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

3

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13

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36 **Abstract**

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

51

52 **Significance statement**

53

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

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73 **Introduction**

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

82

83 On the other hand, studies reveal significant increases in morbidity and mortality associated with  
84 reduction in dietary breadth and sedentarization (6, 18–22). Research reveals increased prevalence  
85 of tuberculosis, syphilis and the plague (6, 23–25), overall immunological stress (26) and a  
86 deterioration in oral health (16, 27, 28). Farming led to higher population densities,  
87 sedentarization, increased contact with neighboring populations, presence of rodents attracted by  
88 food stores, domestication and fecal pollution (29–31). All those factors facilitated virulent  
89 bacterial and viral pathogens as well as soil-borne helminths (roundworm, hookworm and  
90 whipworm (32–38)). While some argue that Paleolithic foragers experienced high helminths loads  
91 (37, 39, 40), archaeological data shows instead an increase in helminths associated with farming  
92 (33, 41–45) compared to mobile, low-density hunter-gatherers. In summary, the overall effect of  
93 agriculture on health was a trend towards increasing morbidity and mortality (16, 19, 28, 46),  
94 although its intensity exhibits some regional variation and inconsistent trends (47–56)).

95

96 Given this significant increase in disease burden, why farming arose independently and expanded  
97 in diverse geographical regions (57, 58) remains a puzzle. Here we propose that settled  
98 agriculture was accompanied by a life history trade-off, whereby mothers switch strategy to invest  
99 in offspring quantity rather than quality and thereby increase their reproductive fitness. A  
100 quantity-quality trade-off is an adaptive process based on a principle of optimal distribution of  
101 limited resources: parents must either allocate finite resources to a few higher quality offspring or  
102 to multiple lower quality ones (59–64). By proposing that a quantity-quality trade-off provides an  
103 explanation for the transition to agriculture, we provide an adaptive mechanism that reconciles  
104 the decline in population health with increases in mortality during the Neolithic transition. We  
105 test this hypothesis with data from extant Palanan Agta foragers in the Philippines (hence forth  
106 referred to as Agta), a diverse group varying in mobility, foraging, wealth accumulation and camp  
107 permanence; traits all attributed to the Neolithic revolution (1, 3, 6, 7). Residing completely  
108 within the Northern Sierra Madre Natural Park the Palanan Agta have remained mostly separated

109 from other Agta populations who reside outside the park limits and further south in Casiguran  
110 (65–67). By measuring fertility, mortality alongside viral, bacterial and helminth markers in  
111 different Agta camps, we found that sedentarization is associated with increased morbidity and  
112 mortality, yet both sedentarization and involvement in non-foraging activities are both associated  
113 with even further increases in fertility, resulting in higher reproductive fitness. Our results  
114 provide evidence that a quality-quantity trade-off was adaptive and suggests a pathway through  
115 which, despite poor health, farming could have become the dominant subsistence system after its  
116 origin in the Neolithic. Thus, we demonstrate how exploring the mechanisms that lead extant  
117 foragers to seek increased settlement and food production is a theoretically informative approach  
118 to test key archaeological predictions (6, 8, 19).

119

## 120 **Results**

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

129

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

141

142 ***Settled Agta exhibit increased fertility.*** The total fertility rate (TFR) among the Agta based on  
143 41 live births in 2013-2014 was 7.7, one of the highest reported in foragers (68). For 117 women  
144 we interviewed (aged between 16-75 years), the mean number of live births was 4.4 (ranging from  
145 0 to 13). Residuals from a linear regression of offspring count and maternal age, including a

