Reproductive trade-offs in extant hunter-gatherers suggest adaptive mechanisms for the Neolithic expansion

Abigail E. Page, Sylvain Viguier, Mark Dyble, Daniel Smith, Nikhil Chaudhary, Gul. D. Salali, James Thompson, Lucio Vinicius, Ruth Mace and Andrea. B. Migliano

Authors' affiliation: Department of Anthropology, University College London, 14 Taviton Street, London WC1H 0BW, UK.

Corresponding Author: Abigail Page; Department of Anthropology, University College London, 14 Taviton Street, London WC1H 0BW, UK; +44(0)7588810936; abigail.page.10@ucl.ac.uk

Keywords: Hunter-gatherers; quality-quantity trade-off; epidemiological transition; Neolithic revolution

Classification: Biological Sciences, Anthropology.

Abstract

The Neolithic demographic transition remains a paradox, as it is associated with both positive effects, such as higher population growth as well as negative effects, such as increased morbidity and mortality rates. Here we reconcile the conflicting evidence by proposing that the spread of agriculture involved a life history quality-quantity trade-off whereby mothers traded offspring survival for increased fertility, achieving greater reproductive success in spite of deteriorating health. We test this hypothesis by investigating fertility, mortality, health and overall reproductive success in Agta hunter-gatherers whose camps exhibit variable levels of sedentarization, mobility and involvement in agricultural activities. We conducted blood composition tests with 345 Agta and found that viral and helminthic infections as well as child mortality rates were significantly increased with sedentarization. Despite this, age-controlled fertility and overall reproductive success are both positively affected by sedentarization and participation in cultivation. Thus, we provide the first empirical evidence of an adaptive mechanism in foragers which reconciles the decline in health and child survival with the observed demographic expansion during the Neolithic.

Significance statement

The rise of agriculture during the Neolithic period has paradoxically been associated with worldwide population growth in spite of increases in disease and mortality. We examine the effects of sedentarization and cultivation on disease load, mortality and fertility among Agta foragers. We report increased disease and mortality rates associated with sedentarization alongside an even larger increase in fertility associated with both participation in cultivation and sedentarization. Thus, mothers who transition to agriculture have higher reproductive fitness. We provide the first empirical evidence of an adaptive mechanism behind the expansion of agriculture, explaining how we can reconcile the Neolithic increase in morbidity and mortality with the observed demographic expansion.

\body

Introduction

Agriculture appeared in multiple locations from around 10–12,000 BP before slowly spreading to become the dominant subsistence system by 5000 BP (1–5). The Neolithic transition was associated with sedentarization, food storage, wealth accumulation and inequality as well as increasing population size (3, 4, 6, 7). It has been suggested that an increased availability of calories combined with a reduction in energy expenditure due to sedentarization led to increased energy availability for reproduction (8–10). As a result, while exact estimates vary, it has been argued that average population growth rates rose from <0.001% per year to approximately 0.04% during the early Neolithic (6, 8, 11–17).

On the other hand, studies reveal significant increases in morbidity and mortality associated with reduction in dietary breadth and sedentarization (6, 18–22). Research reveals increased prevalence of tuberculosis, syphilis and the plague (6, 23–25), overall immunological stress (26) and a deterioration in oral health (16, 27, 28). Farming led to higher population densities, sedentarization, increased contact with neighboring populations, presence of rodents attracted by food stores, domestication and fecal pollution (29–31). All those factors facilitated virulent bacterial and viral pathogens as well as soil-borne helminths (roundworm, hookworm and whipworm (32–38)). While some argue that Paleolithic foragers experienced high helminths loads (37, 39, 40), archaeological data shows instead an increase in helminths associated with farming (33, 41–45) compared to mobile, low-density hunter-gatherers. In summary, the overall effect of agriculture on health was a trend towards increasing morbidity and mortality (16, 19, 28, 46), although its intensity exhibits some regional variation and inconsistent trends (47–56)).

Given this significant increase in disease burden, why farming arose independently and expanded in diverse geographical regions (57, 58) remains a puzzle. Here we propose that settled agriculture was accompanied by a life history trade-off, whereby mothers switch strategy to invest in offspring quantity rather than quality and thereby increase their reproductive fitness. A quantity-quality trade-off is an adaptive process based on a principle of optimal distribution of limited resources: parents must either allocate finite resources to a few higher quality offspring or to multiple lower quality ones (59–64). By proposing that a quantity-quality trade-off provides an explanation for the transition to agriculture, we provide an adaptive mechanism that reconciles the decline in population health with increases in mortality during the Neolithic transition. We test this hypothesis with data from extant Palanan Agta foragers in the Philippines (hence forth referred to as Agta), a diverse group varying in mobility, foraging, wealth accumulation and camp permanence; traits all attributed to the Neolithic revolution (1, 3, 6, 7). Residing completely within the Northern Sierra Madre Natural Park the Palanan Agta have remained mostly separated from other Agta populations who reside outside the park limits and further south in Casiguran (65–67). By measuring fertility, mortality alongside viral, bacterial and helminth markers in different Agta camps, we found that sedentarization is associated with increased morbidity and mortality, yet both sedentarization and involvement in non-foraging activities are both associated with even further increases in fertility, resulting in higher reproductive fitness. Our results provide evidence that a quality-quantity trade-off was adaptive and suggests a pathway through which, despite poor health, farming could have become the dominant subsistence system after its origin in the Neolithic. Thus, we demonstrate how exploring the mechanisms that lead extant foragers to seek increased settlement and food production is a theoretically informative approach to test key archaeological predictions (6, 8, 19).

