CHAPTER 12

THE CAUSAL RELATIONSHIP BETWEEN FERTILITY AND INFANT MORTALITY

prospective analyses of a population in transition

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12.1 INTRODUCTION

UNDERSTANDING the relationship between fertility rates and infant and juvenile mortality risks has been a long-standing interest of demographers and biologists. Standard demographic transition theory is one classic approach (Coale 1973; Coale and Watkins 1987; Davis 1945, 1963). This theory posits that mortality rates for infants and children drive fertility rates, mediated through cultural, social, and psychological processes. Those social processes have the effect of keeping population size stable. Under conditions of high mortality, high fertility rates are required to keep populations from shrinking. When there is a transition from high to low mortality rates, cultural processes, albeit with some lag, will result in reduced fertility rates. After a period of rapid growth, the population returns to stable equilibrium.

Life history theory derived from evolutionary biology posits a bidirectional relationship between fertility and juvenile mortality risks (Blurton Jones 1986; Cole 1954; Kaplan 1996; Smith and Fretwell 1974). According to the theory, organisms have limited budgets and face a trade-off between quantity and quality of offspring. Increasing fertility reduces available time and energy to invest in each individual offspring, increasing their likelihood of dying. At the same time, for organisms that engage in postnatal investment in offspring (including all birds and mammals), the death of an

existing offspring releases time and energy for the mother to invest in new replacement offspring. The theory proposes that natural selection results in organisms possessing characteristics that will tend to maximize biological fitness, often measured by the number of surviving offspring they produce. According to the theory, the effect of an exogenous reduction in mortality risks to offspring will depend on how it affects the trade-off between quantity and quality of offspring. By increasing the number of existing offspring demands on the mother, reductions in mortality will tend to reduce fertility, but if the cause of reduced mortality is due to an increase in available resources, fitness-maximizing organisms may respond by increasing fertility. For most organisms, populations will eventually return to equilibrium due to resource constraints.

Many traditional native South Americans living in the lowland areas of Amazonia are currently undergoing a transition in mortality rates. The demographic history of those groups reveals large swings in population size, due to the effects of contact with Europeans. During the first centuries of contact, there were large demographic collapses throughout the Americas, due to both introduced diseases and economic, social, and political disruption (see Livi Bacci 2007 for a review). The rubber boom in the late nineteenth century caused further demographic disorder. The effects of these disruptions were greater for settled groups than for small-scale nomadic societies, living on small water courses in the interior of the forest. Many of those small-scale societies continued to live traditional lifestyles until the middle or latter part of the twentieth century. As they make increasing contact with global forces (including change in access to land and resources, schooling, and public health), they are now experiencing demographic change; in many cases, the result is rapid population growth as high as 3–5% annually (Perz et al. 2008).

The aim of this paper is to examine the causal processes underlying recent change in demographic outcomes in one traditional native South American society, the Tsimane of lowland Bolivia, with the specific goal of shedding light on the relationship between fertility and mortality. While the vast majority of Tsimane remain subsistence-level forager-farmers, people and communities vary in distance from the nearest town, their ability to speak Spanish (from none to fluent), their access to medical care, their educational level (from none to completion of secondary school), and their degree of economic exchange with outsiders (Gurven et al. 2007). Using prospective data collected between 2002 and 2010, we first present descriptive data on age-specific fertility and total fertility rates (TFR), and how they vary by distance from the town of San Borja (population approximately 23,000). We then examine the determinants of parity progressions among parous women, using a proportional hazards approach. Next, a comparable analysis is given regarding the transition to first birth. The subsequent section examines the determinants of mortality risks for infants, first for higher-order births and then for firstborn children. Finally, we compare secular change in mortality and fertility rates among the Tsimane to Bolivia as a whole, using historical demographic data.

12.2 Methods

Longitudinal data on health status, fertility, and mortality were collected from 2002 to 2010 under the aegis of the Tsimane Health and Life History Project (www.unm.edu/~tsimane/). Census data were maintained throughout this period, documenting the age, sex, community membership, and parents of each individual born or living in the sample villages. Retrospective reproductive histories were collected from a subset of adults in this sample according to methods described in Gurven et al. (2007). Yearly medical exams and interviews were conducted by a mobile team of Bolivian physicians and biochemists. These exams recorded height, weight, pregnancy status, and parity. White blood cell count was quantified by biochemists using a microscope or a portable dry hematology analysis machine (QBC Diagnostics). Spanish-speaking ability and completed years of schooling were also recorded.