146 logarithmic term, were used to control for age effects on fertility and reproductive success, while  
147 an exponential term was included for child mortality (see SI appendix). Settled mothers had  
148 significantly higher fertility than women who moved camp at least once ( $\beta = 1.3 \pm 0.6, p =$   
149  $0.04$ ). Correspondingly, increases in household belongings were positively associated with  
150 fertility ( $\beta = 0.5 + 0.2, p = 0.005$ ). This relationship is further confirmed by examining TFR:  
151 settled mothers had 16.7% higher TFR (7.7) compared to mobile mothers TFR (6.6). Similarly,  
152 for all live births settled mothers had 20.5% more offspring (5.3) than mobile mothers (4.4; SI  
153 appendix table S6). A possible pathway may be that settled mothers are able to accumulate more  
154 somatic resources for reproduction. Accordingly, settlement was a significant predictor of  
155 maternal BMI (i.e. mothers never witness to move camp,  $\beta = 1.7 \pm 0.6, p = 0.004$ ), and BMI  
156 positively predicts fertility ( $\beta = 0.3 \pm 0.1, p = 0.02$ ).

157

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

165

166 ***Sedentarization is associated with health deterioration.*** We examined the effects of  
167 cultivation and sedentarization on three white blood cell types – lymphocytes, neutrophils and  
168 eosinophils - as proxies for different immunological attacks: viral, bacterial and helminthic,  
169 respectively (see SI appendix). Our sample consisted of 345 Agta, 140 of which were adults  
170 (48.6% males) and 205 children under 16 (60% males). Due to inconclusive test results missing  
171 data reduced the sample to 293, consisting of 117 adults (47% males) and 176 children (59%  
172 males). Table 1 shows that people in large camps with low out-of-camp mobility had 2.8 times  
173 higher chances of presenting with lymphocytosis compared to mobile camps. People residing in  
174 camps with permanent and semi-permanent houses had significantly higher eosinophil  
175 concentrations than individuals in temporary camps. Severe eosinophilia ( $>5 \times 10^9/L$ ) is  
176 indicative of extreme helminth infestations and only found in sedentarized camps. In contrast,  
177 people residing in sedentarized camps with some form of infrastructure (i.e. church or water  
178 pump) had lower odds (by 80%) of neutrophilia. One major bacterial disease among the Agta is  
179 *Mycobacterium tuberculosis* (TB), demonstrated by the fact that 41.7% of the 24 individuals suffering  
180 from neutrophilia had clinically diagnosed or suspected TB. In contrast, percentage of time  
181 spent foraging had little effect on health. Individuals in households who foraged more had a 76%  
182 reduction in odds of presenting with lymphocytosis than households who foraged less. However,

183 indicators of helminthic or bacterial infections were not affected by percentage of time spent  
184 foraging (SI appendix tables S11-13).

185

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

199

200 ***Child mortality is increased in settled camps.*** We examined whether the negative effects of  
201 settlement on health also extended to child mortality rates (including all post-natal deaths until  
202 age 16). Out of 520 reported live births from 124 mothers, 19% of children died before age one,  
203 13.9% from one to five and 6% from five to fifteen years. Those rates are lower than the 28-29%  
204 previously reported for neighboring Agta (65, 69). Mothers residing in camps with permanent  
205 housing experienced significantly higher childhood mortality rates, compared to mothers living in  
206 camps with temporary housing ( $\beta = 0.7 \pm 0.3$ ,  $p = 0.005$ ). The relationship for semi-permanent  
207 camps was in the same direction but of marginal significance ( $\beta = 0.5 \pm 0.3$ ,  $p = 0.08$ ). This  
208 relationship results in a 63.2% increase in mortality rates for settled mothers living in  
209 sedentarized camps (0.93) when compared to nomadic mothers in temporary camps (0.57). Thus,  
210 the sedentarized camps with the highest helminth and viral disease rates also experience the  
211 highest childhood mortality rates. Following the morbidity results, proportion of time spent in  
212 cultivation had no significant relationship with child mortality ( $\beta = 0.01 \pm 0.04$ ,  $p = 0.8$ ).