Results

Palanan Agta exhibit a suite of traits attributed to the Neolithic transition. Archaeological studies have shown that the Neolithic transition from hunter-gathering to agriculture is associated with a suite of traits (3, 7) that are also present across Agta camps. Figure 1 shows significant correlations between proportion of food produced in cultivation and key 'transition' traits. These correlations indicate that while extensive foraging, small size, high mobility and few belongings characterize some Agta camps; others exhibit more food production, larger camp size, little mobility and many belongings. Thus, the variability present within the Agta today allows us to test to influence of 'transition' on fitness related outcomes.

We used these 'transition' variables associated with the Neolithic revolution in multilevel analysis to examine fertility, morbidity and mortality. Due to covariance two models were produced for each analysis: one exploring the effects of *household mobility* (whether an household moved camp at least once or not during two years of fieldwork) and the second, exploring the effects of *household foraging* (binary measure, 1 = more than 75% of maternal time spent in foraging as opposed to cultivation and wage labor). Both these models included one camp settlement variable, chosen based on lowest AIC score in univariate regressions (SI appendix table S4), and included: *i*) *camp housing type* (temporary, semi-permanent or permanent); *ii*) a binary *sedentarized camp* variable denoted by the presence of permanent camp infrastructures; and *iii*) *out-of-camp mobility* over two years, 0 representing camp abandonment. AICs and full model results are reported in the SI appendix tables S8-14.

Settled Agta exhibit increased fertility. The total fertility rate (TFR) among the Agta based on 41 live births in 2013-2014 was 7.7, one of the highest reported in foragers (68). For 117 women we interviewed (aged between 16-75 years), the mean number of live births was 4.4 (ranging from 0 to 13). Residuals from a linear regression of offspring count and maternal age, including a logarithmic term, were used to control for age effects on fertility and reproductive success, while an exponential term was included for child mortality (see SI appendix). Settled mothers had significantly higher fertility than women who moved camp at least once (β = 1.3 $\pm$ 0.6, p = 0.04). Correspondingly, increases in household belongings were positively associated with fertility (β = 0.5 + 0.2, p = 0.005). This relationship is further confirmed by examining TFR: settled mothers had 16.7% higher TFR (7.7) compared to mobile mothers TFR (6.6). Similarly, for all live births settled mothers had 20.5% more offspring (5.3) than mobile mothers (4.4; SI appendix table S6). A possible pathway may be that settled mothers are able to accumulate more somatic resources for reproduction. Accordingly, settlement was a significant predictor of maternal BMI (i.e. mothers never witness to move camp, β = 1.7 $\pm$ 0.6, p = 0.004), and BMI positively predicts fertility (β = 0.3 $\pm$ 0.1, p = 0.02).

Mothers who forage more exhibit lower fertility. A high degree of foraging also significantly predicts fertility (β = -1.4 $\pm$ 0.7, p = 0.04). As a result, mothers who spent less than 75% of their time foraging experience 0.23 higher fertility residuals than expected for their age. Mothers who spent more than 75% of their time foraging had 0.85 less offspring, given their age (SI appendix table S7). Women who spent more time foraging also had marginally lower BMI (β = -1.5 $\pm$ 0.9, p = 0.08). Therefore, transition to farming as measured by both increasing cultivation and sedentarization are positively associated with fertility, perhaps due to increased somatic resources.

Sedentarization is associated with health deterioration. We examined the effects of cultivation and sedentarization on three white blood cell types – lymphocytes, neutrophils and eosinophils - as proxies for different immunological attacks: viral, bacterial and helminthic, respectively (see SI appendix). Our sample consisted of 345 Agta, 140 of which were adults (48.6% males) and 205 children under 16 (60% males). Due to inconclusive test results missing data reduced the sample to 293, consisting of 117 adults (47% males) and 176 children (59% males). Table 1 shows that people in large camps with low out-of-camp mobility had 2.8 times higher chances of presenting with lymphocytosis compared to mobile camps. People residing in camps with permanent and semi-permanent houses had significantly higher eosinophil concentrations than individuals in temporary camps. Severe eosinophilia (>5 x 10^9/L) is indicative of extreme helminth infestations and only found in sedentarized camps. In contrast, people residing in sedentarized camps with some form of infrastructure (i.e. church or water pump) had lower odds (by 80%) of neutrophilia. One major bacterial disease among the Agta is *Mycobacterium tuberculosis* (TB), demonstrated by the fact that 41.7% of the 24 individuals suffering from neutrophilia had clinically diagnosed or suspected TB. In contrast, percentage of time spent foraging had little effect on health. Individuals in households who foraged more had a 76% reduction in odds of presenting with lymphocytosis than households who foraged less. However, indicators of helminthic or bacterial infections were not affected by percentage of time spent foraging (SI appendix tables S11-13).

To explore helminth burden further we collected 30 fecal samples from Agta who had presented with eosinophilia. All 30 samples tested positive for helminth ova. The mean number of species was 1.6 ± 0.7 and included: roundworm (*Ascaris Lumbricoides,* 83.3%); hookworm (*Ancylostoma duodenale* or *Necator americanus,* 46.7%); and whipworm (*Trichuris trichiura*, 30%). Due to the small sample size non-parametric Kruskal-Wallis tests were run on three measures of transition. Living in a sedentarized camp was associated with a 0.65 mean increase in parasite species number compared to living in mobile camps ($\chi^2 = 5.9$, df = 1, $p = 0.02$). Household participation in cash labor decreased helminth loads by 37.4% ($\chi^2 = 8.9$, df = 1, $p = 0.003$) indicating that families who interact with the wider economy may be more able, financially and/or behaviorally, to acquire anthelmintic medicines. While cash labor is a positive predictor, the proportion of time spent foraging is not ($\chi^2 = 3.3$, df = 1, $p = 0.2$). Our results indicate that although increased helminthic load is likely to be a consequence of transition to agriculture, it is settlement, rather than cultivation, which predicts helminth infestation.

