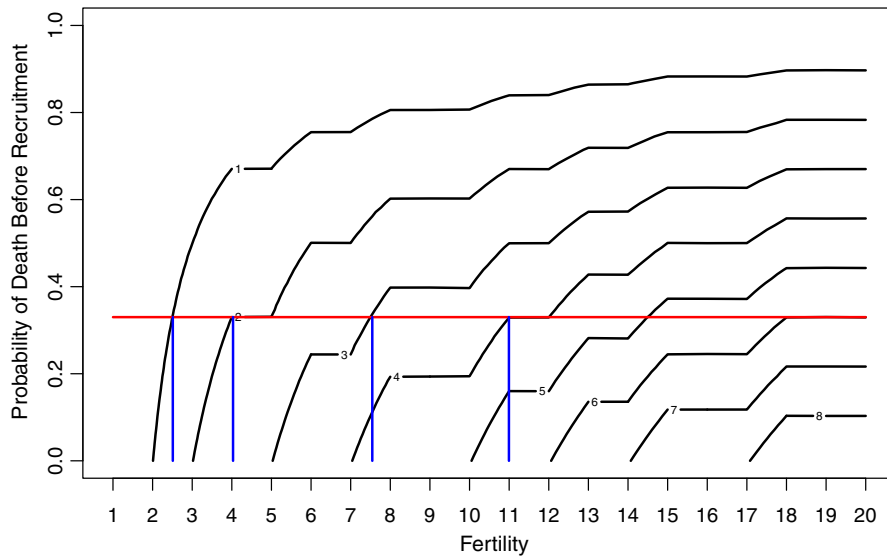
(d) Estimated value functions (and ninety-five percent PCIs) linking pregnancies to recruited offspring in the SIA (green) and CA (orange), phase 2.

Fig. 5. The effects of stochastic outcome variance and elevation of the value function on fertility: Frames 5(a) and 5(b) plot the kernel density estimates of the variance of the residuals from the quantity–quality trade-off models in the SIA (green) and CA (orange), for phase 1 and phase 2, respectively. The area of the central ninety-five percent of each distribution is delineated by the shaded regions. There is reduced variance in the residuals from the quantity–quality trade-off model in the CA compared to the SIA, regardless of phase. Frames 5(c) and 5(d) plot the estimated value functions (and PCI95s) linking pregnancies to recruited offspring in the SIA (green) and CA (orange), for phase 1 and phase 2, respectively. 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 offspring recruitment (see discussion in text), and the dashed vertical bars are PCI95s.

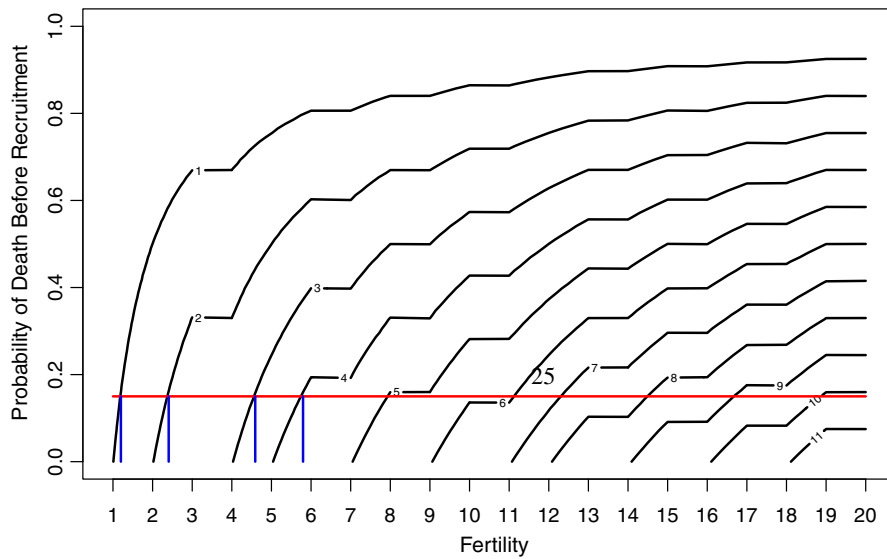
4. Discussion

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. It is becoming increasingly clear (e.g., [Lawson](#)

[et al., 2013](#); [Moorad et al., 2011](#); [Zietsch et al., 2014](#)) that empirical assessments of the various life-history trade-offs that an organism faces must integrate different components of such models. Here we investigate, within the framework of human behavioral ecology and life-history theory, predictions of several models concerning heterogeneity in mortality



(a) Full VCH analysis, SIA phase 1.



(b) Full VCH analysis, CA phase 1.