213

214 ***A quantity-quality trade-off explains higher reproductive success in transitioning Agta.***  
215 Our results show that women who settle down trade child survival for fertility, increasing their  
216 overall reproductive success (Figure 2a). Settled women ( $\beta = 0.8 \pm 0.4$ ,  $p = 0.03$ ) had significantly  
217 more children surviving to age 16 (our measure of reproductive fitness) than mobile women.  
218 Although these settled women faced higher child mortality rates, they also experienced extremely  
219 high fertility. As a result of the negative morbidity effect of sedentarized camps compared to the

220 positive fertility effect of settled households, women residing in permanent camps suffered lower  
221 child survival ( $\beta = -1.2 \pm 0.5, p = 0.01$ ) compared to temporary camps, once household mobility  
222 has been controlled for. Figure 2a demonstrates that mobile women living in sedentarized camps  
223 faced the worst situation as they experienced both higher mortality rates associated with  
224 permanent camps and the lower fertility rates associated with high mobility. Thus, they  
225 experienced 0.73 lower fitness, given their age. Overall, our results show that settled mothers, in  
226 spite of the higher mortality rates, had an extra 0.59 offspring (4.4) surviving to age 16 compared  
227 to mobile women (3.8), a relative increase of 15.8% in reproductive fitness.

228

229 Our other indicator of 'transition', the percentage of time involved in foraging, also predicted  
230 reproductive success ( $\beta = -1.2 \pm 0.6, p = 0.05$ ). We find that mothers who foraged more than  
231 75% of the time had 0.74 less children surviving to age 16 given their age, while mothers who  
232 spent less time foraging experienced 0.04 more children surviving to age 16 (figure 2b). Thus,  
233 while abandoning foraging does not significantly affect child mortality rates, it does increase  
234 fertility, and consequently mother's reproductive success. Consequently, while cultivation is  
235 associated with increased fertility, sedentarization is associated with both increased fertility and  
236 increased morbidity and mortality. The overall consequence of this combined process is a  
237 reproductive trade-off where settled mothers involved in cultivation have the highest  
238 reproductive fitness, despite increased morbidity and mortality.

239

## 240 **Discussion**

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

253

254 Our data indicates that sedentarization was associated with increased risk of infectious  
255 disease. Viral infections were higher in the larger, less mobile camps, with increased cultivation.  
256 Camp size and population density (measured here through out-of-camp mobility) were



257 significantly correlated with viral infections in our data. This follows expectations of transmission  
258 of viruses such as *Caliciviruses* and *Rotoviruses*, causing gastroenteritis and influenza (38), both  
259 common among settled Agta and dependent on higher population densities (70). This mirrors  
260 the finding of increased risk of high C-reactive protein concentrations (indicative of an  
261 inflammatory response) in children among more acculturated Tsimane forager-horticulturalists  
262 (71). In particular, cultivation may independently predict increased viral load (indicated by the  
263 association between lymphocytosis and foraging) due to poorer nutritional quality of agricultural  
264 staples. Increased consumption of rice with cultivation entails a loss of dietary breadth and  
265 macro- and micro-nutritional quality (72, 73) leading to malnutrition, which is a significant  
266 predictor of disease and mortality (74).

267

268 As with viral infections, Agta living in more permanent camps (as predicted by camp housing  
269 type) were also worse off in terms of helminthic infections, matching theoretical predictions (29,  
270 33, 43, 44, 75). Contrary to this, some studies have argued the high helminth burden was a major  
271 selective pressure before the Neolithic (37, 39, 76) due to extreme helminth rates in many semi-  
272 sedentarized, farmer-foragers (31, 37, 77). However, these groups are no longer fully  
273 mobile. Supporting our interpretation and findings, researchers observed a near absence of  
274 helminths in an isolated Amazonian group (78), Hadza children (79) and lower helminth loads  
275 among isolated and mobile Saluma and Yanomama groups (80). While some parasitic species  
276 were hosted by our hominid ancestors (29, 81, 82), there is little archaeological evidence for an  
277 extreme intestinal parasite burden predating agriculture (33, 41–43, 45, 81). Thus, increased viral  
278 and helminth burdens are costs associated with sedentarization. It should be noted that settled  
279 Agta did not, however show an increased incidence of neutrophilia, which in our sample is often  
280 caused by TB. Chronic bacterial infections, such as TB, have evolved to survive at low  
281 population densities, thus likely predate agriculture (83, 84). The lower incidence of neutrophilia  
282 in settled Agta camps is likely due to the limited access to medical care, which might also explain  
283 the finding that cash labor decreased helminth loads by 37.4%. Since westernized medicine is a  
284 recent occurrence, the overall increased helminthic load in sedentarized camps may be  
285 underestimating the effect that settlement had on human populations during the Neolithic  
286 transition.