Child mortality is increased in settled camps. We examined whether the negative effects of settlement on health also extended to child mortality rates (including all post-natal deaths until age 16). Out of 520 reported live births from 124 mothers, 19% of children died before age one, 13.9% from one to five and 6% from five to fifteen years. Those rates are lower than the 28-29% previously reported for neighboring Agta (65, 69). Mothers residing in camps with permanent housing experienced significantly higher childhood mortality rates, compared to mothers living in camps with temporary housing ($\beta = 0.7 \pm 0.3, p = 0.005$). The relationship for semi-permanent camps was in the same direction but of marginal significance ($\beta = 0.5 \pm 0.3$, $p = 0.08$). This relationship results in a 63.2% increase in mortality rates for settled mothers living in sedentarized camps (0.93) when compared to nomadic mothers in temporary camps (0.57). Thus, the sedentarized camps with the highest helminth and viral disease rates also experience the highest childhood mortality rates. Following the morbidity results, proportion of time spent in cultivation had no significant relationship with child mortality ($\beta = 0.01 \pm 0.04, p = 0.8$).

A quantity-quality trade-off explains higher reproductive success in transitioning Agta. Our results show that women who settle down trade child survival for fertility, increasing their overall reproductive success (Figure 2a). Settled women ($\beta = 0.8 \pm 0.4, p = 0.03$) had significantly more children surviving to age 16 (our measure of reproductive fitness) than mobile women. Although these settled women faced higher child mortality rates, they also experienced extremely high fertility. As a result of the negative morbidity effect of sedentarized camps compared to the positive fertility effect of settled households, women residing in permanent camps suffered lower child survival ($\beta = -1.2 \pm 0.5$, $p = 0.01$) compared to temporary camps, once household mobility has been controlled for. Figure 2a demonstrates that mobile women living in sedentarized camps faced the worst situation as they experienced both higher mortality rates associated with permanent camps and the lower fertility rates associated with high mobility. Thus, they experienced 0.73 lower fitness, given their age. Overall, our results show that settled mothers, in spite of the higher mortality rates, had an extra 0.59 offspring (4.4) surviving to age 16 compared to mobile women (3.8), a relative increase of 15.8% in reproductive fitness.

Our other indicator of 'transition', the percentage of time involved in foraging, also predicted reproductive success ($\beta = -1.2 \pm 0.6$, $p = 0.05$). We find that mothers who foraged more than 75% of the time had 0.74 less children surviving to age 16 given their age, while mothers who spent less time foraging experienced 0.04 more children surviving to age 16 (figure 2b). Thus, while abandoning foraging does not significantly affect child mortality rates, it does increase fertility, and consequently mother's reproductive success. Consequently, while cultivation is associated with increased fertility, sedentarization is associated with both increased fertility and increased morbidity and mortality. The overall consequence of this combined process is a reproductive trade-off where settled mothers involved in cultivation have the highest reproductive fitness, despite increased morbidity and mortality.

Discussion

The variability of lifestyles currently observed within the Agta allows the testing of hypothesis proposed by archaeologists to explain the demographic processes taking place during the Neolithic transition (8, 29). Current evidence from archaeology and other sources suggests a Neolithic paradox as fertility increased alongside morbidity (58). Here we have tried to shed light on this debate by offering an adaptive explanation for the Neolithic transition. We propose that a life history trade-off between offspring quantity and quality is able to explain a suite of traits including higher fertility, mortality, morbidity and overall reproductive success observed in sedentarized Agta practicing cultivation. In so far that variability observed within the Agta is reflective of Neolithic trends, our results illuminate the adaptive mechanisms involved in transition to sedentarized food production. In doing so we provide empirical evidence that a quantity-quality trade-off can explain the demographic changes associated with cultivation and sedentism.

Our data indicates that sedentarization was associated with increased risk of infectious disease. Viral infections were higher in the larger, less mobile camps, with increased cultivation. Camp size and population density (measured here through out-of-camp mobility) were significantly correlated with viral infections in our data. This follows expectations of transmission of viruses such as *Caliciviruses* and *Rotoviruses,* causing gastroenteritis and influenza (38)*,* both common among settled Agta and dependent on higher population densities (70). This mirrors the finding of increased risk of high C-reactive protein concentrations (indicative of an inflammatory response) in children among more acculturated Tsimane forager-horticulturalists (71). In particular, cultivation may independently predict increased viral load (indicated by the association between lymphocytosis and foraging) due to poorer nutritional quality of agricultural staples. Increased consumption of rice with cultivation entails a loss of dietary breadth and macro- and micro-nutritional quality (72, 73) leading to malnutrition, which is a significant predictor of disease and mortality (74).

