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The Demographic Transition Influences Variance in Fitness and Selection on Height and BMI in Rural Gambia

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Summary

Recent human history is marked by demographic transitions characterized by declines in mortality and fertility [1]. By influencing the variance in those fitness components, demographic transitions can affect selection on other traits [2]. Parallel to changes in selection triggered by demography per se, relationships between fitness and anthropometric traits are also expected to change due to modification of the environment. Here we explore for the first time these two main evolutionary consequences of demographic transitions using a unique data set containing survival, fertility, and anthropometric data for thousands of women in rural Gambia from 1956–2010 [3]. We show how the demographic transition influenced directional selection on height and body mass index (BMI). We observed a change in selection for both traits mediated by variation in fertility: selection initially favored short females with high BMI values but shifted across the demographic transition to favor tall females with low BMI values. We demonstrate that these differences resulted both from changes in fitness variance that shape the strength of selection and from shifts in selective pressures triggered by environmental changes. These results suggest that demographic and environmental trends encountered by current human populations worldwide are likely to modify, but not stop, natural selection in humans.

Results and Discussion

Human societies have recently experienced striking declines in mortality and fertility rates [1]. While this “demographic transition” has received attention from demographers [4, 5], economists [6, 7], and evolutionary biologists [8], little effort has been put into investigating its evolutionary consequences [2]. The evolutionary dynamics of a population encountering

demographic change are interesting for at least two reasons. First, as fertility and mortality decline, the total variance in relative fitness [9–14] and thus the “opportunity” for selection both change [9, 15]. This change in opportunity for selection can significantly affect the strength of total selection on other traits. Furthermore, changes in the relative contributions of fertility and mortality to fitness can also change the net selection gradient, making predictions of evolutionary change difficult. Second, shifts in the selection gradient may occur as biological relationships between traits and fitness are modified by the profound social, cultural, medical, and economic changes (hereafter referred as *environment*) that are associated with demographic transitions but are not directly related to changes in survival and fertility rates. In population genetic terms [16, 17], demographic transitions can influence selection because (1) the variance in fitness can constrain the covariance between traits and fitness and (2) environmental changes independently shape the covariance between traits and fitness. Here we investigate and disentangle these two distinct effects of the demographic transition on selection.

Using individual-based data collected on women by the Medical Research Council (MRC) over a 55 year period from two rural villages in the West Kiang district of Gambia [3, 18], we present here a detailed investigation of the role of rapid demographic change in influencing the strength and direction of selection on traits in humans. Specifically, we first investigate how changes in survival and fertility rates (i.e., vital rates) across the demographic transition translate into changes in variance of relative fitness and fitness components; second, we study changes in directional selection on height and body mass index (BMI); and third, we assess how changes in selection on these anthropometric traits are explained by both change in fitness variance and the net effect on trait-fitness covariance associated with secular changes over this period, largely as a result of alterations to nutrition, infrastructure, and health provision. Our data set is uniquely well suited to addressing these questions. First, the period of data collection coincides with significant shifts in population vital rates [3], starting with the high mortality and fertility rates characteristic of most preindustrial societies [18], and more recently exhibiting much lower mortality and fertility rates (see below). A clinic was established in 1974 to provide free medical care to residents of the villages and the surrounding area. Second, because the data collected include records of individual reproductive events and deaths together with anthropometric data (height and weight) [19, 20], we had the unique opportunity to measure how the strength of selection on traits varies across the demographic transition. Third, the MRC staff focused on collecting data on women’s reproductive history and the health of neonates, which strongly limits the selective disappearance of individuals that biases most selection studies performed in natural populations. This started at the beginning of the study when regular surveys were carried out under the supervision of Sir Ian McGregor and continued after the establishment of the clinic.

First, the changes that we observed in variance in relative fitness and its components over the study period follow