287

288 We found that more permanent camps had significantly higher childhood mortality rates,  
289 matching archaeological evidence from the Neolithic (6). Our results also revealed significantly  
290 higher fertility rates in settled women, particularly those transitioning from foraging to  
291 cultivation. Agriculture has been associated with fertility increases (85, 86) as the reduction in  
292 energy expenditure with settlement (87) and increased carbohydrate consumption (10, 88) are  
293 associated with increased BMI, which correlates with shorter inter-birth intervals and higher

294 fertility (89). This suggests a pathway through which increased cultivation could lead to increased  
295 fertility. An additional pathway, as suggested by Kramer and Boone (90), considers the increased  
296 economic productivity of children in agriculture which reduces maternal constraints and thus,  
297 increases her fertility. Our study remains correlative, which leaves unanswered the question of  
298 the causal direction between fertility, sedentarization and food production. Since sedentarization  
299 correlates with food production in the Agta, with more sedentarized households abandoning  
300 foraging, it seems that these two process are interdependent, and thus are treated here as part of  
301 a process that involved a cluster of ‘transition’ traits. This is likely to be the case for the Neolithic  
302 transition as well, as many have reported the interplay between sedentarization and food  
303 production leading to the demographic changes associated in the origins of agriculture (4, 7).  
304 Further limitations stem from using a cross-sectional study design to explore longer-term trends,  
305 thus, it is unclear to what degree sedentism is reflective of mobility trends beyond our two-year  
306 sample period. However, a cross-sectional study design does permit the exploration of intra-  
307 population variability without requiring this variability to be recent or unilineal. Furthermore,  
308 foraging and mobility behaviors are likely altered during the heavy rainy and typhoon season not  
309 captured here as data collection occurred during the dry period. However, this does mean there is  
310 no systemic temporal bias in the data as camps were visited within the same season. Finally, more  
311 detailed dietary data would be required to explore these questions in more depth, allowing us to  
312 better separate the effects of ‘transition’.

313

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

322

### 323 **Methods**

324 Data collection occurred over two field seasons from April to June 2013 and February to  
325 October 2014 during the Isabela dry season. There are around 1,000 Agta living in Palanan  
326 municipality, Isabela Province, located in northeastern Luzon. The Agta are primarily fisher-  
327 foragers, residing either at the coast or inland watersheds. Hunting does occur, however fishing is  
328 far more common: out of 2168 work activities 54% were spent fishing, 20% gathering and 3%  
329 hunting. The remaining ‘non-foraging’ activities consist of cultivation (13.5%) and wage labor  
330 (9.5%). There is, however significant variance in diet (Figure S1) and activities between

331 households: mobile households spent only 3.5% of their work activities in cultivation and 0% of  
332 time in wage labor. Comparatively, settled households spend 11.6% and 10% of their work  
333 activities in cultivation and wage labor, respectively. We found 26% Agta moved camp at least  
334 once during our fieldwork, resulting in an average camp move of once every 10 days. Similarly,  
335 the degree of camp sedentarization varies drastically as some camps change daily and consists of  
336 temporary shelters while others consist of permanent wooden structures built around churches  
337 and cultivation plots. Some Agta living in permanent camps closer to town have limited access to  
338 medical care and government provisioning. However, the effects of these sporadic interventions  
339 on the Agta health are limited (see SI appendix for further ethnographic description). We stayed  
340 around 14 days in each of the 13 camps and conducted reproductive histories to quantify  
341 demographics and interviews to produce an index of household belongings. After creating an  
342 emic-sourced list of ‘important’ belongings we asked each household whether they had each of  
343 the 14 objects, and if so how many. This was then weighted based on how many times each item  
344 were mentioned (SI appendix table S1). We also conducted four daily camp scans at staggered  
345 time intervals based on spot observation techniques (SI appendix figure S4). We categorized each  
346 individual’s activity at the allocated time, separating hunting, fishing, foraging, wage labor and  
347 cultivation. Thus, we can quantify the proportion of time individuals spent in foraging activities  
348 versus cultivation and wage labor. Finally we recorded key features of the camp and its changing  
349 composition as we visited each camp two to three times (depending on whether it had dissolved  
350 into new camps).