As with viral infections, Agta living in more permanent camps (as predicted by camp housing type) were also worse off in terms of helminthic infections, matching theoretical predictions (29, 33, 43, 44, 75). Contrary to this, some studies have argued the high helminth burden was a major selective pressure before the Neolithic (37, 39, 76) due to extreme helminth rates in many semi-sedentarized, farmer-foragers (31, 37, 77). However, these groups are no longer fully mobile. Supporting our interpretation and findings, researchers observed a near absence of helminths in an isolated Amazonian group (78), Hadza children (79) and lower helminth loads among isolated and mobile Saluma and Yanomama groups (80). While some parasitic species were hosted by our hominid ancestors (29, 81, 82), there is little archaeological evidence for an extreme intestinal parasite burden predating agriculture (33, 41–43, 45, 81). Thus, increased viral and helminth burdens are costs associated with sedentarization. It should be noted that settled Agta did not, however show an increased incidence of neutrophilia, which in our sample is often caused by TB. Chronic bacterial infections, such as TB, have evolved to survive at low population densities, thus likely predate agriculture (83, 84). The lower incidence of neutrophilia in settled Agta camps is likely due to the limited access to medical care, which might also explain the finding that cash labor decreased helminth loads by 37.4%. Since westernized medicine is a recent occurrence, the overall increased helminthic load in sedentarized camps may be underestimating the effect that settlement had on human populations during the Neolithic transition.

We found that more permanent camps had significantly higher childhood mortality rates, matching archaeological evidence from the Neolithic (6). Our results also revealed significantly higher fertility rates in settled women, particularly those transitioning from foraging to cultivation. Agriculture has been associated with fertility increases (85, 86) as the reduction in energy expenditure with settlement (87) and increased carbohydrate consumption (10, 88) are associated with increased BMI, which correlates with shorter inter-birth intervals and higher fertility (89). This suggests a pathway through which increased cultivation could lead to increased fertility. An additional pathway, as suggested by Kramer and Boone (90), considers the increased economic productivity of children in agriculture which reduces maternal constraints and thus, increases her fertility. Our study remains correlative, which leaves unanswered the question of the causal direction between fertility, sedentarization and food production. Since sedentarization correlates with food production in the Agta, with more sedentarized households abandoning foraging, it seems that these two process are interdependent, and thus are treated here as part of a process that involved a cluster of 'transition' traits. This is likely to be the case for the Neolithic transition as well, as many have reported the interplay between sedentarization and food production leading to the demographic changes associated in the origins of agriculture (4, 7). Further limitations stem from using a cross-sectional study design to explore longer-term trends, thus, it is unclear to what degree sedentism is reflective of mobility trends beyond our two-year sample period. However, a cross-sectional study design does permit the exploration of intra-population variability without requiring this variability to be recent or unilineal. Furthermore, foraging and mobility behaviors are likely altered during the heavy rainy and typhoon season not captured here as data collection occurred during the dry period. However, this does mean there is no systemic temporal bias in the data as camps were visited within the same season. Finally, more detailed dietary data would be required to explore these questions in more depth, allowing us to better separate the effects of 'transition'.

In summary, our study of the Agta provides evidence supporting the hypothesis that while the transition to agriculture in the Neolithic significantly depressed health, the overall fitness payoff was greater. Therefore, our proposed quality-quantity trade-off provides an adaptive mechanism that reconciles deteriorating health, increased mortality and demographic expansion following the spread of agriculture in the Neolithic. Finally, since high fertility rates were accompanied by relatively high mortality rates, the trade-off also explains why population numbers did not explode during the Neolithic but instead increased relatively slowly (8), perhaps as large increases in fertility were matched by increases in mortality (17).

Methods

Data collection occurred over two field seasons from April to June 2013 and February to October 2014 during the Isabela dry season. There are around 1,000 Agta living in Palanan municipality, Isabela Province, located in northeastern Luzon. The Agta are primarily fisher-foragers, residing either at the coast or inland watersheds. Hunting does occur, however fishing is far more common: out of 2168 work activities 54% were spent fishing, 20% gathering and 3% hunting. The remaining 'non-foraging' activities consist of cultivation (13.5%) and wage labor (9.5%). There is, however significant variance in diet (Figure S1) and activities between households: mobile households spent only 3.5% of their work activities in cultivation and 0% of time in wage labor. Comparatively, settled households spend 11.6% and 10% of their work activities in cultivation and wage labor, respectively. We found 26% Agta moved camp at least once during our fieldwork, resulting in an average camp move of once every 10 days. Similarly, the degree of camp sedentarization varies drastically as some camps change daily and consists of temporary shelters while others consist of permanent wooden structures built around churches and cultivation plots. Some Agta living in permanent camps closer to town have limited access to medical care and government provisioning. However, the effects of these sporadic interventions on the Agta health are limited (see SI appendix for further ethnographic description). We stayed around 14 days in each of the 13 camps and conducted reproductive histories to quantify demographics and interviews to produce an index of household belongings. After creating an emic-sourced list of 'important' belongings we asked each household whether they had each of the 14 objects, and if so how many. This was then weighted based on how many times each item were mentioned (SI appendix table S1). We also conducted four daily camp scans at staggered time intervals based on spot observation techniques (SI appendix figure S4). We categorized each individual's activity at the allocated time, separating hunting, fishing, foraging, wage labor and cultivation. Thus, we can quantify the proportion of time individuals spent in foraging activities versus cultivation and wage labor. Finally we recorded key features of the camp and its changing composition as we visited each camp two to three times (depending on whether it had dissolved into new camps).