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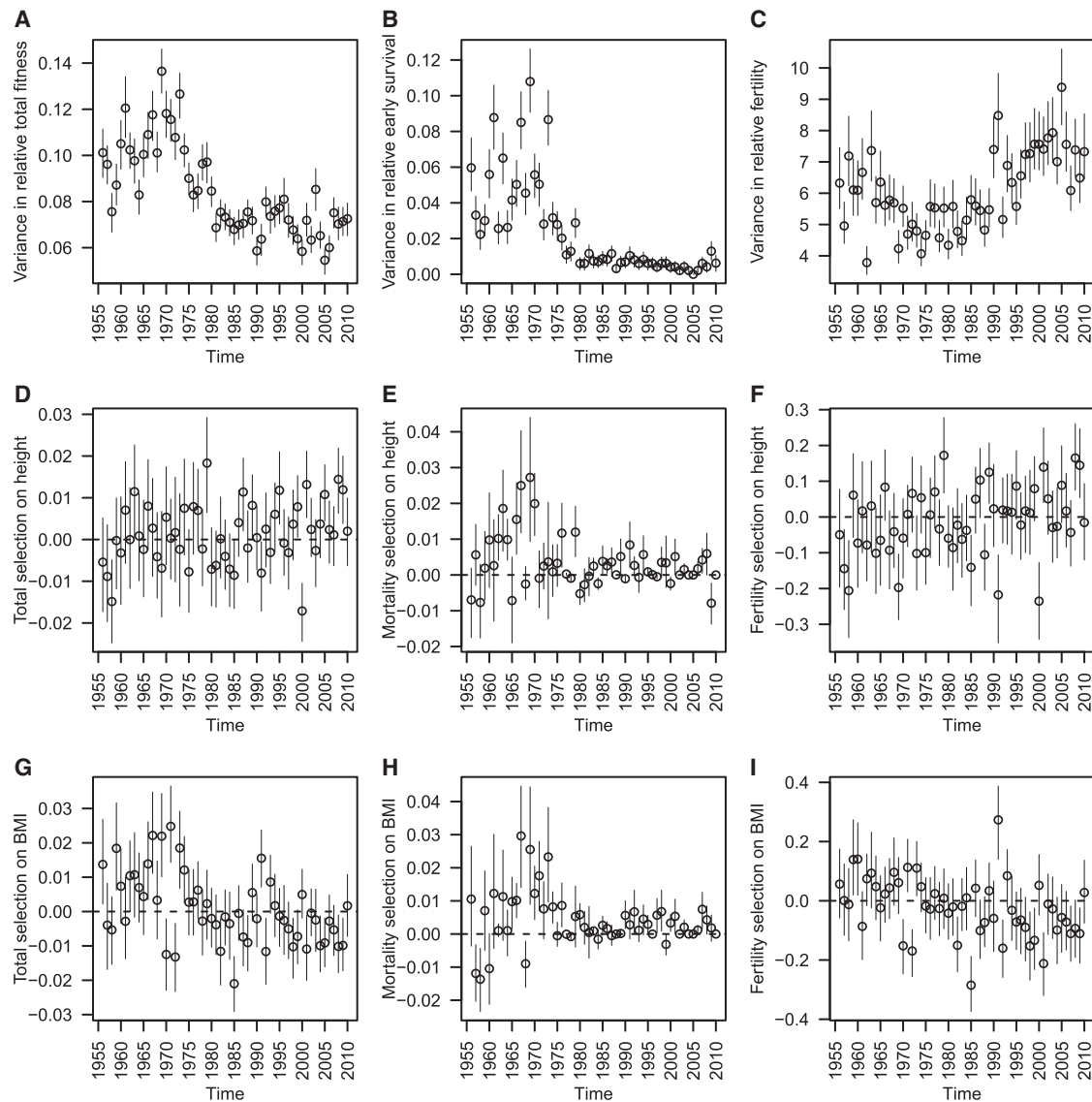


Figure 1. Changes in Fitness Variance and Linear Selection Acting on Height and BMI across the Demographic Transition in Rural Gambia

Rows represent successively, from top to bottom, changes in fitness variance and its components (A–C), linear selection acting on height (D–F), and linear selection acting on BMI (G–I). For all plots, changes are represented as a function of years (x axis). The columns represent successively, from left to right, changes in fitness variance or selection mediated by differences in total selection (A, D, and G), differences in early mortality (B, E, and H), and differences in fertility (C, F, and I). For each year, bars indicate the mean \pm 1 SE (estimated by bootstraps). In plots (D)–(I), the horizontal dashed line corresponds to a null selection gradient.