Fig. 6. Variance compensation and demographic transition in the Agta: Frames 6(a) and 6(b) plot the number of pregnancies (X-intercepts of the vertical blue bars) needed to meet risk-sensitive target outcomes of recruited offspring (black contours for target recruited offspring = {1, 2, 3, ...}), conditional on the empirical level of stochastic probability of death before recruitment in the subpopulation (horizontal red bar), and the subpopulation-specific value function of fertility in terms of recruited offspring estimated in the quantity–quality trade-off model. Read the figure this way: imagine that a woman in the SIA phase 1 – Frame 6(a) – has a target of 3 recruited offspring, then if stochastic mortality were zero (i.e. the red bar were moved down to 0 on the Y-axis), she would need 5 pregnancies to reach such an outcome given value function linking pregnancies to recruited offspring in the SIA phase 1, since the contour for recruited offspring = 3 intersects the X-axis at the value of 5 pregnancies. Now, assume that stochastic mortality increases, such that the red bar is set to some empirical level of stochastic mortality risk, 0.33 in this example. In this case, the woman now must compensate by increasing fertility to offset for offspring lost due to stochastic mortality; specifically, she now needs about 7.6 pregnancies on average to meet her target goal of 3 recruited offspring, as indicated by the intersection of the vertical blue bar and the target contour. Thus, a woman must increase fertility by 2.6 pregnancies on average to compensate for the effects of stochastic mortality, even though her expected offspring loss due to stochastic mortality is only 1 (3 target offspring times the stochastic mortality risk of 0.33); the additional 1.6 pregnancies are variance compensation. In these figures, we hypothetically assume that the level of stochastic mortality in a given subpopulation can be described by the cumulative probability of death conditional on surviving to the age of 1 year (0.33 for the SIA and 0.15 for the CA, in phase 1; these are approximately the mean values of CPD15|S1 in Table 1), and we also hypothetically assume that the mortality captured by the value function is due purely to infant mortality. These are not necessarily empirically-supported assumptions, but they allow us to demonstrate how mortality, fertility, and the quantity–quality trade-off interact in a unified model. Disentangling these effects might be empirically challenging, but we can still hope to gain an understanding of the system dynamics using the simple assumptions we make here. We only plot phase 1 outcomes here, but include the results from both phase 1 and 2 in Table 4. See Supplementary Model Code to produce plots for phase 2. Table 4 provides the numerical results of our model, and partitions excess fertility relative to a target number of recruited offspring into mean and variance compensation. See Table 4 for further discussion.

and fertility. We then combine different components of these analyses in order to address research questions – for example, the role of variance compensation in driving demographic transition – that cannot be broached in an analysis focused on a single kind of outcome.

In the subsections that follow, we contextualize the findings of each of our models. The survival analysis explores the structuring of

mortality, and is discussed in terms of constraints on, and strategic options open to, foraging and post-foraging populations; this analysis highlights the importance of heavy investment in first-born daughters in populations undergoing hypergynous interethnic integration. Our results are consistent with studies of other population undergoing such transitions (e.g., in Berezkei & Dunbar, 1997; Bailey, 1988; Cronk,

Table 4
Variance compensation and demographic transition in the Agta: We present the total number of pregnancies needed to reach a target outcome of recruited offspring for each location (Loc) and phase (P) assuming zero probability of stochastic mortality before recruitment. We then present the same estimates when the probability of stochastic mortality before recruitment is set to the empirical levels estimated using the survival analysis model (CPD15|S1, see Table 1).

Loc	P	Target Number of Recruited Offspring	Total Fertility Needed at Zero Stochastic Mortality	Offset at Zero Stochastic Mortality	Variance Compensation at Zero Stochastic Mortality	Total Fertility Needed at Empirical Mortality	Additional Offset to Compensate for Empirical Mortality	Mean Compensation at Empirical Mortality	Variance Compensation at Empirical Mortality
SIA	1	1	2	1	0	2.5	0.5	0.33	0.17
SIA	1	2	3	1	0	4	1	0.66	0.34
SIA	1	3	5	2	0	7.6	2.6	1	1.6
SIA	1	4	7	3	0	10.9	3.9	1.33	2.57
SIA	2	1	3	2	0	3.2	0.2	0.16	0.04
SIA	2	2	5	3	0	5.4	0.4	0.32	0.08
SIA	2	3	8	5	0	8.6	0.6	0.48	0.12
SIA	2	4	11	7	0	11.8	0.8	0.64	0.16
CA	1	1	1	0	0	1.2	0.2	0.15	0.05
CA	1	2	2	0	0	2.4	0.4	0.3	0.1
CA	1	3	4	1	0	4.6	0.6	0.45	0.15
CA	1	4	5	1	0	5.8	0.8	0.6	0.2
CA	2	1	2	1	0	2.15	0.15	0.12	0.03
CA	2	2	3	1	0	3.25	0.25	0.24	0.01
CA	2	3	5	2	0	5.4	0.4	0.36	0.04
CA	2	4	7	3	0	7.6	0.6	0.48	0.12