These data created the 'transition' variables which were broken into: a) *camp sedentarization* measured by *i*) *camp housing type* (temporary, semi-permanent or permanent), *ii*) a binary *sedentarized camp* variable denoted by the presence of church and/or water pump and *iii*) *out-of-camp mobility* between three visits, 0 representing camp abandonment, 0.5 when 50% of individuals remained and 1 when no one leaves; b) *household mobility* established by whether an individual moved camp or not during two years of fieldwork; c) *household belongings* a emic based list of common objects; and d) *household foraging*, a binary variable in which 1 equals when mothers spent more than 75% of food production activities in foraging compared to those who spend more time in cultivation and wage labor. Due to multicollinearity, only one of the variables in the *camp sedentarization* group was entered into each model, chosen by the lowest AIC in univariate regressions. White blood cell composition analysis was conducted on HemoCue® WBC DIFF and we collected fecal samples from 30 individuals with intestinal parasites symptoms. Further information and descriptive statistics for these variables can be found in SI appendix tables S2 and S3. Logistic and linear multilevel models (MLM) were conducted in R version 3.1.2 (92) using the lme4 package (93). All models were originally run with level 1 as the individual, level 2 as the household and level 3 as the camp. Levels that failed to improve the model were removed to produce the most parsimonious model. Only theoretically informed variables were entered into the model; however, as many variables co-vary, the maximal model suffered from multicollinearity (variance inflation factor scores of more than 2.5 (94)). Therefore, two models were produced, separating *household mobility* from *household foraging*, to correct for any remaining covariance. Otherwise all models contained all appropriate controls (age, sex, mean relatedness and household dependents and belongings) and the best predictor variable for camp sedentarization. As the proportion of each leukocyte is dependent on the circulating levels of other leukocytes, whether an individual had abnormally high levels of any white blood cell types was controlled for as well as total white blood cell count in each analysis. Due to the smaller sample size, non-parametric Kruskal-Wallis tests were used to examine the data on polyparasitic infections. All model betas are reported in text alongside standard errors. This research and fieldwork was approved by UCL Ethics Committee (UCL Ethics code 3086/003) and carried out with permission from local government and tribal leaders in Palanan. Informed consent was obtained from all participants, and parents signed the informed consents for their children (after group and individual consultation and explanation of the research objectives in the Agta language). As part of the process, people identified as having any disease were provided with medical care in partnership with the local government.

Acknowledgements

This project was funded by the Leverhulme Trust grant RP2011-R-045 to A.B.M., R.M. also received funding from European Research Council Advanced Grant AdG 249347. We thank the Human Evolutionary Ecology and Hunter-Gatherer groups at UCL and Matt Thomas for their comments on earlier drafts, the three reviewers for their constructive critique, our assistants in the Philippines, and most importantly, the Agta.

References

1. Bar-Yosef O, Meadow RH (1995) The origins of agriculture in the near east. *Last Hunters-First Farmers*, eds Price D, Gebauer AB (School of American Research Press, Santa Fe), pp 39–94.
2. Bollongino R, et al. (2013) Stone Age Central Europe. *Science (80)* 342:479–481.
3. Piperno D, Pearsall DM (1998) *The origins of agriculture in the Lowland Neotropics* (Academic Press, London).
4. Price DT, Gebauer AB (1995) New perspectives on the transition to agriculture. *Last Hunters-First Farmers*, eds Price DT, Gebauer AB (School of American Research Press, Santa Fe), pp 3–20.
5. Richerson PJ, Boyd R, Bettinger RL (2001) Was Agriculture Impossible during the Pleistocene but Mandatory during the Holocene ? A Climate Change Hypothesis. *Am Antiq* 66(3):387–411.
6. Cohen MN, Crane-Kramer GMM (2007) *Ancient Health: Skeletal indicators of agricultural and economic intensification* (University Press of Florida, Gainesville).
7. Hayden B (1995) A new overview of domestication. *Last Hunters-First Farmers*, eds Price D, Gebauer AB (School of American Research Press, Santa Fe), pp 215–242.
8. Bocquet- Appel J, Naji S (2006) Testing the Hypothesis of a Worldwide Neolithic Demographic Transition: Corroboration from American Cemeteries. *Curr Anthropol* 47(2):341–365.
9. Starling AP, Stock JT (2007) Dental indicators of health and stress in early Egyptian and Nubian agriculturalists: A difficult transition and gradual recovery. *Am J Phys Anthropol* 134(4):520–528.
10. Herrera E (2000) Metabolic adaptations in pregnancy and their implications for the availability of substrates to the fetus. *Eur J Clin Nutr* 54 Suppl 1:S47–S51.
11. Wells JCK, Stock JT (2007) The biology of the colonizing ape. *Yearb Phys Anthropol* 50:191–222.
12. Bandy MS (2005) New World settlement evidence for a two-stage Neolithic Demographic

Transition. *Curr Anthropol* 46(S):S109–S115.

