

RESEARCH PAPER



The ex-pat effect: presence of recent Western immigrants is associated with changes in age at first birth and birth rate in a Maya population from rural Guatemala

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ABSTRACT

Background: Economic transitions expose indigenous populations to a variety of ecological and cultural challenges, especially regarding diet and stress. These kinds of challenges are predicted by evolutionary ecological theory to have fitness consequences (differential reproduction) and, indeed, are often associated with changes in fertility dynamics. It is currently unclear whether international immigration might impact the nature of such an economic transition or its consequences for fertility.

Aim: To examine measures of fertility, diet and stress in two economically transitioning Maya villages in Guatemala that have been differentially exposed to immigration by Westerners.

Subjects and methods: This study compared Maya women's ages at first birth and birth rates between villages and investigated whether these fertility indicators changed through time. It also explored whether the villages differed in relation to diet and/or a proxy of stress.

Results: It was found that, in the village directly impacted by immigration, first births occurred earlier, but birth rate was slower. In both villages, over the sampled time window, age at first birth increased, while birth rate decreased. The villages do not differ significantly in dietary indicators, but the immigration-affected village scored higher on the stress proxy.

Conclusion: Immigration can affect fertility in host communities. This relationship between immigration and fertility dynamics may be partly attributable to stress, but this possibility should be evaluated prospectively in future research.

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Introduction

For many indigenous peoples, increased interaction with urban centres and integration into regional, national or global market economies is associated with changes in cultural identity and knowledge, as well as in patterns of learning (Berry, 2008; Godoy et al., 2005; Peña, 2005). Such changes are often associated with increases in socioeconomic inequality and psychosocial stress (Hill et al., 2010; Paradies, 2006a). At the same time, participation in wage labour and market economies increases access to mass-produced foodstuffs, which are often energy-dense and long-lasting, but nutrient-poor (Cordain et al., 2005). In turn, these kinds of changes can impact reproductive patterns and have demographic effects (e.g. Ellison, 1995; Lagranja et al., 2015; McSweeney & Arps, 2005; Nag et al., 1980; Vitzthum, 2009).

In particular, both increased stress and increased availability of calories can lead to increased adiposity during development, through adulthood, and even across generations (Hanson & Gluckman, 2014; Wells, 2006, 2012). Adiposity, in turn, is one of the most important predictors of the timing of key life history events for girls and women. Specifically,

variation in adiposity deposition is associated with variation in girls' age at menarche and girls'/women's age at first birth and lengths of subsequent inter-birth intervals (IBIs) (Ellison et al., 1993; Frisch, 1974, 1975; Frisch & Revelle, 1971; Vallengia & Ellison, 2001, 2004, 2009; Wells, 2006; Worthman et al., 1993; Yermachenko & Dvornyk, 2014). These variables directly affect fertility, because women who begin giving birth earlier and who space births closer together are likely to have more children over the courses of their lives (Ellison 2008; Ellison et al., 1993; Frisch, 1975). Notably, both adiposity deposition patterns and the scheduling of women's life history events are closely correlated with numerous health measures, with excess adiposity and high fertility generally associated with worse overall health outcomes for both women and their children (Heerwagen et al., 2010).

Given the potential demographic and health consequences of rapid market integration for indigenous peoples, it is important that we understand the extent to and ways in which such development may impact reproductive biology (Stephens et al., 2006). Such understanding can be used in the development of long-term public policy pertaining to

health and education tailored to the size, structure, and cultural ecology of a transitioning population (Gracey & King, 2009; King et al., 2009; Mowbray, 2007). Currently, however, there are a number of gaps in our understanding of the cultural ecology of indigenous demography during economic transition.

One problem that warrants attention is that we have not yet been able to discriminate between the two main evolutionary hypotheses put forward to explain fertility increases in indigenous populations undergoing socioeconomic transition (Sear et al., 2016; Snopkowski & Kaplan, 2014; Snopkowski et al., 2016). The first of these can be called the 'energy access hypothesis'. It assumes that fertility increases associated with increased market integration are the result of more energetically-abundant conditions, enabled by increases in access to calorie-dense foods and sedentism, and the introduction of labour saving technology (Ellison, 2008; Kramer, 2005; Kramer & Ellison, 2010). This hypothesis is based on the observations that: (1) increases in somatic energy stores during ontogeny are associated with earlier sexual maturity, earlier marriage, and earlier first conception and birth (Frisch, 1974, 1984; Frisch & Revelle, 1971; Nettle, 2010; Walker et al., 2006) and (2) increases in energy stored as fat in adulthood facilitates earlier resumption of ovarian function after giving birth, and thus shorter IBIs (Ellison et al., 1993; Vallenggia & Ellison, 2001, 2004, 2009; Vitzthum, 2009; Worthman et al., 1993). In keeping with this view, a number of human biology field projects focusing on indigenous populations in transition have provided evidence that increased market integration is associated with increased energy access, surplus somatic energy and increased fertility (e.g. Kramer, 2005, 2017; Lanza & Vallenggia, 2014; Mcallister et al., 2012). However, there are also cases where it is less clear-cut that energy access is the main driver of fertility changes related to market integration (e.g. see Migliano, 2005). This suggests that other, non-energy-related factors should also be considered.

The other main evolutionary hypothesis offered to explain high fertility in indigenous populations, especially those in economic transition, is the 'live fast–die young hypothesis' (Charnov & Berrigan, 1993, see also Coall et al., 2016; Gawlik et al., 2011; Migliano, 2005; Migliano et al., 2007, 2010; Quinlan, 2007; Walker et al. 2006). Unlike the energy access hypothesis, the live fast–die young hypothesis assumes that the emergence of markers of increased fertility (e.g. younger age at first birth) is driven by poor conditions. It holds that indicators of high extrinsic morbidity and mortality (stressors) should cue women to reproduce as early and as often as possible before death or severe illness forecloses all reproductive opportunities, independent of energy availability (Coall et al., 2016; Walker et al., 2006). Mechanistically, the hypothalamic-pituitary-adrenal axis (HPAA) is responsible for hormonally disrupting or terminating linear somatic growth (Tsigos & Chrousos, 2002), in effect switching allocation of limited energy from growth to reproductive readiness. In line with this, Gawlik et al. (2011) found in a sample of 22 indigenous human populations that IBI was shorter in population-dense environments assumed to be stressful nutritionally and psychosocially. Similarly, a number of studies have found

that indigenous populations undergoing socioeconomic transition are often characterised by high psychosocial stress, early age at first birth, young age structure, and high fertility (e.g. Kramer, 2017; Kramer & Greaves, 2017; Moisan et al., 2016, see also Bombay et al., 2009, 2011, 2014 regarding stress and psychometric outcomes). However, while these results are intriguing, most of the relevant studies have not adequately accounted for energy availability and consumption, so the energy access hypothesis cannot be ruled out (see Becker et al., 2010 for a critique of the work of Migliano and colleagues). Moreover, there is a need for work that investigates the role of both energy and stress—which are mechanistically related to one another via HPAA function—in mediating the relationship between market integration and demographic change.