The subsequent analyses of age at first birth, parity progressions, and infant mortality draw on the census data collected during the sample period (2002–2010), supplemented by retrospective demographic interview data where available. In order to understand the patterning of variance in demographic outcomes across individuals and communities, multilevel models (Gelman and Hill 2007; Hox 2002) were estimated, including individual- and community-level predictors and random effects. Mixed-effects Cox proportional hazards models (Therneau 2012) were employed to predict time to next birth following a birth that occurred during or immediately preceding the sample period, and to predict age at first birth. Mixed-effects logistic regression models (Bates et al. 2012) were employed to predict the likelihood of each child born dying within one year of birth, with separate models for higher-order births and first births. Total fertility and infant mortality rates before 2002 were drawn exclusively from retrospective demographic interviews. Nation-wide Bolivian demographic data were obtained from the UN Common Database, UNICEF.

12.3 Results

The total fertility rate for the entire sample of Tsimane from 2002 to 2010, based on 5,730 risk years for births, is 8.8. Figure 12.1 shows the age-specific fertility rates from which the TFR is derived. There is some evidence of regional variation in age-specific fertility. If we divide the population into the more remote Tsimane villages and those that are either near the town of San Borja or at a large Catholic mission settlement, fertility rates are somewhat higher for women in more remote communities during peak reproductive years (Figure 12.2), resulting in TFRs of 9.3 and 8.4 for remote and near villages, respectively.

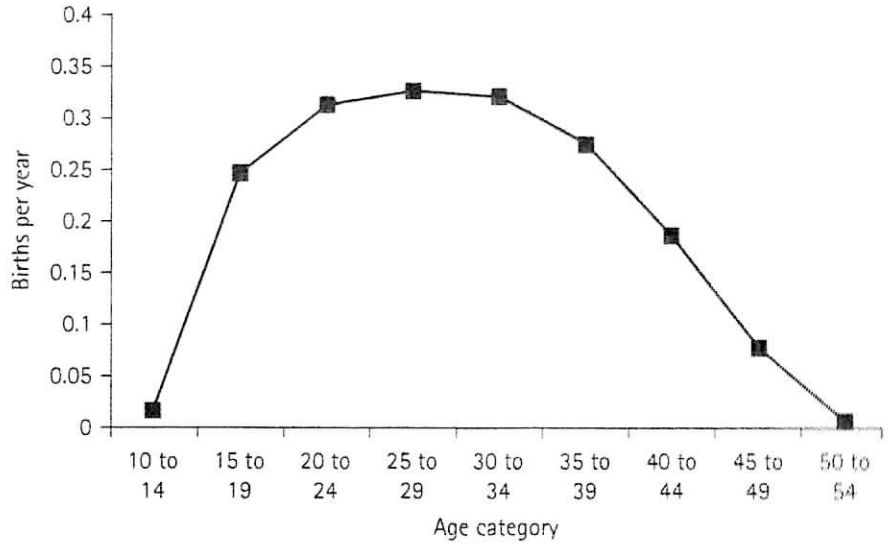

FIG. 12.1 Age-specific fertility rate among Tsimane women.

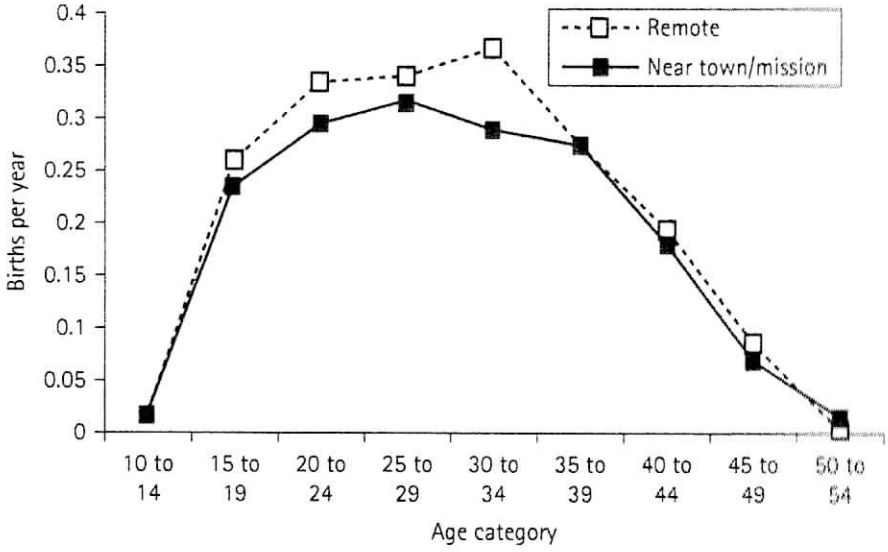

FIG. 12.2 Regional variation in age-specific fertility rate.