patterns similar to those documented for most other demographic transitions [9–14, 21] (Figures 1A–1C). Because the period under study is recent and therefore many individuals have not yet completed their lifetime reproductive success, we used an annual measure of fitness that represents the contribution of each individual to the population in the next calendar year [22–24] (see the [Supplemental Experimental Procedures](#) available online) to extract the maximal amount of information from our data. While precluding a self-consistent demographic analysis like that carried out by Moorad [2], this approach did allow us to capture rapid changes in selective pressures with time that may not have been detectable using a lifetime measure of fitness and to reduce potential biases triggered by nonrandom emigration. From those annual fitness measures, we derived variance in

relative fitness, which is qualitatively similar to the “opportunity for selection” derived from lifetime fitness measures that is traditionally used to estimate the upper limit for selection [9, 15] (for a formal relationship, see [2]). Variance in total relative fitness declined steeply over time (average up to 1974, 10.5×10^{-2} ; 1975 onward, 7.34×10^{-2} ; overall Spearman’s correlation, $\rho = -0.75$; $p < 0.001$; Figure 1A), indicating that the opportunity for selection declined. This result contrasts with a recent study showing a marked increase in opportunity for selection observed across the 19th century in the Utah population [2], where the demographic transition co-occurred with the settlement of pioneers. Although mortality and fertility rates declined in both of these populations, the growth rate of the Utah population decreased with time, which could explain differences between the studies. Overall,

a decrease in variance in relative fitness across the transition has been documented for most populations studied [9–11, 13, 14, 21], including the United States (as a whole), Italy, Finland, Sweden, and India, suggesting that it is a general feature of demographic transitions.

We analyzed variance in relative fitness mediated by early survival and by adult fertility separately, as did other demographic studies involving lifetime fitness measurements [10–14, 25]. The decline in variance in relative fitness was mostly explained by the decrease in variance in relative child survival (up to 1974, 5.20×10^{-2} ; 1975 onward, 8.15×10^{-3} ; $\rho = -0.84$; $p < 0.001$; Figure 1B), itself the result of the decrease in mean child mortality (Figure S1). Annual survival rates for individuals under 15 years old averaged before and after the establishment of the clinic in 1974 increased from 0.951 to 0.992, respectively. (Accumulated over 15 years, such rates would represent a transition from 47% to 89% survival at 15 years. The real value may differ slightly since this estimate neglects the variation of survival rates with age; however, the estimate is consistent with lifetime-based estimates [26].) In contrast, we did not find that survival of adults changed over the course of the study period ($\rho = -0.18$, $p = 0.19$, Figure S1), which is not surprising since the adult survival rate was already relatively high in the early years.

Although reductions in prereproductive mortality drove the decline in variance in relative total fitness, we observed an increase in the variance of relative fertility (up to 1974, 5.57; 1975 onward, 6.32; $\rho = +0.49$; $p < 0.001$; Figure 1C), a pattern that also marks the first stages of other demographic transitions [2, 10, 13]. The variance in relative fertility corresponds to the variance in absolute fertility divided by the mean fertility squared (see the Supplemental Experimental Procedures). We measured decreases in both absolute variance ($\rho = -0.50$, $p < 0.001$) and mean fertility ($\rho = -0.49$, $p < 0.001$, Figure S1), which combine here to produce the observed increase in the variance of relative fertility. Thus, although both villages underwent rapid demographic change, analyzing annual fitness allowed us to detect the changes in variance in relative fitness and fitness components in a manner equivalent to other studies of the demographic transition that used lifetime fitness measures and were carried out over a longer temporal and a larger spatial scale [2, 10, 11, 13, 14].

Second, we measured how selection on height and BMI changed across the demographic transition. Throughout the study period, the MRC staff has routinely measured individuals for several anthropometric traits. We focused on height and BMI (weight / height²) because those traits were most reliably sampled and because previous studies have shown them to be associated with lifetime survival and reproductive success in this population [19, 20]. Although BMI is a function of height, those two traits are weakly correlated at the phenotypic level in contrast to height and weight, making BMI a better alternative for statistical analyses than weight. Because traits were measured at different ages within and across individuals, we derived for each individual a unique index for each trait that represents their relative lifetime height/BMI. This method assumes parallel growth curves and is as independent as possible from age and cohort effects (see the Supplemental Experimental Procedures). Selection gradients were then calculated for each year of the study period to allow us to determine how they changed with time [27, 28]. Because selection gradients were built with annual fitness measures, whereas height/BMI indices applied across the lifetime of each individual, our analysis does not achieve the fine-tuned