Another unresolved issue concerning the demographic impacts of socioeconomic transition is how market integration results in demographic change. Formal models and some preliminary evidence suggest that a change in cultural learning processes may be an important part of the picture (Snopkowski & Kaplan, 2014; Snopkowski et al., 2016). There is reason to think that the source from which an idea or behaviour is obtained influences its likelihood, rate, and extent of uptake (Broesch & Hadley, 2012; Henrich & Gil-White, 2001; Richerson & Boyd, 2005). For example, several laboratory studies indicate that a source's prestige, power, and similarity to self affect whether or not an idea or behaviour will be adopted (e.g. Chudek & Henrich, 2011; Chudek et al., 2012; Mesoudi et al. 2006). One implication of this is that *who* indigenous people interact with while undergoing socioeconomic transition may affect the scale and pace of change. However, previous work has examined only a relatively narrow range of sources of cultural information. These studies have focused on cases in which market integration has involved interaction between rural and urban people from the same state (Kramer, 2017; Kramer & Greaves, 2017, e.g. Lanza & Vallenggia, 2014; Mcallister et al., 2012; Vallenggia & Lanza 2007, Veile & Kramer, 2015; Veile et al., 2014). Based on the aforementioned laboratory findings, we might expect Westerners, who are often viewed as prestigious (given their access to relative wealth and power), to have different impacts. Currently, we do not know whether this is the case, because no studies have been conducted in circumstances in which the main cultural learning sources are from the West. While some previously studied populations have been missionized, in these cases, missionization long preceded demographic study (e.g. the Argentinian Toba, described in Vallenggia & Lanza, 2007).

To begin to address these gaps in the literature, we report a study that examined fertility markers in relation to both stress and nutritional ecology in an indigenous population that is currently undergoing rapid socioeconomic change. The study population lives in an area that has a relatively large number of recent Western immigrants, who bring with them substantial economic resources. Specifically, we carried out our work with a population of indigenous Maya people from rural Guatemala. Sub-sets of the study population have been differentially exposed to a wave of immigration by North Americans and Europeans that began in the wake of

the 30-year-long Guatemalan civil war, which ended in 1996. We took advantage of this fact in designing the study. We compared indigenous women from a village that had been directly affected by Western immigration to indigenous women from a village that had only been indirectly affected by Western immigration, as of the time the data reported here were collected. Thus, the study can be thought of as a natural experiment.

The study had two main aims. One was to assess whether economic change and increasing market integration related to Western immigration is associated with changes in life history variables in Maya women. The markers we focused on were age at first birth and reported number of live births. The other aim was to assess whether the energy access hypothesis (diet) or the live fast-die young hypothesis (stress) accounts for any observed impacts of immigration on the life history variables. To this end, we evaluated two predictions. The first was that Maya people living close to Western immigrants would be more likely to show signs of eating a calorie-rich, nutrient-poor diet. The second prediction was that Maya interacting more extensively with the Westerners would exhibit stronger indicators of psychosocial stress, resulting from higher levels of socioeconomic inequality and a faster rate of culture change.

Subjects and methods

Sample

The data were collected as part of an on-going, long-term field study led by PN called 'Society, Environment, and Reproduction (SER)'. SER investigates the ecology, demography, economy, and health of indigenous Maya women, men, and children living in two villages in the Department of Sololá in Guatemala's Central Highlands.

The two study villages, hereafter Village A and Village B, are part of a municipality of five villages that collectively house ~4200 people, according to the 2002 census (Herrington, 2010). Both villages are situated in mountainous terrain at ~1500 metres above sea level, and are a short walk from the edge of a large, freshwater lake (Atyeo et al., 2017; Herrington, 2010). The villages were somewhat isolated, but not inaccessible, as of the time data were collected for this study (Berry, 2010; Nepomnaschy, 2005).

Villages A and B are very similar genealogically, culturally, and linguistically (Berry, 2010; Nepomnaschy, 2005). As of the time the data reported in this study were collected (2013), there were, however, differences between the two villages in terms of economy and structure of the labour force. These appear to relate to proximity to, and interaction with, immigrants from North America and Europe, who began arriving in the region in relatively large numbers in the late 1990s, following the end of the civil war (Berry, 2010).

Village A remained relatively economically and socially insulated from the Western immigrants, as of 2013. Related to this insulation, the majority of families in Village A lived primarily traditional, subsistence-level lives, owning or leasing land to raise chickens and to grow corn, beans, coffee, and vegetables and fruit for household consumption. A little over

one third of families from this village made regular trips to market in nearby cities to sell surplus produce. Only ~15% of male heads of household engaged in non-farm-related wage labour such as construction, taxi-driving, and shop-keeping (unpublished data).

The economic situation in Village B was rather different by 2013. As of the time of data collection, a growing community of North American and European immigrants had been based within a kilometre of the village for ~15 years. This immigrant community has employed and continues to employ many locals from Village B in wage labour, has attracted increasing numbers of tourists to the area, and has also invested in educational, health, and other infrastructure in and around the village. One consequence of this is that a relatively small proportion of families in Village B operate at subsistence level. Thirty-one per cent of households surveyed did not engage in any cultivation of crops for subsistence or sale by 2013 (unpublished data). Additionally, 59% of male household-heads were employed in trades or other kinds of non-farm-related labour for large portions of the year. Lastly, Village B was and is more densely populated than Village A, with many villagers reporting living in small compounds with insufficient space for cultivation or husbandry (Berry, 2010).