12.3.1 Parity Progressions for Parous Women

Table 12.1 shows the results of a Cox proportional hazards analysis of 1,159 risk intervals for the progression from one birth to the next birth among parous women in 14 communities (of which 659 intervals terminated with a birth). Model A examines the variance captured by the individual- and community-level random-effect terms with no predictor variables, and shows that the individual-level variance is much greater than the community-level variance. Model B examines the ability of individual-level variables to predict fertility. It shows that (a) rates of progression decrease with a woman's age, radically after age 35 (see Figure 12.3a for the corresponding functions); (b) the death of

Table 12.1 Multilevel Cox proportional hazard models of probability of giving birth among parous women

	Model A	Model B				Model C				Model D			
Fixed effects		B	exp(B)	SE	p	B	exp(B)	SE	p	B	exp(B)	SE	p
Age 20–24 (baseline)	–	0	1	–	–	–	–	–	–	0	1	–	–
Age 25–29	–	−0.220	0.802	0.121	0.069	–	–	–	–	−0.221	0.802	0.121	0.069
Age 30–34	–	−0.431	0.650	0.142	0.002	–	–	–	–	−0.439	0.645	0.142	0.002
Age 35–39	–	−1.072	0.342	0.160	<0.001	–	–	–	–	−1.078	0.340	0.160	<0.001
Age 40–44	–	−2.338	0.097	0.228	<0.001	–	–	–	–	−2.347	0.096	0.229	<0.001
Age 45–49	–	−2.131	0.119	0.407	<0.001	–	–	–	–	−2.156	0.116	0.409	<0.001
Prev. infant survives (baseline)	–	0	1	–	–	–	–	–	–	0	1	–	–
Prev. infant does not survive	–	1.020	2.774	0.225	<0.001	–	–	–	–	1.023	2.781	0.226	<0.001
BMI < 20.5 (baseline)	–	0	1	–	–	–	–	–	–	0	1	–	–
BMI ≥ 20.5	–	0.352	1.422	0.159	0.027	–	–	–	–	0.346	1.414	0.159	0.030
Spanish fluency: none (baseline)	–	0	1	–	–	–	–	–	–	0	1	–	–
Spanish fluency: moderate	–	−0.042	0.959	0.124	0.740	–	–	–	–	−0.035	0.966	0.130	0.790
Spanish fluency: high	–	−0.558	0.573	0.183	0.002	–	–	–	–	−0.561	0.571	0.198	0.005
Community mean age	–	–	–	–	–	−0.026	0.974	0.095	0.780	0.057	1.058	0.096	0.550
Community mean BMI	–	–	–	–	–	0.234	1.263	0.268	0.380	0.187	1.206	0.270	0.490
Community mean Spanish fluency	–	–	–	–	–	0.047	1.048	0.299	0.880	0.173	1.189	0.311	0.580
Community distance from town (km)	–	–	–	–	–	0.004	1.004	0.004	0.400	0.003	1.003	0.004	0.500
Random effects	Variance	Variance				Variance				Variance			
Individual	0.760	0.571				0.745				0.571			
Community	0.044	0.050				0.039				0.042			

Notes: N = 1159 risk intervals belonging to 575 females aged 20–49 in 14 communities.

the infant whose birth began the interval increases the likelihood of progression to the next birth (Figure 12.3b); (c) women with Body Mass Index (BMI) less than 20.5 (one standard deviation below the mean) also have lower progression rates (Figure 12.3c); and (d) women who speak Spanish fluently have significantly lower rates of progression to next birth than do women who speak some or no Spanish (Figure 12.3d). Model C examines community-level predictors, and shows them to be generally weak. Model D combines individual- and community-level effects simultaneously; this model yields no substantial improvement over the individual-level Model B, suggesting that the regional effects in Figure 12.2 are due to individual factors that vary by region.

12.3.2 Progression to First Birth for Nulliparous Women

Table 12.2 shows a Cox proportional hazards analysis of the predictors of first birth. Again, Model A shows much larger individual variance than community variance. Model B, with individual-level predictors, shows that (a) there is a general trend to earlier first birth over time; (b) BMI higher than the early adolescent female mean of 18.1 is associated with faster transition to first birth (Figure 12.4a); and (c) education has a large effect on the transition to first birth (although the direction of causality may be unclear). Those with no or one year of education undergo transition first; those with two or three years of education experience transition slightly later; while those with four or more years of education have their transition last (Figure 12.4b). While Model C shows some association between mean community values (particularly mean birth year) and age of first birth, Model D indicates that these effects are better attributed to individual-level rather than community-level characteristics.

12.3.3 Infant Mortality Rates: Higher-Order Births

Table 12.3 presents an analysis of the predictors of infant mortality in the first year of life using mixed-effects logistic regression (N=747 births of which 4.6% died in the first year of life). It shows that (a) children born to mothers over age 35 have about twice the mortality risk of children born to younger mothers; (b) mother's BMI negatively predicts infant death, with the odds ratio decreasing by 14% for each additional unit of BMI; and (c) there is a strong interaction between the length of the preceding birth interval and geographical region of residence in determining mortality: short intervals of less than two years increase mortality hazards by more than fourfold in remote regions with no access to medical treatment, but do not affect mortality rates in regions with greater access. Neither maternal education nor the ability to speak Spanish are significantly related to mortality rates (results not shown). The multilevel random-effect terms in model A though D capture effectively zero variance in mortality, while the community-level predictors included in models C and D show little predictive ability.