Table 1. Time Changes in Linear Selection by Fitness Components

Fitness Component	Average Selection Gradient		Overall Time Trend	
	Up to 1974	1975 Onward	ρ	p Value
Height				
Total	-1.82×10^{-4}	$+1.98 \times 10^{-3}$	+0.29	0.031
Early survival	$+6.73 \times 10^{-2}$	$+1.77 \times 10^{-2}$	-0.19	0.10
Fertility	-4.69×10^{-2}	$+4.44 \times 10^{-3}$	+0.36	<0.01
BMI				
Total	$+7.94 \times 10^{-3}$	-3.12×10^{-3}	-0.46	<0.001
Early survival	$+7.48 \times 10^{-3}$	$+2.30 \times 10^{-3}$	-0.20	0.42
Fertility	$+3.18 \times 10^{-2}$	-4.89×10^{-2}	-0.48	<0.001

Standardized linear selection gradients are averaged over the period preceding (1956–1974) and following (1975–2010) the establishment of a clinic in 1974. Spearman correlation coefficients and the associated p values are also provided to characterize the overall trend in selection gradients over years. p values were obtained by permutations on bootstrapped data in order to capture uncertainty caused by sampling and measurement errors (see the Supplemental Experimental Procedures).

characterization of change in selection within the life of individuals that would be possible with annual measurements of anthropometrics for each individual. We were still able to decompose the trends in selection into changes in selection caused by early survival per se (survival to age 15) and changes in selection caused by fertility variation among adults, which therefore captures the likely main contribution of age structure to the evolutionary consequences of the demographic transition (see also [2]).

Temporal changes in selection gradients are represented in Figures 1D–1I. We observed a shift across the demographic transition from negative to positive selection on height coupled with a shift from positive to negative selection on BMI. The change in total selection on height was due to a shift from a negative to a positive relationship between height and adult fertility, which ran counter to a slight decrease in the positive relationship between height and early survival (see Table 1 for details). For BMI, the change in total linear selection was also triggered by the shift in selection mediated by adult fertility, but here selection shifted from positive to negative. As for height, positive linear selection on BMI mediated by child survival decreased only slightly, on average, but absolute values of selection gradients became much closer to zero from 1975 onward for both traits (Figures 1E and 1H). To summarize, whereas at the start of the study period selection favored short females with high BMI values (i.e., approximately <157 cm and >21 kg/m² for adults up to 1974), this changed so that selection now favors tall females with low BMI values (i.e., approximately >158 cm and <21 kg/m² for adults from 1975 onward).

Changes in selection on traits (i.e., the covariance between trait and relative fitness) may occur independently of changes in opportunity for selection (i.e. the variance in relative fitness) (cf. the opportunity-outcome conundrum: [29–32]). We therefore studied the extent to which temporal changes in selection could be accounted for by temporal trends in variance in relative total fitness or its components (demographic factors per se) versus temporal trends due to changing biological relationships between traits and fitness triggered by environmental change not directly related to changes in vital rates. To do this, we built linear models in which annual selection gradients were predicted from both the variance in relative fitness (or its components) and from “time” as such and estimated temporal trends independently from changes in

Table 2. Influence of Variance in Relative Fitness and Other Time Changes on the Annual Variation in the Intensity of Linear Selection

Fitness Component	Proportion of Variation in Annual Linear Selection Coefficients Explained (R^2)				
	By Variance in Fitness Components Alone	By Years Alone	By Variance in Fitness Components Controlling for Years	By Years Controlling for Variance in Fitness Components	By Variance in Fitness Components and Years
Height					
Total	0.03	0.06	0.02	0.04	0.10
Early survival	0.18	0.05	0.09	0.02	0.20
Fertility	0.03	0.08	0.02	0.06	0.10
BMI					
Total	0.16	0.14	0.03	0.02	0.19
Early survival	0.24	0.03	0.17	0.06	0.32
Fertility	0.02	0.11	0.03	0.10	0.14

Values correspond to R^2 and partial R^2 obtained from linear models where selection coefficients for a given trait and for a given fitness component are regressed against two covariates: one describing the corresponding amount of fitness variation, and another representing the years allowing to capture other changes across time affecting selection. Computations were performed on bootstrapped data in order to capture uncertainty caused by sampling and measurement errors (see the Supplemental Experimental Procedures).

fitness variance and vice versa (Table 2). Together, linear trends in variance in relative total fitness and “time” accounted for 10% of interannual variation in total linear selection on height with only 2%–4% explained by each factor separately (controlling for the other, i.e., partial correlation). The respective values for selection on BMI were 19% (combined), 3% (relative fitness only), and 2% (time only). Hence, changes in fitness variance and direct change in covariance between traits and fitness only weakly predicted changes in selection when their respective effects were partitioned but captured a nonnegligible part of variation in selection across the demographic transition when they were combined.