During the period of study, fertility was generally 'natural' in Village A, with only ~22% of surveyed women reporting or inferred (from unpublished endocrinological and birth spacing data) to be using or to have at any time used any form of contraception. On average, women from this village gave birth to 8.2 children by the end of their reproductive career, and had 6.8 children who had survived until at least age 5 years. By the end of the study period, ~45% of women in Village B reported and/or can be inferred to have been using reliable forms of contraception. The average number of births by reproductive senescence in Village B was 6.7, which is substantially lower than in Village A. On average, mothers at the end of their reproductive career in Village B had 6.2 children who had survived until at least age 5 years (unpublished data).

As of 2013, diets in both villages were heavily corn-based, with corn tortillas and corn porridges providing the majority of calories for surveyed individuals (Mckerracher et al. in unpublished data). Importantly, sometime between the early 2000s and 2013, imported rice, oatmeal, and wheat products (e.g. breads, noodles, instant porridges) also began to make substantial caloric contributions to diets in many households, and our general impression was that imported foodstuffs were eaten more frequently in Village B than A. Protein derives mainly from beans, eggs from husbanded chickens, and, traditionally, small fish and invertebrates from the lake. Locally-grown fruits, vegetables and herbs yield dietary fibre and a range of micronutrients.

Data collection

We used interview, biomolecular, and anthropometric data collected from 89 parous (i.e. having given birth at least once was requisite for participation in the study), Kakchiquel-speaking Maya women from the two study villages. The data

pertain to the women, as well as their husbands ($n = 83$) and their children ($n = 428$). This sub-set of SER participants were recruited because longitudinal demographic and anthropometric data were available for them.

All participants provided written or thumb-printed consent before commencement of the study, and all were made aware in both Spanish and Kakchiquel that they had the right to withdraw at any point during the study. The data collection protocol was approved by Simon Fraser University's Research Ethics Board (study # 2012so668).

The interviews used in this particular study were carried out in 2013. Each participant was interviewed about the demographic and economic composition of her household. Trained local field-assistants conducted the interviews in Kakchiquel. Field-assistants translated participant responses on the fly and recorded them in Spanish. Our team then translated the Spanish responses to English in preparation for coding and analysis. We assessed the quality of Spanish–English translations using a standard translation-back translation method for a 10% sub-sample, and did not discover any meaningful discrepancies between the Spanish and English responses.

Anthropometric data (height and weight) were collected monthly throughout 1999–2000 and in a single session in 2013. All measurements were taken three times per observation session and then averaged. Observations regarding weight for participants known to be pregnant at the time of measurement were excluded, because pregnancy weights are unlikely to reflect weight gain patterns related to the variables of interest for this study—namely, inter-individual and inter-village variation in energy access.

Biomolecular data concern ratios of rare stable isotopes of carbon and nitrogen relative to more common ones, hereafter expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Such stable isotope data can be used to coarsely estimate the proportion of a person's bulk dietary protein derived from tropical grasses relative to other plant foods (in the case of $\delta^{13}\text{C}$) and the proportion of bulk dietary protein derived from a particular trophic level (in the case of $\delta^{15}\text{N}$, Schwarcz & Schoeninger, 1991). The isotope data were obtained in 2013 through collection and analysis of fingernail samples from participating women. Details on nail sample collection, preparation, and measurement are available in the Supplementary materials (S1).

Data management and statistical analyses

The final dataset comprises information on 11 variables for all 89 participating mothers and their children. These include two outcome demographic variables and nine variables related to immigration, energy access, and psychosocial stress.

The two outcome variables are:

1. mother's age (years) when she first gave birth (hereafter, age at first birth); and
2. mother's reported number of live births relative to her number of childbearing years at the time of study (hereafter, birth rate).

The nine explanatory (and control) variables are:

1. village (A or B), a geographic proxy for proximity to and interaction with North American and European immigrants;
2. year in which a mother first gave birth, a temporal proxy for proximity to and interaction with North American and European immigrants during a mother's development and/or reproductive career;
3. participant's height (cm);
4. participant's weight (kg) in 1999–2000 and in 2013, used in conjunction with height in 2013 and mother's and children's ages to calculate four proxies for availability of energy-dense foods (details on calculation of subsidiary variables available in the Supplementary materials (S2)):
 - a. participant's body mass index (BMI) in 2000;
 - b. participant's BMI in 2013;
 - c. participant's average annual weight gain (kg); and
 - d. participant's estimated weight at the time of her first conception, assuming a constant annual rate of weight gain;
5. participant's self-reported overall health in 2013, assessed on a five-point Likert scale: 1 = very poor, 5 = very good;
6. participant's age (years);
7. participant's $\delta^{13}\text{C}$ value;
8. participant's $\delta^{15}\text{N}$ value; and
9. whether or not the participant reported or was inferred to have ever used contraception.

We carried out three sets of analyses. In the first, we compared mean age at first birth and birth rate between villages using the linear and Poisson regression models, respectively. We also visually inspected plots of variation in age at first birth and observed birth rate by village through time, marked by year of first birth. In the second set of analyses, we used a linear regression model to describe age at first birth as a function of village and mother's year of first birth, and a Poisson regression model to describe mean number of live births as a function of village, mother's year of first birth, and whether or not the mother had reported ever using or been inferred to have ever used any form of contraception. In the latter model, we treated the length of her observed reproductive career (age in 2013 minus her age at first birth, unless she was post-menopausal, in which case we used 45 minus her age at first birth) as exposure time, and included an appropriate offset term in the model. In the third and final set of analyses, we used the Wilcoxon ranked sum test and the t -test (depending on the proximity of the variable's distribution to the normal distribution) to compare village means for our indicators of energy access (BMI in 2000, BMI in 2013, average annual weight gain, estimated weight at the time of first conception, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$) and for our indicator of contemporary psychosocial stress (self-reported overall health in 2013).

The study was conducted with the aid of Excel and R's stat and ggplot2 packages (R Development Core Team, 2014; Wickham, 2009).

Results

Variation in ages at first birth and birth rate

Age at first birth ranges from 14–28 years for the full sample, with a mean of 19.5 years, a median of 19 years, and an interquartile range of 18–21 years. Observed birth rate ranges from 0.125–0.769 children per year, with mean and median values of 0.328 and 0.299, respectively.