Table 12.2 Multilevel Cox proportional hazard models of probability of first birth among nulliparous females

	Model A	Model B				Model C				Model D			
Fixed effects		B	exp(B)	SE	p	B	exp(B)	SE	p	B	exp(B)	SE	p
Year of birth	–	0.118	1.125	0.027	<0.001	–	–	–	–	0.112	1.118	0.028	<0.001
BMI < 18.1 (baseline)	–	0	1	–	–	–	–	–	–	0	1	–	–
BMI ≥ 18.1	–	0.770	2.159	0.194	<0.001	–	–	–	–	0.673	1.959	0.218	0.002
Education: ≤ 1 year (baseline)	–	0	1	–	–	–	–	–	–	0	1	–	–
Education: 2–3 years	–	–0.016	0.984	0.170	0.930	–	–	–	–	–0.089	0.915	0.185	0.630
Education: ≥ 4 years	–	–0.615	0.541	0.192	0.001	–	–	–	–	–0.670	0.512	0.226	0.003
Community mean year of birth	–	–	–	–	–	0.247	1.280	0.108	0.023	0.063	1.065	0.102	0.530
Community mean BMI	–	–	–	–	–	0.332	1.393	0.304	0.270	0.070	1.073	0.268	0.790
Community mean education (years)	–	–	–	–	–	–0.129	0.879	0.088	0.140	–0.013	0.987	0.084	0.880
Community distance from town (km)	–	–	–	–	–	0.000	1.000	0.005	0.970	–0.002	0.998	0.004	0.640
Random effects	Variance	Variance				Variance				Variance			
Community	0.119	0.019				0.039				0.005			

Notes: N = 590 females aged 10–20 in 14 communities.

Table 12.3 Multilevel logistic regression models of infant mortality in the first year of life

	Model A				Model B				Model C				Model D			
Fixed effects	B	exp(B)	SE	p	B	exp(B)	SE	p	B	exp(B)	SE	p	B	exp(B)	SE	p
(Intercept)	-3.074	0.046	0.178	<0.001	0.006	1.006	1.570	0.997	-13.116	0.000	12.310	0.287	-10.719	0.000	12.088	0.375
Maternal age ≤ 35	-	-	-	-	0	1	-	-	-	-	-	-	0	1	-	-
Maternal age > 35	-	-	-	-	0.825	2.281	0.394	0.036	-	-	-	-	0.825	2.283	0.396	0.037
Maternal BMI	-	-	-	-	-0.152	0.859	0.070	0.030	-	-	-	-	-0.161	0.851	0.071	0.024
Near town/mission × long IBI[a] (baseline)	-	-	-	-	0	1	-	-	-	-	-	-	0	1	-	-
Near town/mission × short IBI[b]	-	-	-	-	-0.508	0.602	0.641	0.428	-	-	-	-	-0.556	0.574	0.646	0.390
Remote × long IBI[a]	-	-	-	-	-0.019	0.981	0.525	0.971	-	-	-	-	-0.128	0.880	0.633	0.839
Remote × short IBI[b]	-	-	-	-	1.455	4.284	0.450	0.001	-	-	-	-	1.348	3.850	0.611	0.027
Community mean age	-	-	-	-	-	-	-	-	0.092	1.096	0.168	0.586	0.082	1.085	0.172	0.635
Community mean BMI	-	-	-	-	-	-	-	-	0.434	1.544	0.499	0.384	0.379	1.460	0.531	0.476
Community mean IBI (months)	-	-	-	-	-	-	-	-	-0.090	0.914	0.063	0.155	-0.013	0.987	0.081	0.869
Community distance from town (km)	-	-	-	-	-	-	-	-	0.002	1.002	0.006	0.796	0.003	1.003	0.006	0.574
Random effects	Variance				Variance				Variance				Variance			
Mother	0.000				7.55E-15				0.000				1.33E-12			
Community	2.11E-14				6.49E-11				0.000				1.05E-11			

Notes: N = 747 later-born infants belonging to 461 mothers in 14 communities.

[a] long IBI = preceding interbirth interval ≥ 24 months.

[b] short IBI = preceding interbirth interval < 24 months.