In addition, decomposing the analysis of the determinants of changes in selection revealed important differences between trends in selection mediated by early mortality versus fertility. Variation in selection mediated by early mortality was particularly well explained by variance in relative survival and by linear trends in time, with 20% and 32% of variation explained for height and BMI, respectively (Table 2). In both of these cases, more was explained by variance alone than by time alone (9% versus 2% and 17% versus 6%, respectively), indicating that temporal changes in selection mediated by survival were mainly due to changes in the variance in relative survival rather than other environmental effects on the selection gradient. Figure 1A shows that a sudden drop in variance in early survival occurred in the early 1970s. Because this date corresponds to increased medical care delivered by the establishment of the clinic, our results suggest that this may be responsible for the large co-occurring drop in selective pressures mediated by early mortality on height and BMI.

Variation in linear selection mediated by fertility was less explained by time and variance in relative fertility and reached 10% and 14% for height and BMI, respectively. In contrast to selection mediated by early survival, variation in the linear selection gradients were less explained by variance in fertility than by time alone (3% versus 8% and 2% versus 11%), indicating that temporal linear trends in the selection gradients were not accounted for by changes in the variance in relative fertility alone. Thus, the temporal change in fertility-mediated selection on height from negative to positive, or on BMI from positive to negative, could not have been predicted from the study of demographic processes alone. These changes in selection may also be due to health care improvements that affect how health relates to height and BMI and thus indirectly to women’s fecundability.

Our findings speak to the relevance of studies using fitness variance to study selection [33, 34] and to the concerns raised by critics [29–32]. Moorad and Wade [35] recently showed how the proportion of changes in fitness variances triggered by selection on traits could be measured; here, we chose the reciprocal approach of measuring the proportion of change in selection on traits triggered by changes in fitness variances. Selection on traits necessarily shapes fitness variance, which in turn can impose constraints on selection. Therefore, both approaches are useful, and the choice that is made between them depends on whether one wants to put the emphasis on change in fitness or change in other traits. Taking the standard phenotypic selection standpoint, we show that changes in phenotypic fitness variance can predict changes in selection. This increases the credibility of studies that have only measured the opportunity for selection, by indicating that such an approach does have predictive power in the context of understanding selection. On the other hand, our results also show changes in selection that occurred independently of changes in total fitness variance, suggesting that measuring fitness variance is insufficient to fully understand temporal changes in selection on morphological traits. The fact that the change in fitness variance was more important in modifying selection mediated by survival, whereas other temporal trends were more influential in modifying selection mediated by fertility, may or may not be generalizable to other populations that undergo similar demographic trends.

Conclusions

In this study investigating the evolutionary consequences of demographic transition in a contemporary human population, we have, for two morphological traits, documented several types of changes in selection. We found cases in which such changes can and cannot be predicted by the change in fitness variance alone. We also linked environmental change (*sensu lato*, i.e., including sociocultural effects) to trait selection. Our results are important because the majority of human populations have either recently undergone or are currently undergoing a demographic transition from high to low fertility and mortality rates. Thus the temporal dynamics of the evolutionary processes revealed here may reflect the shifts in evolutionary pressures being experienced by human societies generally. A major implication is that, given the known heritability of the traits involved, such shifts in selection can be expected to be influencing genetic evolution. Knowledge of

how human phenotypes and genotypes respond to these sorts of environmental changes helps us to predict how human biology will interact with changing environments in the future, with implications for global public health and predictions of demographic change. In particular, the relaxation of early mortality selection triggered by improved health is likely to lead to an increase in maladaptations, some of which are known to be of medical importance [36]. That the duration of demographic transitions is particularly reduced in populations from the emerging world [1] potentially brings novel challenges for those populations. Importantly, we did not find evidence for the decline in overall selective pressures across the demographic transition that could be expected from observing the decline in variance in relative total fitness with time. Like other species, humans are still evolving. Human evolution did not stop with the advent of agriculture [37–41], nor do we expect that it will stop after demographic transitions have been completed. Changes in the strength and character of natural selection are likely to be the major component of such evolutionary change, and those changes are, in humans, increasingly driven by changes in culture, in particular by medical practice and public health measures.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and two figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.04.006>.

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