Unadjusted comparisons of mean ages at first birth and birth rate between villages and through time

The results of the first set of analyses are summarised in Table 1 and Figures 1 and 2. Age at first birth in Village A ranged from 15–25 years, whereas this variable ranged from 14–22 years in Village B. Mean age at first birth in Village A between 1980 and 2001 was 20.0 (SE = ±0.30), whereas mean age at first birth in Village B across this time period was 18.3 (±0.38). This difference is highly significant ($p = .001$). The linear effect of year of first birth on age at first birth was significant and positive (Figure 1(a)). We also fit village-specific loess curves to the same plot. These curves visually suggest that average age at first birth may have decreased and then increased sharply in Village B during the mid-1990s, while Village A did not experience any oscillations in age at first birth during this time period (Figure 1(b)). A larger

sample size would be required to confirm these deviations from the assumed linear trend.

The mean observed birth rate was 0.34 (SE = ±0.018, range = 0.13–0.77) in Village A and 0.26 (SE = ±0.019, range = 0.14–0.64) in Village B ($p = .001$) during the study period, indicating that, on average, the birth rate was higher in Village A than in Village B. The effect of year of first birth on birth rate was significant and negative, indicating that fertility may have decreased in both villages during the time period of interest (Figure 2(a)). The loess curves tentatively hint that birth rate in Village B may have decreased sharply through the 1990s and then begun to increase thereafter (Figure 2(b)). Again, additional data would be needed to confirm these patterns.

Full models for variation in age at first birth and birth rate

The full model for age at first birth is summarised in Table 2. Living in Village A and giving birth for the first time at a later point in time were both associated with later ages at first birth.

The full model for birth rate is summarised in Table 3. Living in Village B and giving birth for the first time at a later point in time were both associated with lower birth rates. There was no evidence that birth rate was associated with reported/inferred contraceptive use.

Comparison of indicators of energy access and stress between villages

Table 4 summarises the findings of the second set of analyses pertaining to inter-village differences in indicators of diet/energy and psychosocial stress. The means for BMI in 2000, BMI in 2013, average annual weight gain, and mean predicted weight at the time of first conception did not differ

Table 1. Summary of comparison of fertility indicators between Villages A and B.

Fertility indicator	Mean (SE)		p
	Village A	Village B	
Age at first birth	20.6 (±0.30)	18.3 (±0.38)	.001**
Birth rate	0.36 (±0.02)	0.27 (±0.02)	.001**

*** $p > .001$, ** $p > .010$, * $p > .05$, $p > .1$

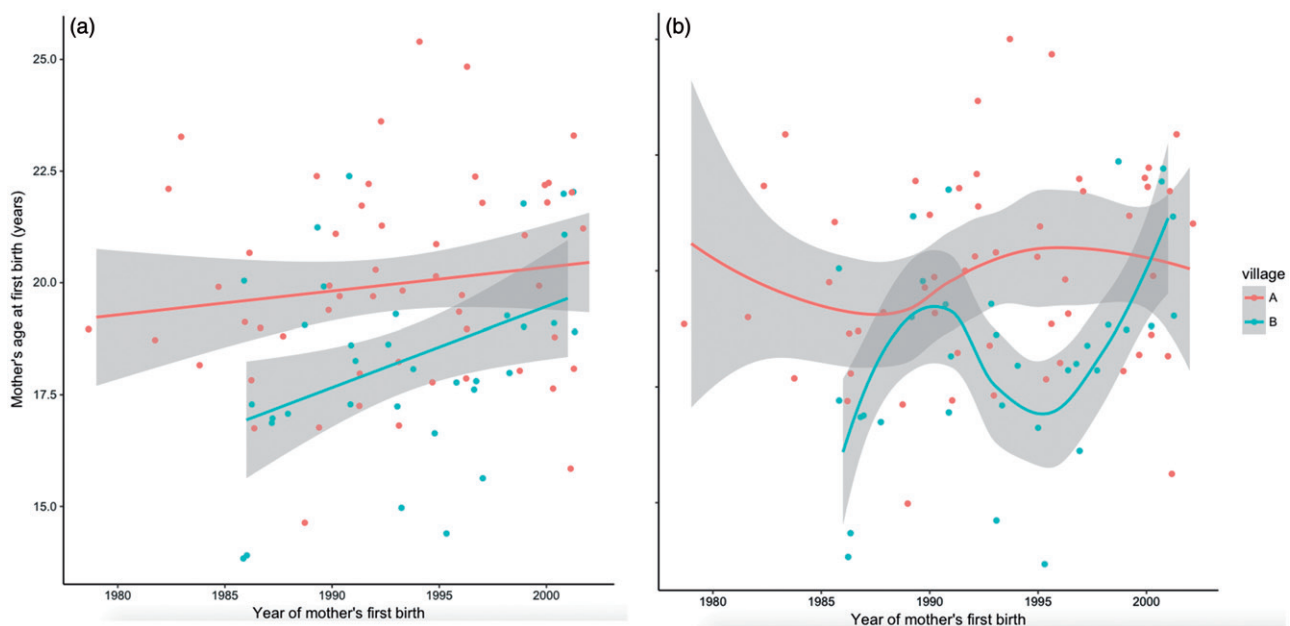


Figure 1. Mother's age at first birth as a function of year of mother's first birth, (a) with a linear trend and (b) with Loess curves and 95% CIs fit for each village.