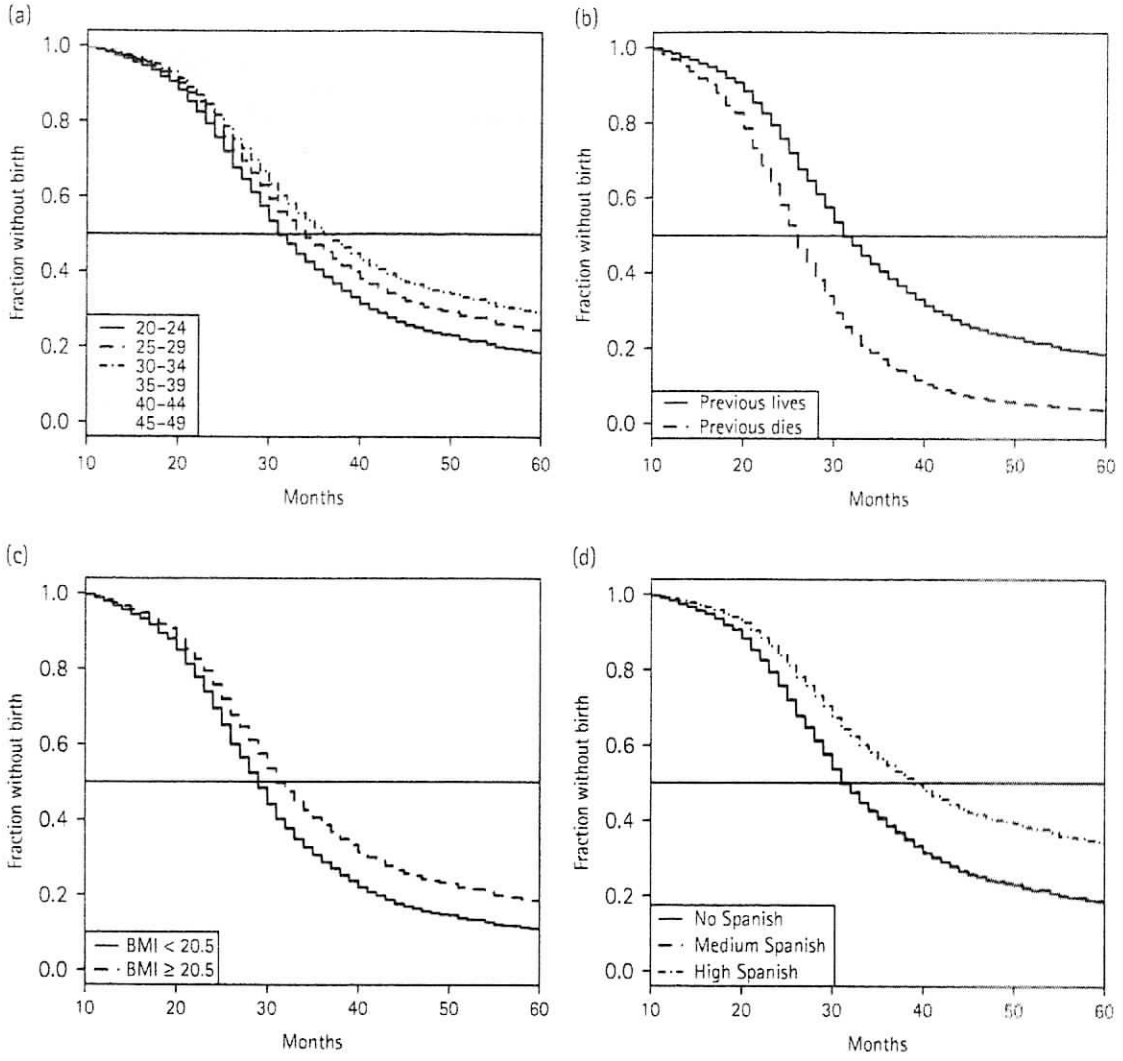

FIG. 12.3 Progression to next birth for parous women as a function of (a) age, (b) survival of previous infant, (c) BMI, and (d) Spanish fluency.

12.3.4 Mortality Risks for Firstborn Infants

Firstborn children die at almost twice the rate of later-born children (7.9% vs 4.6%). Table 12.4 shows the predictors of infant mortality for 198 firstborn children. It shows (a) a strong effect of mother's age at birth on mortality risk, with the odds ratio decreasing by 24% with each additional year of age; (b) a counter-intuitive impact of maternal BMI (unlike older mothers), where heavier mothers have higher infant mortality rates; and (c) the infants of mothers with high white blood cell counts are more likely to die, with an odds ratio of 1.15 for each additional 1,000 cells per cubic millimeter of blood. Neither maternal education nor the ability to speak Spanish were significantly related to mortality rates (results not shown). The variance attributed to the community-level random effect in Model A is obviated with inclusion of individual- and community-level predictors, although none of the community-level fixed effects is statistically significant.