351

352 These data created the ‘transition’ variables which were broken into: a) *camp sedentarization*  
353 measured by *i) camp housing type* (temporary, semi-permanent or permanent), *ii) a binary sedentarized*  
354 *camp* variable denoted by the presence of church and/or water pump and *iii) out-of-camp mobility*  
355 between three visits, 0 representing camp abandonment, 0.5 when 50% of individuals remained  
356 and 1 when no one leaves; b) *household mobility* established by whether an individual moved camp  
357 or not during two years of fieldwork; c) *household belongings* a emic based list of common objects;  
358 and d) *household foraging*, a binary variable in which 1 equals when mothers spent more than 75%  
359 of food production activities in foraging compared to those who spend more time in cultivation  
360 and wage labor. Due to multicollinearity, only one of the variables in the *camp sedentarization* group  
361 was entered into each model, chosen by the lowest AIC in univariate regressions. White blood  
362 cell composition analysis was conducted on HemoCue® WBC DIFF and we collected fecal  
363 samples from 30 individuals with intestinal parasites symptoms. Further information and  
364 descriptive statistics for these variables can be found in SI appendix tables S2 and S3. Logistic  
365 and linear multilevel models (MLM) were conducted in R version 3.1.2 (92) using the lme4  
366 package (93). All models were originally run with level 1 as the individual, level 2 as the  
367 household and level 3 as the camp. Levels that failed to improve the model were removed to

368 produce the most parsimonious model. Only theoretically informed variables were entered into  
369 the model; however, as many variables co-vary, the maximal model suffered from  
370 multicollinearity (variance inflation factor scores of more than 2.5 (94)). Therefore, two models  
371 were produced, separating *household mobility* from *household foraging*, to correct for any remaining  
372 covariance. Otherwise all models contained all appropriate controls (age, sex, mean relatedness  
373 and household dependents and belongings) and the best predictor variable for camp  
374 sedentarization. As the proportion of each leukocyte is dependent on the circulating levels of  
375 other leukocytes, whether an individual had abnormally high levels of any white blood cell types  
376 was controlled for as well as total white blood cell count in each analysis. Due to the smaller  
377 sample size, non-parametric Kruskal-Wallis tests were used to examine the data on polyparasitic  
378 infections. All model betas are reported in text alongside standard errors. This research and  
379 fieldwork was approved by UCL Ethics Committee (UCL Ethics code 3086/003) and carried out  
380 with permission from local government and tribal leaders in Palanan. Informed consent was  
381 obtained from all participants, and parents signed the informed consents for their children (after  
382 group and individual consultation and explanation of the research objectives in the Agta  
383 language). As part of the process, people identified as having any disease were provided with  
384 medical care in partnership with the local government.

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391

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### 618 **Figure legends**

619 **Figure 1:** Correlation plot for six key predictor variables ( $n = 345$ ). Positive correlations are marked in blue  
620 shades, negative in red shades. All correlations are statistically significant at  $p < 0.05$ . Variables are: settled  
621 camp (number of permanent structures within a camp); wealth (an index quantifying household  
622 belongings); mobility (whether an individual was ever witnessed to move camp over a two year period, 0 =  
623 never moved); turnover (number of people leaving a camp); and foraging (proportion of food that  
624 individuals acquired from foraging activities versus food production and wage labor).  
625

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