The offset at zero stochastic mortality is the excess number of births needed on average to yield a target number of recruited offspring given the value function linking pregnancies to expected recruited offspring in the hypothetical absence of stochastic mortality. In the model, we assume that all fertility compensation occurring when stochastic mortality is set to zero arises from the predictable mortality described by the quantity–quality trade-off value function. Thus, when there is no stochastic mortality, there is no variance compensation. Next, we calculate how many additional births are required to offset the empirical levels of stochastic mortality relative to the mean offset that would be required at zero risk of stochastic mortality. We partition this quantity into that which is needed to offset the mean effects of stochastic mortality, and that which is needed to offset the effect of variance in stochastic mortality given an asymmetrical value function; we call this quantity “variance compensation.” As an example, in the SIA phase 1, to reach a risk-sensitive target of 3 recruited offspring (at zero stochastic mortality) one would need 5 pregnancies on average, given the shape of the quantity–quality trade-off value function. This implies a mean offset of 2 additional pregnancies to compensate for the reduced value of pregnancies relative to recruited offspring. Next, if we set stochastic mortality before recruitment equal to the empirical levels estimated in the survival analysis model, we find that we need 7.6 pregnancies to reach a risk-sensitive target of 3 recruited offspring. This implies that an additional 2.6 pregnancies are needed to offset stochastic mortality risks. If we were to hypothetically assume that all mortality under age 1 is predictable and a result of the quantity–quality trade-off value function, and that all mortality between the ages of 1 and 15 is stochastic, then we can decompose the additional offset needed to compensate for empirical mortality into mean and variance compensation by subtracting mean compensation – the product of the target number of offspring and the stochastic mortality rate – from the total additional offset. In our example, the offset of 2.6 additional pregnancies can be decomposed into 1 additional pregnancy of mean compensation, and 1.6 additional pregnancies of variance compensation. In both phases, the empirical difference in completed fertility between the SIA and CA is numerically consistent with the relative levels of predicted mean and variance compensation arising from differences in fertility payoffs and mortality regimes between the SIA and CA.

1991). The fertility model directly compares fertility rates across locations and phases. From our findings and ethnographic descriptions of Agta life in each location and phase, we infer that extrinsic mortality is a more important driver of fertility decisions than budgetary constraints, but we acknowledge that the evidence for this is somewhat indirect. The quantity–quality model is designed to investigate the trade-off between the number of children produced by a mother and the number recruited to reproductive age. The greater prominence of the quantity–quality trade-off in the SIA population suggests that budgetary constraints may be an important factor affecting child survival in large families. Additionally, we show that quantity–quality trade-offs are insufficiently strong, and incorrectly structured across CA and SIA populations, to account for the demographic transition observed in the CA relative to the SIA. Finally, by integrating model-based inference on pre-recruitment mortality, the quantity–quality trade-off value function, and completed fertility, we can demonstrate for the first time empirically that the VCH is capable of explaining demographic transition to lowered fertility. In short, we have attempted to use the Agta Demographic Database to examine how changes in reproductive decision-making across locations and temporal phases are consistent (or not) with different predictions based on life-history theory. Furthermore, we illustrate key methodological advances by deriving problem-specific Bayesian models that incorporate and control for multi-level structuring of data and integrate over uncertainty due to missing, censored, and/or partially known 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 of the CA is generally consistent with studies showing elevated mortality rates among foragers (e.g., Hill & Hurtado, 1996). The SIA experience relatively high mortality during both infancy and childhood, but there is some patterning by phase. Only the SIA in phase 1 can be seen as undisturbed foragers, and we find that mortality risk is especially high in the interval from age 1 to age 15 in the SIA phase 1 (see Fig. 2(d)). Our findings here echo the results of Sellen and Mace (1997) who found that the elevated mortality of foragers is often due to increased hazard post-infancy.
- (2) Elevated infant mortality in the SIA and CA phase 2 relative to phase 1 is unexpected on the basis of production system changes (Sellen & Mace, 1997). It is, however, understandable in light of ecological damage and displacement, and the abuse of the Agta by settlers, loggers, and miners (Early & Headland, 1998; Headland, 2002, 2004). Although the Agta appear to be shifting away from foraging, their socio-economic subjugation as landless peasants obviates any potential mortality reduction which might be associated with the subsistence change. 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 appears not to be the most important factor in the Agta demographic experience there.
- (3) Decreased mortality before age 45 in the CA during phase 2 is expected on the basis of acculturation and hypergenous marriage patterns (Early & Headland, 1998; Headland & Headland, 1998). This change may be driven by economic status, specifically the increased access of some acculturating or interethnic Agta

to the resources held by lowlander families, as well as the associated cultural capital (Early & Headland, 1998) and increased access to western medical facilities (Headland, 2004).