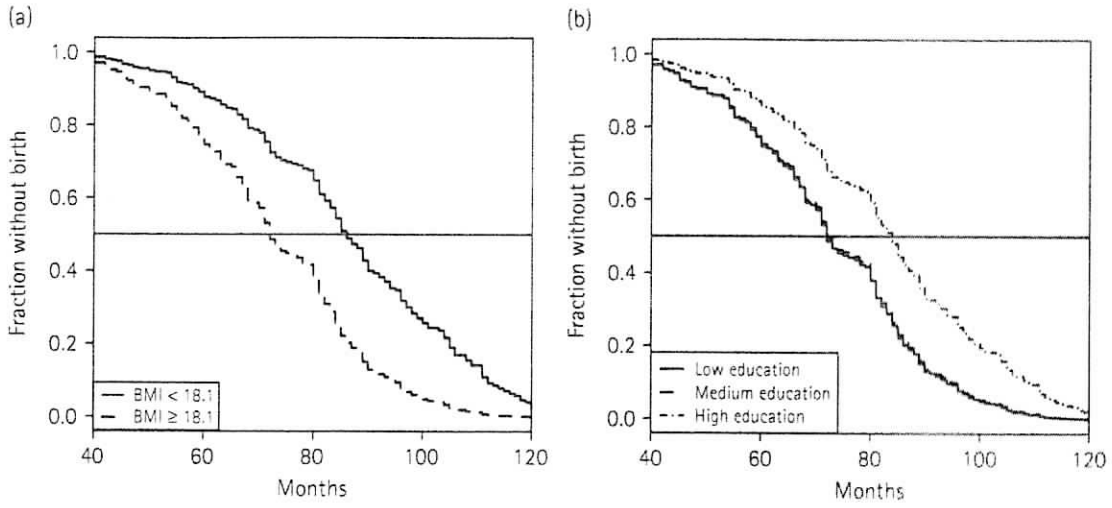

FIG. 12.4 Progression to first birth for nulliparous women as a function of (a) BMI and (b) education.

12.3.5 Changes in Fertility and Infant Mortality over Time: Tsimane and Bolivia Compared

Figure 12.5 shows a comparison between mortality and fertility rates of the Tsimane and the rest of Bolivia, using historical demographic data. There is a general similarity in the downward trajectory of infant mortality rates in both populations. Tsimane infant mortality increased slightly in the 1970s, when roads were built connecting La Paz to San Borja, potentially increasing pathogen exposure due to an influx of highland migrants to the region. The steady decrease in Tsimane infant mortality appears only after 1990, when the first health clinic 'Horeb' was created 6 kilometers from San Borja. By 2009, we find that the infant mortality rate has dropped to about 4–6% for both the Tsimane and for Bolivia as a whole.

The historical trajectories of fertility rates in the two populations, while moving in the same direction, are more dissimilar. From 1975 to 2009 the TFR in Bolivia as a whole dropped by 46% (from 6.6 to 3.5), while there has been relatively little change in the Tsimane TFR over time. By 2009, the gap in TFR between Tsimane and Bolivia is almost six births.

12.4 Discussion

These results provide some fundamental insights into the determinants of fertility and mortality in natural fertility populations undergoing socio-economic and epidemiologic transition. Physiological energy stores appear to play an important role in determining fertility. Women with greater energetic reserves (as indexed by BMI) had an

Table 12.4 Multilevel logistic regression models of firstborn infant mortality in the first year of life

	Model A				Model B				Model C				Model D			
Fixed effects	B	exp(B)	SE	p	B	exp(B)	SE	p	B	exp(B)	SE	p	B	exp(B)	SE	p
(Intercept)	−2.541	0.079	0.294	<2e−16	−5.559	0.004	3.076	0.071	32.814	1.8E+14	20.438	0.108	31.407	4.4E+13	20.413	0.124
Maternal age	–	–	–	–	−0.276	0.759	0.145	0.058	–	–	–	–	−0.278	0.757	0.158	0.078
Maternal BMI	–	–	–	–	0.269	1.309	0.098	0.006	–	–	–	–	0.286	1.332	0.099	0.004
Maternal WBC[a] ($\times 10^3/mm^3$)	–	–	–	–	0.140	1.151	0.076	0.064	–	–	–	–	0.127	1.136	0.087	0.145
Community mean age	–	–	–	–	–	–	–	–	−0.611	0.543	0.533	0.252	−0.308	0.735	0.558	0.581
Community mean BMI	–	–	–	–	–	–	–	–	−0.913	0.401	0.637	0.152	−1.177	0.308	0.663	0.076
Community mean WBC[a] ($\times 10^3/mm^3$)	–	–	–	–	–	–	–	–	−0.463	0.630	0.401	0.249	−0.578	0.561	0.438	0.187
Community distance to town (km)	–	–	–	–	–	–	–	–	0.015	1.015	0.013	0.239	0.015	1.015	0.014	0.283
Random effects	Variance				Variance				Variance				Variance			
Community	0.144				0.053				0.000				0.000			

Notes: N = 198 firstborn infants in 14 communities.

[a] WBC = white blood cell count.