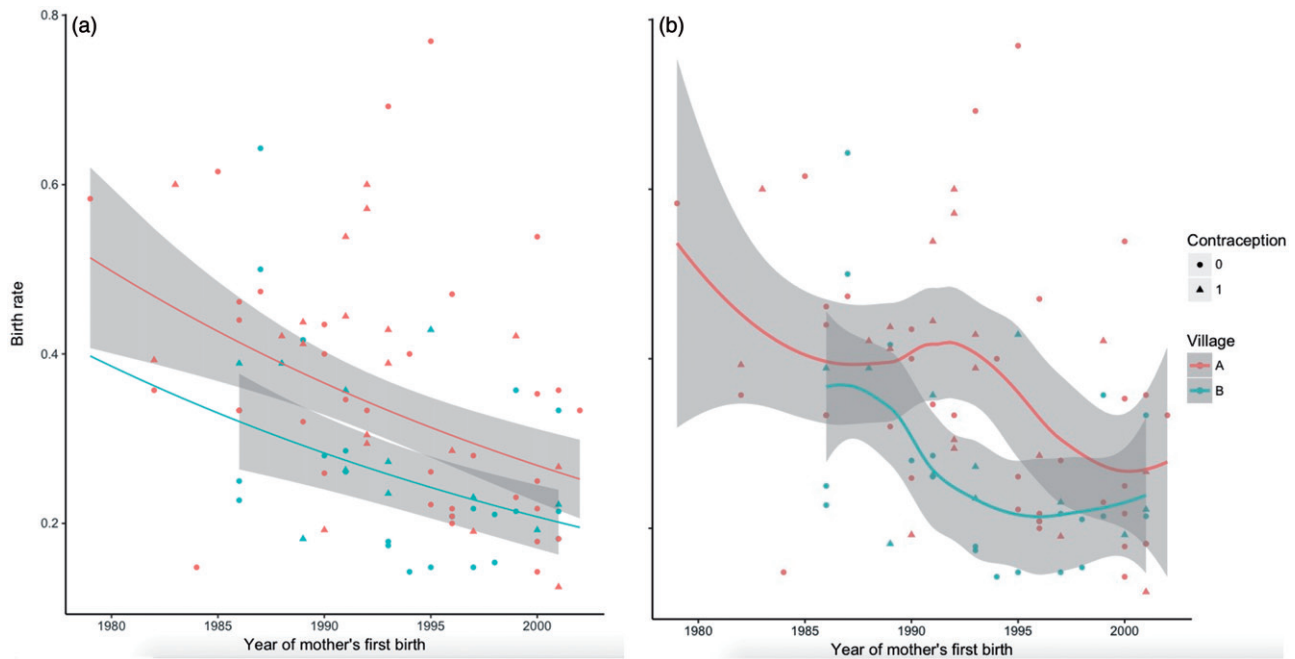


Figure 2. Birth rate as a function of year of mother's first birth, (a) with Poisson curves and (b) with Loess curves and 95% CIs fit for each village.

Table 2. Summary of linear regression results evaluating the relationships between mother's age at first birth, village, and the year in which she first gave birth.

Predictor	Estimate	95% CI	<i>p</i>
Village B	−1.74	−2.67 to −0.80	.000***
Year of first birth	0.09	0.01 to 0.18	.028*

****p* > .001, ***p* > .010, **p* > .05, *p* > .1

Table 3. Summary of the Poisson regression results evaluating the relationships between mother's live birth rate, village, the year in which she first gave birth, and whether or not she has likely ever used any contraception.

Predictor	Estimate	95% CI	<i>p</i>
Village B	−0.25	−0.43 to −0.07	.006**
Year of first birth	−0.03	−0.05 to −0.02	.000
Contraception use	0.10	−0.07 to 0.27	.255

****p* > .001, ***p* > .010, **p* > .05, *p* > .1

Table 4. Summary of comparison of ecological (diet and stress) proxy indicators between Villages A and B.

Ecological (energy or stress) indicator	Mean (SE)		<i>p</i>
	Village A	Village B	
BMI 2000	22.0 (0.46)	21.5 (0.45)	.444
BMI 2013	25.1 (0.64)	26.7 (0.69)	.112
Average annual weight gain (kg)	0.64 (0.08)	0.80 (0.09)	.198
Predicted weight at time of first conception	41.3 (4.40)	41.7 (5.07)	.866
$\delta^{13}\text{C}$	−13.4 (0.11)	−13.0 (0.19)	.134
$\delta^{15}\text{N}$	8.4 (0.06)	8.4 (0.08)	.462
Self-reported overall health	2.5 (0.14)	2.0 (0.11)	.002**

****p* > .001, ***p* > .010, **p* > .05, *p* > .1

between villages ($p > .1$ in all cases). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ also did not differ between villages (again, $p > .1$ in all cases). In contrast, self-reported overall health was lower in Village B (2.0) than in Village A (2.5; $p = .002$). This relationship held after adjusting for two obvious potential confounders, mother's age and BMI in 2013.

Discussion

Summary of main findings

We compared two Maya villages in rural Guatemala in relation to two fertility-related variables—the timing of age at first birth and number of births per woman per reproductive lifespan year (birth rate). There has been substantial growth in immigration by Europeans and North Americans to the region since the end of the Guatemalan civil war in 1996 (Moreno & Littrell, 2001), but the two study villages (A and B) have not been equally exposed to the influx of Westerners. Villagers from Village B have interacted with immigrants from North America and Europe far more extensively and directly than have villagers from Village A. Furthermore, Village B shows clear signs of recent economic and infrastructural change (e.g. a newly upgraded and fully-staffed health post, a small vocational school) related to its proximity to the Western immigrant community. From both theory and previous empirical studies of transitioning indigenous populations, we predicted that through-time and inter-village differences in immigration history would have affected age at first birth and birth rate. Previous research indicates that any changes in fertility we observed would most likely be driven via impacts of immigration on energy access and/or psychosocial stress, not withstanding any cultural changes related to contraception.

Our results were mixed. As predicted, we found that there were systematic differences in age at first birth between the two villages in the expected direction. Women from Village B generally begin their reproductive careers earlier than women from Village A. However, contrary to our initial expectations, women from Village A generally give birth at faster rates than women from Village B once they have begun their reproductive careers. Furthermore, we found that fertility generally appears to have decreased in both

villages, and that the fertility decline may have begun earlier in Village B.

The results we obtained in relation to the variables related to diet and/or stress were also mixed. We found no evidence of differences between the two villages in the dietary/energy variables. However, we did find that our proxy for stress—self-reported overall health—differed significantly between the two villages, with women from Village A generally reporting better health than women from Village B.

Taken together, these findings suggest that immigration by Westerners has led to biologically meaningful changes in key demographic markers such as age at first birth and birth rate in the indigenous host population. The analyses reported here do not offer any clear support for the hypothesis that these changes are driven by changes in access to energy. Rather, they could be interpreted as being broadly consistent with the stress-focused ‘live fast–die young’ hypothesis, which holds that high extrinsic mortality and stress drive accelerated reproductive strategies.

Limitations of study

There is reason to be cautious when interpreting the results of this study. In particular, there may be concerns with the reliability and accuracy of the recall-based interview data, the coarseness and inter-relatedness of our measures of diet/energy and psychosocial stress with each other and with fertility, and the small size and non-randomness of our sample of participants. We discuss each of these in turn.