13. Bellwood P, Oxenham M (2008) The expansions of farming societies and the role of the Neolithic Demographic Transition. *The Neolithic Demographic Transition and Its Consequences*, eds Bocquet- Appel J, Bar-Yosef O (Springer, London), pp 13–34.
14. Downey SS, Bocaege E, Kerig T, Edinborough K, Shennan S (2014) The Neolithic Demographic Transition in Europe: Correlation with Juvenility Index Supports Interpretation of the Summed Calibrated Radiocarbon Date Probability Distribution (SCDPD) as a Valid Demographic Proxy. *PLoS One* 9(8):e105730.
15. Hershkovitz I, Gopher A (2008) Demographic, Biological and Cultural Aspects of the Neolithic revolution: A view from the southern Levant. *The Neolithic Demographic Transition and Its Consequences*, eds Bocquet- Appel J, Bar-Yosef O (Springer, London), pp 441–482.
16. Willis A, Oxenham MF (2013) The neolithic demographic transition and oral health: The Southeast Asian experience. *Am J Phys Anthropol* 152(2):197–208.
17. Zahid HJ, Robinson E, Kelly RL (2015) Agriculture, population growth, and statistical analysis of the radiocarbon record. *PNAS*:1517650112.
18. Armelagos GJ, Goodman AH, Harper KN, Blakey ML (2009) Enamel hypoplasia and early mortality: Bioarcheological support for the Barker hypothesis. *Evol Anthropol* 18(6):261–271.
19. Cohen MN, Armelagos GJ (1984) *Paleopathology at the Origins of Agriculture* (Academic Press, Gainesville).
20. Cohen MN (1989) *Health and the rise of civilisation* (Yale University Press, London).
21. Kohler TA, Varien MD (2010) A Scale Model of Seven Hundred Years of Farming Settlements in Southwestern Colorado. *Becoming Villagers*, eds Bandy MS, Fox JR (University of Arizona Press, Tucson), pp 37–61.
22. Richards MP (2002) A brief review of the archaeological evidence for Palaeolithic and Neolithic subsistence. *Eur J Clin Nutr* 56(12):16
23. Hershkovitz I, et al. (2008) Detection and molecular characterization of 9000-year-old Mycobacterium tuberculosis from a neolithic settlement in the Eastern mediterranean. *PLoS One* 3(10):1–6.
24. Greenblatt CL, Spigelman M (2003) *Emerging pathogens: archaeology, ecology and evolution of infectious disease* eds Greenblatt CL, Spigelman M (Oxford University Press, Oxford).
25. Rasmussen S, et al. (2015) Early Divergent Strains of Yersinia pestis in Eurasia 5,000 Years Ago. *Cell* 163(3):571–582.
26. Mathieson I, et al. (2015) Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* advance on.
27. Pechenkina E A., Benfer R a., Zhijun W (2002) Diet and health changes at the end of the Chinese Neolithic: The Yangshao/Longshan transition in Shaanxi province. *Am J Phys Anthropol* 117(1):15–36.
28. Danford ME, Jacobi KP, Wrobel GD, Glassman S (2007) Health and the transition to Horticulture in the south-central United States. *Ancient Health: Skeletal Indicators of Agricultural and Economic Intensification.*, eds Cohen MN, Crane-Kramer GMM (University Press of Florida, Gainesville), pp 65–79.
29. Barrett R, Kuzawa CW, McDade T, Armelagos GJ (1998) Emerging and re-emerging infectious diseases: The Third Epidemiologic Transition. *Annu Rev Anthropol* 27(1):247–271.
30. Cockburn TA (1977) Infectious Diseases in Ancient Populations. *Culture, Disease and Healing. Studies in Medical Anthropology.*, ed Landy D (Macmillan Publishing, New York), pp 83–96.
31. Froment A (2014) Human Biology and Health of African Rainforest Inhabitants. *Hunter-Gatherers of the Congo Basin: Cultures, Histories and Biology of African Pygmies*, ed Hewlett BS (Transaction Publishers, London), pp 117–164.
32. Jackson J a., Friberg IM, Little S, Bradley JE (2009) Review series on helminths, immune modulation and the hygiene hypothesis. *Immunology* 126(1):18–27.
33. Leles D, et al. (2010) A parasitological paradox: Why is ascarid infection so rare in the prehistoric Americas? *J Archaeol Sci* 37(7):1510–1520.
34. Bethony J, et al. (2006) Soil-transmitted helminth infections: ascariasis, trichuriasis, and hookworm. *Lancet* 367(9521):1521–1532.
35. Dounias E, Froment A (2006) When forest-based hunter-gatherers become sedentary: Consequences for diet and health. *Unasylva* 57:26–33.
36. Hotez PJ, Bethony J, Bottazzi ME, Brooker S, Buss P (2005) Hookworm: "The great infection of mankind." *PLoS Med* 2:0187–0191.
37. Hurtado a. M, Frey MA, Hurtado I, Hill KR, Baker J (2008) The role of helminthes in human evolution. *Medicine and Evolution: Current Applications, Future Prospects*, eds Elton S, O'Higgins P (CRC Press, London), pp 153–180.