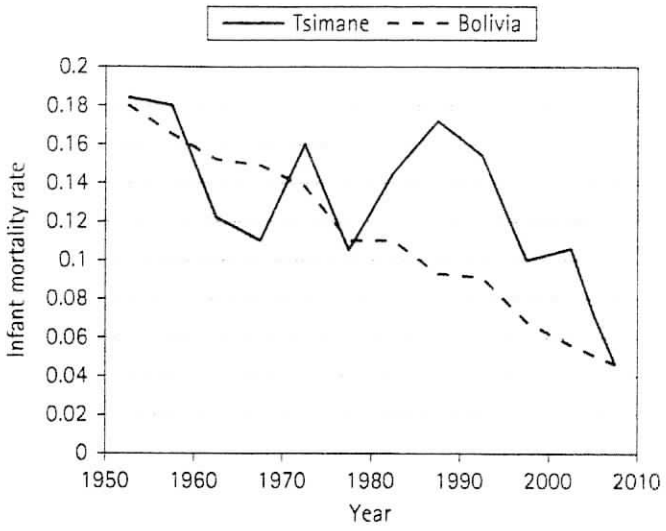

FIG. 12.5 Infant mortality rates of Tsimane and Bolivia by year.

earlier first birth and shorter intervals between subsequent births. As expected from models positing a causal relationship from mortality to fertility, the loss of the previous infant hastens the transition to the next birth, presumably due to the termination of lactation and faster resumption of ovulation (Wood 1994), as expected by models positing a causal relationship from mortality to fertility.

There is also evidence that fertility affects mortality. In remote areas with minimal access to medical services, a short interval between births increases the mortality risk to the subsequent infant about fourfold. Age of first birth also has a significant effect on mortality rates, reducing the mortality risk of the earlier-born infant by a quarter for each additional year that a young women delays reproduction. Thus, with respect to production of surviving offspring, there is a clear trade-off between fertility (both its initiation and its resumption following a birth) and infant survival.

Physiological energy stores also appear to affect mortality. Greater maternal BMI is associated with a lower risk of infant mortality for higher-order births. For first births, the results were counter-intuitive, since maternal BMI is associated with a higher risk of infant mortality. One possible explanation of this result is that there is more competition between maternal and infant energy stores when mothers are adolescents and still increasing in body weight (which continues past age 20 among Tsimane girls). Early maternal physiology may be sequestering more resources for itself at a cost to the infant. It is possible that some of the increased risk of mortality for firstborn children is due to this energy competition, and not just due to the inexperience of young mothers. This counter-intuitive finding does have precedent in developed societies: in the US, obese women experience more neonatal mortality, regardless of weight gain during pregnancy, due to more pregnancy complications related to short gestation and low birth weight, pre-eclampsia, and prolonged labour (Chen et al. 2009).

Taken together, these results provide support for the view that natural selection has acted on the physiological mechanisms governing human fertility to maximize the

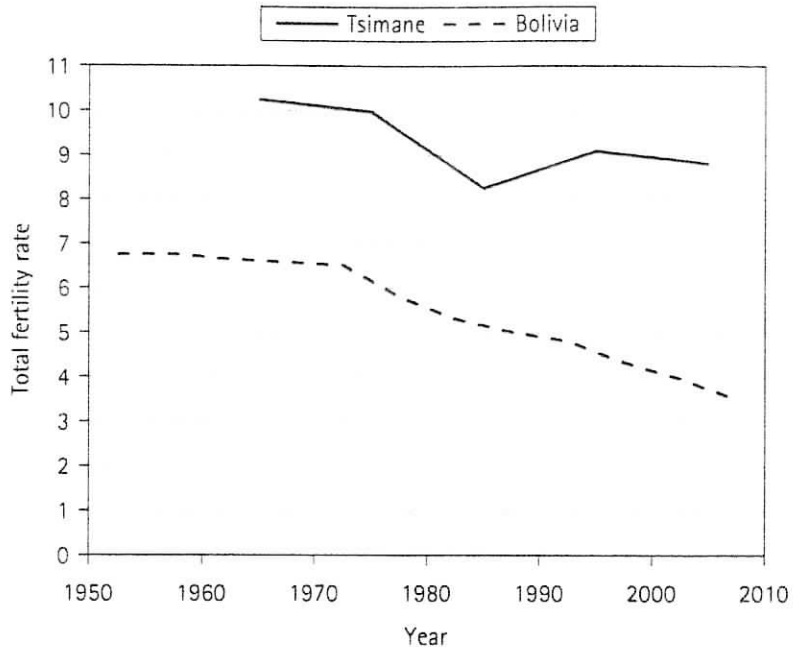

FIG. 12.6 Total fertility rates of Tsimane and Bolivia by year.

production of *surviving* offspring through the optimal combination of fertility and parental investment. The transition to the next birth is affected by both energy stores and whether there is an existing living infant to invest in. Most birth intervals are longer than two years; holding energy stores constant, having a shorter interval results in increased mortality risk.

The effects of secular change also provide support for this view. Mortality has been decreasing rapidly over time. Given the observed regional effects on mortality, it appears that much of the secular trend in mortality rates is due to increased access to Western medical treatment, especially antibiotics and rehydration therapy. One remote area that is served by a medical post with itinerant teams visiting the villages had similar infant mortality rates to villages near the town of San Borja, where there is a hospital.