Our main outcome variables—age at first birth and birth rate—rely on participant’s ability to recall their children’s ages. Age determination can be challenging in non-Western populations such as the study population, since birthdays are generally not marked (e.g. Blurton-Jones, 2016; Goodman et al., 1985; Hill & Hurtado, 1996; Howell, 1979, 2010; Marlowe, 2010; Migliano et al., 2007). However, this seems unlikely to be a major issue for this study. Participants were asked to report their own ages; reported ages were later crosschecked by examining government-issued birth records of participating mothers. In all but one case, participants reported their own ages accurately. This suggests they can be relied on to recall and report the ages of their children accurately. Furthermore, 34 known-age children of participating mothers were involved in a separate study by Nepomnaschy et al. (2014), and the mothers accurately reported these children’s ages in years, suggesting that the women in this population can recall their fertility histories by year. So, while it is possible that some women may have made errors in recall, we think these errors are unlikely to be frequent or large enough to affect any overall patterns in the data.

Two other potential problems with the interview data concern contraceptive use. Sex and contraception are generally regarded as taboo subjects among rural Guatemalan Maya peoples (Berry, 2010; Ward & Pauc, 2003), suggesting that under-reporting may impede our understanding of changing fertility dynamics in the study population. With this in mind, we adjusted not only for self-reported contraceptive

use in our models, but also counted women who had both unusually long IBIs and unusually flat hormonal profiles during the 1999–2001 field season as probable long-term contraceptive users. Making this statistical adjustment did not have any significant effect on our main results, suggesting that the trends we observed are unlikely to be mainly due to contraceptive use. The second contraception-related problem, however, is a more complicated one. Previous work on other Latin American populations indicates that there can be considerable lag-time between when a population, a village, or even an individual is introduced to a new contraceptive technology and when that technology begins to be used effectively (Paxman et al., 1993). So, it is possible that a non-trivial number of the women who reported having used contraception may have, in fact, been misusing it. We do not yet have data of sufficiently fine grain to investigate this possibility further. In the meantime, though, we suggest that our approach in which we adjusted for any possible contraceptive use introduces a conservative bias against the main predictions of the hypotheses we evaluated. We nevertheless recommend that future work: (1) corrects for contraceptive use by longitudinally tracking women’s hormonal profiles through multiple time points; and (2) directly investigates the possible role of lag-time in cultural learning of contraceptive technologies in driving proximate, short-term fertility trends.

Turning now to the coarseness of our measures of energy and nutrient access, BMI, average annual weight gain, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ may each reflect a range of inputs other than current diet. In particular, environmental exposures during early development, pregnancy and lactation history, age, reproductive career stage, and chronic inflammation are known to influence BMI and weight gain patterns (McDade, 2003, 2005; Valeggia & Ellison, 2004, 2009; Wells, 2006; Worthman et al., 1993). Protein metabolism (anabolism vs catabolism) appears to affect $\delta^{15}\text{N}$ and may also influence $\delta^{13}\text{C}$ (D’Ortenzio et al., 2015; Fuller et al., 2004, 2006; Mekota et al., 2006). Thus, it may be that we did not find differences in mean values for these variables between villages, because the variables are not reflecting energy access, but rather other variables related to reproduction and energy balance. However, previous work in other indigenous populations undergoing nutritional ecological transitions have used fewer or coarser indicators and have observed variation in them among villages or sub-sets of a population (Hedges et al., 2009; Lanza et al., 2013; Mcallister et al., 2012; Nagata et al., 2009; Valeggia et al., 2010). This suggests that the variables are adequate for detecting the effects of interest. Nonetheless, we cannot discount the possibility that energy access does indeed differ between the villages, and that the two groups of women are simply allocating energy differently in ways that makes inter-village differences difficult to detect without longitudinal diet data. As such, future studies should investigate longitudinal inter-village patterns in body size, diet, and diet-related biomolecules in this population and in similar transitioning populations.

Regarding the coarseness of our measure of psychosocial stress—self-reported overall health—we acknowledge that the most compelling approach would be to use a

psychometric instrument specifically designed to assess psychosocial stress, combined with one or more stress biomarkers. Our catchall proxy probably reflects a suite of states related to somatic stress (e.g. nutritional shortfall, disease) and psychological stress (e.g. anxiety). We further acknowledge that a validated approach specifically targeting measurement of psychosocial stress could help circumvent any systematic differences between individuals and/or villages in the ability to articulate concerns about health or wellbeing. That said, meta-analytic studies demonstrate that, across a number of cultural contexts, objective and subjective measures of stress are negatively associated with self-reported overall health (e.g. Cella et al., 2010; Idler & Benyamini, 1997; Miilunpalo et al., 1997; Paradies 2006b). Moreover, despite the coarseness of our measure, we did find differences in health between villages, independent of age and BMI, suggesting the presence of a strong signal detectable through what we assume is heavy noise.

Lastly, there is the size and structure of the sample. To reiterate, we used longitudinal data from women who were recruited randomly in the first field season of a study that was initiated in 1999 and continues to the present. While this means that we have pertinent information from these participants that extends for 12–14 years, it also means that our study does not include any women that conceived for their first time after 2001. As such, our sample is small and biased towards older women. However, we do not think that this undercuts our main results. Rather, size and structure of the sample used likely impose a conservative bias against our main hypotheses regarding village and through-time patterns. That is, the youngest participants in our sample gave birth for the first time in the mid or late 1990s, slightly after the first small wave of Western immigrants began to buy properties in the region but before these Westerners had had opportunity to impact local infrastructure (e.g. before ensuring that the health post in Village B was fully staffed). In spite of this, we detected effects of village and time on the variables of interest. Thus, we are reasonably confident about our main results. That being said, additional work with a sample more representative of the whole population is required before we can assume that the factors that appear to affect variation in age at first birth and birth rate among older women also affect variation in those variables in the general population.

Why might age at first birth and birth rate change with increases in market integration: energy access or stress?