38. Van Blerkom LM (2003) Role of Viruses in Human Evolution. *Am J Phys Anthropol* 122:14–46.
39. Rook GAW (2009) Review series on helminths, immune modulation and the hygiene hypothesis: The broader implications of the hygiene hypothesis. *Immunology* 126(1):3–11.
40. Stearns SC (2012) Evolutionary medicine: its scope, interest and potential. *Proc R Soc B Biol Sci* 279(1746):4305–4321.
41. Hugot JP, Reinhard KJ, Gardner SL, Morand S (1999) Human enterobiasis in evolution: origin, specificity and transmission. *Parasite* 6(3):201–8.
42. Reinhard K, Ambler JR, Mcguffie M (1985) Diet and Parasitism at Dust Devil cave. *Am Antiq* 50(4):819–824.
43. Reinhard KJ, Araujo A (2012) Synthesining parasitology with archaeology in paleopathology. *The Global History of Paleapathology*, eds Buikstra JE, Roberts C (Oxford University Press, Oxford), pp 751–764.
44. Reinhard KJ (1988) Cultural ecology of prehistoric parasitism on the Colorado Plateau as evidenced by coprology. *Am J Phys Anthropol* 77(3):355–366.
45. Santoro C, Dorsey Vinton S, Reinhard KJ (2003) Inca Expansion and Parasitism in the Lluta Valley: Preliminary Data. *Mem Inst Oswaldo Cruz* 98:161–163.
46. Cohen MN (2009) Introduction: Rethinking the Origins of Agriculture. *Curr Anthropol* 50(5):591–595.
47. Hutchinson DL, Norr L, Teaford MF (2007) Outer Coast Foragers and Inner Coast Farmers in Late Prehistoric North Carolina. *Ancient Health: Skeletal Indicators of Agricultural and Economic Intensification.*, eds Cohen MN, Crane-Kramer GMM (University Press of Florida, Gainesville), pp 52–64.
48. Pinhasi R, Stock JT (2011) *Human Bioarchaeology of the Transition to Agriculture*.
49. Douglas MT (2006) Subsistence change and dental health in the people of Non Nok Tha, northeast Thailand. *Bioarchaeology of Southeast Asia*, eds Oxenham MF, Tayles N (Cambridge University Press, Cambridge), pp 191–219.
50. Humphrey LT, et al. (2014) Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-gatherers from Morocco. *Proc Natl Acad Sci* 111(3):954–959.
51. Lukacs JR (1992) Dental paleopathology and agricultural intensification in south Asia: new evidence from Bronze Age Harappa. *Am J Phys Anthropol* 87(2):133–150.
52. Oxenham MF, Tayles N (2006) Synthesising Southeast Asian population history and palaeohealth. *Bioarchaeology of Southeast Asia*, eds Oxenham MF, Tayles N (Cambridge University Press, Cambridge), pp 335–349.
53. Oxenham MF, Nguyen LC, Nguyen KD (2008) Oral health in northern Vietnam. *Bull Indo-Pacific Prehist Assoc* 22:121–134.
54. Pietrusewsky M, Ikehara-Quebral R (2007) The bioarchaeology of the Vat Kommou cemetry, Angkor Borei, Cambodia. *Bull Indo-Pacific Prehist Assoc* 26:86–97.
55. Tayles N, Domett KM, Halcrow S (2009) Can dental caries be interpreted as evidence of farming? The Asian experience. *Comparative Dental Morpohology*, eds Koppe T, Meyer G, Alt KW (Karger, Basel), pp 162–166.
56. Walker P, Hewlett B (1990) Dental health diet and social status among Central African foragers and farmers. *Am Anthropol* 92(2):383–398.
57. Diamond J (2002) Evolution, consequences and future of plant and animal domestication. *Nature* 418(6898):700–7.
58. Lambert PM (2009) Health versus fitness: competing themes in the origins and spread of agriculture? *Curr Anthropol* 50(5):603–608.
59. Borgerhoff Mulder M (2000) Optimizing Offspring: The Quantity-Quality Trade-off in Agropastoral Kipsigis. *Evol Hum Behav* 21(6):391–410.
60. Draper P, Hames R (2000) Birth order, sibling investment, and fertility among Ju/'Hoansi (!Kung). *Hum Nat* 11(2):117–156.
61. Gillespie DO., Russell AF, Lummaa V (2008) When fecundity does not equal fitness: evidence of an offspring quantity versus quality trade-off in pre-industrial humans. *Proc R Soc B Biol Sci* 275(1635):713–722.
62. Hagen EH, Barrett HC, Price ME (2006) Do human parents face a quantity-quality tradeoff?: Evidence from a shuar community. *Am J Phys Anthropol* 130:405–418.
63. Hill K, Hurtado AM (1996) *Aché Life History: The Ecology and Demography of a Foraging People* (Aldine de Gruyter, New Haven).
64. Lawson DW, Alvergne A., Gibson M. (2012) The life-history trade-off between fertility and child survival. *Proc R Soc B Biol Sci* 279(1748):4755–4764.
65. Minter T (2010) The Agta of the Northern Sierra Madre. Dissertation (Leiden University).
66. Rai NK (1990) *Living in a lean-to: Philippine Negrito foragers in transition* (University of Michigan, Ann Arbor).