The multilevel models developed here provide additional insights into the processes determining fertility and mortality in natural fertility populations. Results show that the effects of community-level variables are quite weak. Most determinants of fertility and mortality modelled here operate on the individual level, with the exception of regional effects on mortality. Both infant and child mortality from 1950–2000 increased with distance from San Borja. This does not mean that there is little scope for social effects on demographic rates among the Tsimane (and similar groups). We have shown in other papers that kin—especially post-reproductive kin—play a major role in providing the food energy to support reproduction (Hooper 2011; Kaplan et al. 2010). It appears to be the case that, in the present setting, the social effects on fertility and mortality are achieved through social assistance, with impacts on energy and care, rather than through cultural effects based on conformity or other process of value transmission.

The multilevel models also suggest that unobserved heterogeneity is greater at the individual than group level. In relation to the terminology used by Wachter (this volume), it may not be possible to distinguish frailty from life-luck, even with the random effects terms for individual heterogeneity. With few births per woman during the sample period, the differences in women in hazards of fertility and the likelihood of their baby dying could be due to unobserved differences in health, tendency to conceive, parenting abilities, etc.; or alternatively, to differences in life-luck, such as flu epidemics and random variation in chromosomal segregation during meiosis. There does seem to be large scope for unobserved heterogeneity in both the initiation and nature of reproduction. The counter-intuitive relationship between maternal BMI and infant mortality for first births may reflect unobserved heterogeneity in adolescent growth patterns, maternal feeding practices, and perhaps more subtle differences in family assistance. The relatively high risks of fertility for some women in their late 40s may also represent differences among women in health, ovarian follicle number, ovum quality, and perhaps other factors.

The secular change in infant mortality rates among the Tsimane is dramatic and keeping pace with the rest of Bolivia. Nevertheless, infant mortality rates still show large yearly fluctuations, probably reflective of temporal variance in respiratory and diarrheal epidemics (cf. Omran's characterization of the 'Age of Pestilence' where mortality is high and fluctuating; Omran 2005).

In contrast with mortality, there has been little or no change in total fertility rates over time among the Tsimane, whereas TFRs have dropped from 6.6 to 3.6 for Bolivia as a whole. This is likely due to the fact that lowering family size in order to increase parental investment in education still has little pay-off in the context of their isolation and rural lifestyle (McAllister et al. 2012). At the same time, modernization is beginning to affect personal values regarding fertility. McAllister et al. (2012) showed that values about ideal family size are changing among some women, and are affected by education and Spanish-speaking ability. About 10% of parous women in our sample speak Spanish fluently. Their rates of transition to next birth were lower than for women who speak little or some Spanish. Presumably an increasing number of women will speak Spanish as time progresses. Schooling will also be more common for current cohorts; Tsimane girls and boys aged 10–19 now have an average of 3.2 and 3.5 years of schooling, respectively, compared with 0.4 and 1.3 years of schooling among women and men aged 40+. For the transition to first birth, there is also evidence that young women with more education ($\geq$ 4 years) initiate reproduction later. In some cases, however, pregnancy may have terminated schooling rather than vice versa.

In sum, however, the effects of education and Spanish speaking on actual fertility as of yet are quite weak, and do not overshadow the increasing nutritional status of women. For this reason, hazards of births are increasing slightly over time, after controlling for the death of the previous child. This may be reflective of a 'pre-decline rise' in fertility (Dyson and Murphy 1985). It is also noteworthy that over the course of the study, progression rates to first birth increased by about 12% per year (i.e. mothers' average age at first birth decreased). This finding is consistent with the biological view that in

natural fertility populations, the physiological mechanisms underlying fertility regulation should tend to maximize population growth. It is less consistent with the cultural homeostasis view proposed by demographic transition theories (e.g. Coale and Watkins 1987), which argued that cultural institutions will act to maintain population equilibrium by lowering fertility when mortality is low and vice versa. Although the rise in fertility following mortality decline has been observed now among the Tsimane, other transitioning groups in South America, and elsewhere (Dyson and Murphy 1985; McSweeney and Arps 2005), classic demographic transition theories generate the expectation of stable fertility levels that gradually decline following drops in mortality. Our findings highlight the kinds of mechanisms at the individual level that can lead to growing fertility rates as a response to changes in mortality. As the process of modernization continues, we expect greater scope for community and social network effects on fertility as people begin to model and preferentially interact with others sharing similar behavioural strategies (Casterline 2001).

To conclude, we propose that under traditional, natural fertility conditions: (1) fertility and mortality are tightly linked; (2) the physiological processes underlying fertility outputs are tuned to individual condition (in terms of energy inputs and stores), existing vessels of investment, and the environmentally variable connection between birth spacing and subsequent infant mortality; and (3) fertility outputs will tend to maximize descendant production over the long run. With modernization, as populations become more internally structured by socio-economic status and differing strategies for parental investment, the scope for cultural and network effects may be much greater, with less control being exercised by a fitness-maximizing physiology.

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