Previous studies of Latin American indigenous populations undergoing socioeconomic transitions have generally shown that fertility increases with increasing market integration, even when reliable forms of contraception are widely available (Casterline & Mendoza, 2009; McSweeney & Arps, 2005). Specifically, data from the Bolivian Tsimane (Leonard et al., 2015; Liebert et al., 2013; Mcallister et al., 2012), the Argentinian Toba (Lagranja et al., 2015; Lanza & Valeggia 2014; Lanza et al., 2013), the Yucatec Maya (Kramer, 2005; Veile & Kramer, 2015), the Venezuelan/Colombian Pumé

(Kramer, 2008, 2017; Kramer & Greaves, 2017), and the Paraguayan Aché (Hill & Hurtado, 1996) indicate that increasing market integration for these populations is associated with markers of increasing energy availability and/or of reduced energetic expenditures. Women in all of these populations appear to convert these energetic surpluses into higher fertility, via reductions in age at menarche, age at first birth, and/or high birth rate across the reproductive lifespan. These patterns align very well with the package of core predictions from one of the two main evolutionary hypotheses put forward to explain why fertility tends to change during or immediately after socioeconomic transition—the energy access hypothesis (Ellison, 2008; Ellison et al., 1993; Valeggia & Ellison, 2001).

While one of our main findings was consistent with this general pattern (age at first birth is younger in the more immigration-impacted and market-integrated village), our other findings differ from those pertaining to the other transitioning indigenous populations studied to date. In particular, we found evidence that pace of reproduction generally slowed for the Kakchiquel-speaking Maya between 1980 and 2013. Additionally, we found no clear evidence of differences in markers of access to or somatic storage of energy between the two villages. Taken together, these findings suggest that a set of factors other than increased energy availability may account for the through-time changes in fertility dynamics we observed for the study population.

As mentioned earlier, the other main evolutionary hypothesis available in the literature to explain why fertility changes in response to socioeconomic change is the live fast–die young hypothesis. To reiterate, this hypothesis holds that the pace of life history (and, thus, the timing of fertility markers) responds to cues of extrinsic mortality risk (i.e. stressors), so as to maximise limited reproductive opportunities before death. At first blush, the findings reported here regarding overall declines in fertility depart from the predictions of the live fast–die young hypothesis. In particular, the hypothesis predicts that age at first birth should drop and birth rate should increase post-immigration/market integration, whereas the data we reported suggest a fertility trend in the opposite direction.

We suggest, however, that what we view as a special case of the live fast–die young hypothesis, the ‘historical trauma hypothesis’, could offer an explanation for our findings (Heart et al., 2011; Sotero, 2006). This hypothesis extends the general proposal of the live fast–die young hypothesis from the individual to the group. It contends that a shock like the introduction of a new infectious disease or a war can cause group-wide stress (Heart et al., 2011; Sotero, 2006). The shock then impacts ontogeny and demography/life history of the entire group. This hypothesis seems to be supported by well-known historical cases of forced assimilation of indigenous populations such as occurred in North America between the 17th and through the 20th centuries (Bombay et al., 2009, 2011, 2014; Heart et al., 2011; Sotero, 2006).

In keeping with this historical trauma hypothesis, all participants from both of the villages in our study underwent some or all of their development during the Guatemalan civil

war, in which hundreds of thousands of Guatemalans, mostly indigenous Maya from the Central Highlands, were killed or 'disappeared', and at least a million people were internally displaced (Rothenberg, 2016). These are conditions of profound psychosocial stress. This seems to be reflected in the overall health data, since participants from both villages generally described their health status as being less than 'fair'. Participants from Village B were subsequently exposed to the arrival of immigrants from a radically different cultural context and to substantial socioeconomic changes. We view this exposure as another possible historically traumatic shock, stacked on top of the shock of the civil war. This second shock could be reflected in the inter-village differences in overall health scores, in which women from Village B generally reported being in 'poor' health, whereas women from Village A generally reported their health as being relatively closer to 'fair'; although we note again that these differences could partly reflect differences in ability to identify and communicate health concerns.

The apparent overall fertility declines also makes sense in light of this historical traumatic shock hypothesis. The hypothesis predicts that fertility should have been unusually high during the war. With this prediction in mind, the decline in average birth rate from one birth every 2 years to one birth every 3 years might partly reflect a return from a during-war high to a pre-shock, peace-time normal.

While these overall health and fertility decline findings are consistent with the historical trauma hypothesis, we lack: data on the fertility patterns prior to the civil war, data that robustly link the historical shocks of interest to indicators of stress, and data that link indicators of stress mechanistically to life history variables across the villages. As such, we can only point to trends in the age at first birth and birth rate data that hint that: (1) birth rates are generally very high in this sample, with the average woman giving birth about seven times over her reproductive lifespan (as we would expect in a population that has experienced a collective stress event), (2) fertility dynamics were changing around the time of the end of the civil war and through the period of time in which Westerners were beginning to arrive in the region in relatively large numbers, and (3) more marked changes occurred in Village B during the time when the Westerners were beginning to arrive (see Figure 1(b)). So, there is an obvious need for further research that prospectively assesses whether there are systematic differences between the two villages with respect to stress levels (preferably assessed through biomolecular markers of stress and/or validated psychosocial stress evaluation tools) and their effects on fertility-related variables.

Immigration, stress, and fertility?

While previous findings concerning fertility changes in socio-economically transitioning indigenous populations have emphasised the role of changing energy access in relation to market integration, our results for the Kakchiquel-speaking Maya tentatively suggest a role for psychosocial stress in mediating the relationships of interest. There are two obvious

differences between the present study and previous ones that may have contributed to this contrast in findings (and their explanations). The first is the background context of civil war which, as discussed above, makes assessing baseline fertility norms for the study population difficult.

The other major difference between this study and previous ones that may account for the differences in findings is in *who* is driving the economic development and increased market integration. The previous studies, which focused on the Tsimane (Leonard et al., 2015; Liebert et al., 2013; Mcallister et al., 2012), the Toba (Lagranja et al. 2015; Lanza & Vallenggia, 2014; Lanza et al., 2013), the Yucatec Maya (Kramer, 2005; Veile & Kramer, 2015), the Pumé (Kramer, 2008, 2017; Kramer & Greaves, 2017) and the Paraguayan Ache (Hill & Hurtado, 1996), investigated the impact of state-driven development, past missionisation and/or development driven by relatively slow, stochastic processes leading to an increased exchange of ideas, people and money between national urbanites and indigenous peoples. In the Kakchiquel Maya case, however, the health post, vocational school, restaurant and other amenities in Village B are currently managed/owned by Western immigrants to the region. That is, the people bringing in cash, ideas and a desire for cheap labour are linguistically, culturally and physically (as far as superficial, phenotypic cues like stature, hair colour, skin colour) very distinct from the indigenous peoples.