67. Peterson JT (1978) *The Ecology of Social Boundaries: Agta Foragers of the Philippines* (University of Illinois Press, London).
68. Kelly RL (2013) *The Lifeways of Hunter-Gatherers: The Foraging Specturm* (Cambridge University Press, Cambridge).
69. Early JD, Headland TN (1998) *Population Dynamics of a Philippine Rain Forest People: The San Ildefonso Agta* (University Press of Florida, Gainesville).
70. Norrby E, Kovamees J, Blixenkrone-Moller M, Sharma B, Orvell C (1992) Humanized animal viruses with special reference to the primate adaptation to morbillivirus. *Vet Microbiol* 33:275–286.
71. McDade TW, et al. (2005) Predictors of C-reactive protein in Tsimane' 2 to 15 year-olds in lowland Bolivia. *Am J Phys Anthropol* 128(4):906–913.
72. Hurrell RF (2003) Influence of vegetable protein sources on trace element and mineral bioavailability. *J Nutr* 133(9):2973S–7S.
73. Mcdonell A, Oxenham MF (2014) Localised Primary Canine Hypoplasia: Implications for Maternal and Infant Health at Man Bac, Vietnam, 4000-3500years BP. *Int J Osteoarchaeol* 24(4):531–539.
74. Who (2012) WHO Children reducing mortality. *WHO Media Cent*:1.
75. Mascie-Taylor CGN (1993) The Biological Anthropology of Disease. *The Anthropology of Disease*, ed Mascie-Taylor CGN (Oxford University Press, Oxford), pp 1–72.
76. Cooper PJ (2004) Intestinal worms and human allergy. *Parasite Immunol* 26(11-12):455–467.
77. Tanner S, et al. (2009) Influence of helminth infections on childhood nutritional status in lowland Bolivia. *Am J Hum Biol* 21(5):651–656.
78. London D, Hruschka D (2014) Helminths and human ancestral immune ecology: What is the evidence for high helminth loads among foragers? *Am J Hum Biol* 26:124–129.
79. Jelliffe DB (1962) The Children of the Hadza Hunters. *Trop Pediatr* 60:907–913.
80. Confalonieri U, Ferreira LF, Araujo A (1991) Intestinal Helminths in Lowland South American Indians: Some Evolutionary Interpretations. *Hum Biol* 63(6):863–873.
81. Gonçalves MLC, Araújo A, Ferreira LF (2003) Human Intestinal Parasites in the Past: New Findings and a Review. *Mem Inst Oswaldo Cruz* 98(SUPPL. 1):103–118.
82. Sprent JFA (1969) Helminth "zoonoses": an analysis. *Helminthol Abstr* 38:333–351.
83. Armelagos GJ, Harper KN (2005) Genomics at the Origins of Agriculture. *Evol Anthropol* 14:109–121.
84. Sreevatsan S, et al. (1997) Restricted structural gene polymorphism in the Mycobacterium tuberculosis complex indicates evolutionarily recent global dissemination. *Proc Natl Acad Sci U S A* 94(18):9869–74.
85. Bentley GR, Jasienska G, Goldberg T (1993) Is the Fertility Higher Than Agriculturalists That of Nonagriculturalists ?'. *Curr Anthropol* 34(5):778–785.
86. Sellen D, Mace R (1997) Fertility and mode of subsistence: a phylogenetic analysis. *Curr Anthropol* 3(5):878–889.
87. Blurton Jones N (1987) Bushman birth spacing: Direct tests of some simple predictions. *Ethol Sociobiol* 8(3):183–203.
88. Hardy K, Brand-Miller JC, Brown KD, Thomas MG, Copeland L (2015) The importance of dietary carbohydrate in human evolution. *Q Rev Biol* 90(3):251–268.
89. Tracer D (1991) Fertility related changes in maternal body composition among the Au of Papua New Guinea. *Am J Phys Anthropol* 85(4):393–406.
90. Kramer KL, Boone JL (2002) Why Intensive Agriculturalists Have Higher Fertility: A household energy budget approach. *Curr Anthropol* 43(3):511–517.
91. Gibson M, Mace R (2005) Helpful grandmothers in rural Ethiopia: A study of the effect of kin on child survival and growth. *Evol Hum Behav* 26(6):469–482.
92. R Core Team (2012) R: A language and environment for statistical computing.
93. Bates D, Bolker B, Maechler M, Walker S (2013) lme4 R Package.
94. Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1(1):3–14.
95. Griffin PB, Griffin MB (1992) Fathers and Childcare among the Cagayan Agta. *Father-Child Relations: Cultural and Biosocial Contexts*, ed Hewlett BS (Transaction, New Brunswick), pp 297–320.
96. Bion GP, B.Griffin M (1997) Agta Foragers. *Aust J Anthropol* 8:259.
97. Headland TN (1989) Population Decline in a Philippine Negrito Hunter-Gatherer Society. *Am J Hum Biol* 72:59–72.
98. Dyble M, et al. (2015) Sex equality can explain the unique social structure of hunter-gatherer bands. *Science* 348(6236):796–798.
99. Griffin BM (2012) The Cultural Identity of Foragers and the Agta of Palanan, Isabela the Philippines. *Anthropos* 91(1996):111–123.

100. Estioko-Griffin AA, Griffin PB (1981) The beginning of cultivation among Agta hunter-gatherers in Northeast Luzon. *Adaptive Strategies and Change in Philippine Swidden-Based Societies*, ed Olofsen H (Forest Research Institute, Laguna), pp 55–72.
101. Griffin PB (1985) A contemporary view of the shift from hunting to horticulture. *Recent Advances in Indo-Pacific Prehistory*, eds Misra VN, Bellwood P (IBH Publishing, New Delhi), pp 349–352.
102. Headland TN, et al. (1989) Hunter-Gatherers and Their Neighbors from to the Prehistory Present. *Curr Anthropol* 30:43–66.
103. Headland TN (1984) Agta Negritos of the Philippines. *Cult Surv Q* 8(3):29–31.
104. Dounias E, Froment a. (2011) From foraging to farming among present-day forest hunter-gatherers: consequences on diet and health. *Int For Rev* 13(3):294–304.
105. Morris SS, et al. (1999) Precision, accuracy, and reliability of hemoglobin assessment with use of capillary blood. *Am J Clin Nutr* 69(6):1243–1248.
106. Greer PJ, et al. (2013) *Wintrobes Clinical Hemaology* (Lippincott Williams & Wilkins). Thirteenth.
107. Beck N (2008) *Diagnostic Hematology* (Springer, London).
108. van Assendelft OW (2002) Calibration, control of hematology analyzers. *Adv Adm Lab* 22:43–47.
109. Mitaishvili R (2010) *The Human Blood: Composition, Typing, Lab Test Interpretation* (RM Global Health).
110. Wahed A, Dasgupta A (2015) *Hematology and Coagulations: A Comprehensive Review for Board Preparation, Certification and Clinical Practice.* (Elsevier, London).
111. Bentley S, Johnson A, Bishop C (1993) A parallel evaluation of four automated hematology analyzers. *Am J Clin Pathol* 100:626–632.

Figure legends

Figure 1: Correlation plot for six key predictor variables (*n* = 345). Positive correlations are marked in blue shades, negative in red shades. All correlations are statistically significant at $p < 0.05$. Variables are: settled camp (number of permanent structures within a camp); wealth (an index quantifying household belongings); mobility (whether an individual was ever witnessed to move camp over a two year period, 0 = never moved); turnover (number of people leaving a camp); and foraging (proportion of food that individuals acquired from foraging activities versus food production and wage labor).

Figure 2: Relationship between measures of transition and age-specific fertility, mortality and reproductive success (RS) separated by a) individual settlement status and b) degree of foraging. Error bars represent standard errors of the mean and *n* = 90.