- (4) There is evidence for increasing parental favoritism directed toward male offspring in the SIA in phase 2 relative to phase 1, perhaps as a result of the increased value of males as agricultural laborers (Boserup, 2007; Burton & White, 1984). 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.
- (5) In the CA, however, the transition from phase 1 to phase 2 has been marked by a significant decrease in survival for first-born males, but increased survival for females. 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 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 ~1000 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 & 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 completed fertility in the CA relative to the SIA, possibly reflecting an onset of demographic transition that is clearly unrelated to decreased budgets, given the greater material resources of the CA relative to the SIA; and (2) we find a small increase in completed fertility in the SIA between phase 1 and phase 2. This increase is unlikely to reflect relaxed budgetary constraints, insofar as the SIA in phase 2 have experienced considerable disturbance to their 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 & 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 predominantly occurs during phase 1 and is unlikely to be a factor affecting fertility decline, since the minor differences in this trade-off across the SIA and CA illustrate that there are slightly higher quantity–quality trade-offs in the population with elevated fertility rates. The quantity–quality trade-offs during phase 1 are 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 could be important factors in driving mortality as maternal fertility increases.

Our analysis of the quantity–quality trade-off is potentially compromised by the confounding influence of phenotypic correlation (Hill & Hurtado, 1996). If, for instance, Agta mothers vary in their maternal resources, and women with greater resources not only have more children, but are more successful in raising them, then standard regression models will underestimate the possibility of a trade-off. Fortunately, the ADD allows us to test for phenotypic correlation by

controlling for maternal quality operationalized as maternal height, weight, or weight-for-height. We fit basic maximum likelihood Poisson regression models to a subset of the Agta data for which we have complete fertility records and height and weight data (Supplementary Materials Section 1.2). Formal model comparison with AIC indicates that the model with no controls for maternal state is preferred. This indicates that our main findings are not likely to be confounded by maternal embodied capital, at least insofar as it is 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 declining maternal condition. 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 children will survive to recruitment age—in other words, that target reproductive outcomes are affected by stochastic variance (Winterhalder & Leslie, 2002; Leslie & Winterhalder, 2002). Other factors being equal, lower fertility is predicted in contexts where stochastic outcome variance is reduced, and where the lower portion of the fitness value function linking pregnancies to recruited offspring approaches direct proportionality. Both predictions are supported in this study.

Controlling for the mean effects of increasing maternal fertility, 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 – i.e. an increase in the expected number of recruited offspring given a small number of pregnancies – in the CA relative to the SIA.

Furthermore, 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 & Kessler, 1999; Kaplan, 1996; Winterhalder & Leslie, 2002; Smith et al., 2010; Gurven et al., 2010; Bergerhoff Mulder et al., 2009; Snopkowski & Kaplan, 2014). By intermarrying with the Filipino lowlanders and reducing fertility, the acculturating CA could be building more economic and socio-relational security (Headland & 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 the 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 (Leslie & Winterhalder, 2002; Winterhalder & Leslie, 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 & Kessler, 1999). Our successful empirical test of the VCH as an explanation for demographic transition of course does not exclude the possibility that other adaptive (Kaplan, 1996; Kaplan, Lancaster, Johnson, & Bock, 1995) and non-adaptive (Colleran, Jasienska, Nenko, Galbarczyk, & Mace, 2014; Goodman, Koupil, & Lawson, 2012; Pérusse, 1993; Richerson & Boyd, 2008; Richerson et al., 2015) theories for demographic transition might also be consistent with the data.

Variation in behavioral and life history strategies can be strongly affected by the local political economy (Nettle, 2010; Ross & Winterhalder, 2015). 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 have been disastrous for the welfare of the Agta people (Headland et al., 2011).

4.5. The value of Bayesian methods in twenty-first century anthropology

Finally, we have demonstrated how Bayesian model specification allows researchers to create custom statistical tools that account for uncertainty in measurement of covariates and outcomes, missing data, and censored variables like recruited offspring. Demographic and anthropological data on foraging and other subsistence populations, like data on archaeological sites (Winterhalder, Kennett, Grote, & Bartruff, 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.

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Appendix A. Supplementary Materials

Supplementary materials to this article can be found online at <http://dx.doi.org/10.1016/j.evolhumbehav.2016.02.005>.

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