North American and European immigrants might influence the speed and intensity with which market integration impacts demography in at least two ways. One is that there may simply be greater differences in wealth between the Western immigrants and the indigenous people than the differences in wealth between the Guatemalan national urbanites that sometimes work in the district and indigenous peoples. There is now substantial evidence supporting the idea that extreme socioeconomic inequality is stressful and deleterious to health, largely independent of energy access and food security (Brunner, 1997; Krieger, 1999). So, the Kakchiquel Maya, in undergoing economic transition driven partly by relatively wealthy international immigrants (in addition to having just emerged from the throes of civil war), may be experiencing more acute psychosocial stress related to inequality than other Latin American indigenous populations in transition. This stress may be, in effect, swamping any effects of nutritional ecology and energy access in this population.

The other main possibility derives from cultural cognition modeling and manipulation studies, which demonstrate that the likelihood of adopting new ideas and behaviours depends in large part on who is introducing them (Broesch & Hadley, 2012; Henrich & Gil-White, 2001; Richerson & Boyd, 2005). Studies indicate that sources of cultural information viewed as prestigious are more likely to be emulated when the potential consequences of an idea or behaviour in a given environment are complex and uncertain (Henrich & Gil-White, 2001; Richerson & Boyd, 2005). Both the future environment and consequences of behaviour in that future environment are highly uncertain in the context of rapid market integration. As such, emulating prestigious individuals may offer an important shortcut to figuring out how to behave in

a new, less subsistence-agriculture-based, more market-integrated ecological context. According to this view, it is possible that the Western immigrants are viewed as relatively more prestigious than Guatemalan national urbanites, and, therefore, drive relatively rapid economic change and cultural loss when compared to other cases of transition in Latin American.

Regardless of whether the mediating factor is wealth or prestige, the data reported here appear to be consistent with the view that socioeconomic-transition-related stress is associated with fertility changes (statistically independent of reported/inferred contraceptive use). In turn, when compared with other Latin American indigenous contexts, it seems plausible that who drives the socioeconomic transition (state institutions and urbanites of the same nationality vs wealthy international immigrants) affects the contribution of stress relative to energy of fertility dynamics.

Conclusion

Immigration by Europeans and North Americans is associated with earlier ages at first birth, but lower numbers of subsequent births per unit of time in a sample of indigenous, Kakchiquel-speaking Maya women from two villages in rural Guatemala. There is no clear evidence indicating that these patterns are driven by differences in access to diet/energy. Rather, there is some tentative evidence suggesting that these fertility changes may reflect adaptive responses to the increased psychosocial stress of undergoing rapid socioeconomic change and exposure to increasing inequality, on the heels of civil war-related stress.

Unfortunately, we do not yet have an understanding of the physiological, psychological, or cultural mechanisms underpinning the main associations we observed. There are, therefore, several avenues for future inquiry. In particular, it would be useful to compare indicators of stress—both at a biomolecular level and through the collection of detailed, personal histories of development and stress—between the two study villages. Furthermore, expansion of the sample to include individuals who began their reproductive careers after the time periods for which we have data (i.e. after 2001) should clarify whether the effects we observed represent a long-term, historical trajectory resulting from immigration-driven increased market integration or whether they represent a short-term, post-civil-war recovery pattern. There is also a need for studies comparing the recent demographic histories and individual life histories of the members of Villages A and B with those of other Maya villages in the region with varying exposures to immigration, as has been done with the Tsimane and the Pumé (Kramer, 2017; Kramer & Greaves, 2017; Veile et al., 2014). Such work should shed light on the extent to which the patterns we observed are generalisable for the region.

The findings reported here have a number of potential implications for public health and public policy. Specifically, they align with other recent findings to suggest that rapid socioeconomic change, irrespective of cause, can have substantial and biologically-meaningful impacts on pace

of ontogeny and can increase risks of early (i.e. before mid-teenage years) first birth (Kramer & Lancaster, 2010; Migliano et al., 2007). Adolescent motherhood is associated with a number of longer-term health risks to both mothers and infants (Koniak-Griffin & Turner-Pluta, 2001; Makinson, 1985). These increased risks include truncated linear growth and excess adiposity in mothers, reduced educational and financial opportunities for mothers (education and income buffer women against all-cause morbidity and mortality, Furnee et al., 2004), intra-uterine growth restriction, low birth weights, reduced investments in non-essential tissues, and higher infant mortality for foetuses and babies (Chen et al., 2007; Kramer 2008, 2017; Kramer & Lancaster, 2010; Wu et al. 2004). These effects on foetuses and infants are associated with a host of poorer later-life outcomes, at least for highly sedentary populations in environments where calories are cheap and ubiquitous. These outcomes include increased risks of cardiovascular diseases, type 2 diabetes, and some cancers (e.g. Godfrey et al., 2010; Hanson & Gluckman, 2015; Lagranja et al., 2015; Liebert et al., 2013). Given these increased risks—and their substantial concomitant human as well as financial costs—public health policy aimed at increasing family planning services should consider prioritising teens in contexts featuring rapid socioeconomic change.

Our results also draw attention to the idea that immigration is not only of political and economic salience from the perspective of wealthy, developed nations. Immigration to poor, rural, indigenous contexts by people from wealthy, developed nations can have negative biological effects on indigenous populations (Bombay et al., 2009, 2011, 2014; Heart et al., 2011; Sotero, 2006). This suggests that policy should be developed to soften or eliminate some of these impacts. If our proposal that increased social inequality is a factor linking immigration-related socioeconomic change and increased stress is correct, these findings suggest that a policy direction to explore is one that focuses on slowing rates of economic change and/or on maximising redistribution to reduce inequality in the host population. Developing this kind of policy, however, will require careful, prospective, qualitative, and quantitative assessments of the initial and continued effects of immigration-related rapid cultural change on indigenous biodemography, not only in the Maya of Guatemala's Central Highlands, but also in other indigenous populations facing similar socioeconomic challenges.

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