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APPLICATION TO FERTILITY CONTROL: A MODEL
OF EDUCATION AND SOCIAL TRANSMISSION OF
CONTRACEPTIVE USE

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ABSTRACT

The evolution of a cultural trait may be affected by niche construction, or changes in the selective environment of that trait due to the inheritance of other cultural traits that make up a cultural background. This study investigates the evolution of a cultural trait, such as the use of contraception, that is both vertically and horizontally transmitted within a homogeneous social network. Individuals conform to the norm, and adopters of the trait have fewer progeny than others. The study examines the effects of a vertically transmitted aspect of the cultural background, such as the preference for high or low levels of education, on the evolution of contraceptive use. This provides an example of cultural niche construction that facilitates the spread of traits with low Darwinian fitness while providing an environment that counteracts conformity to norms. Thus niche construction can facilitate the 'demographic transition', whereby a reduction in fertility follows a reduction in mortality.

1. INTRODUCTION

Niche construction refers to the ability of organisms to choose, regulate, construct and destroy important components of their environments, and in the process change the selection pressures to which they and other organisms are exposed (Lewontin, 1983, 2000; Odling-Smee, 1988; Odling-Smee *et al.*, 1996; Laland *et al.*, 2000, 2001; Odling-Smee *et al.*, 2003). Humans have constructed or altered many components of their selective environment to a considerable degree. Niche construction by means of innovation and technology, for example, may have had important effects on human evolution (Aunger, 2000). For example, Kwa-speaking yam cultivators of West Africa traditionally cut down the tropical forests for their slash-and-burn agriculture, creating breeding places for malaria-carrying mosquitoes. This may be responsible for the spread of the sickle-cell allele of the hemoglobin locus among those people, since in the heterozygous condition this allele confers resistance against malaria (Livingstone, 1958; Durham, 1991).

Models of human cultural evolution have been criticized for considering the evolution of cultural traits in isolation from the cultural background in a population. Niche construction theory may be particularly applicable to the evolution of cultural traits as the theory can incorporate the effects of the cultural background as a form of constructed niche (Feldman, 2003). For example, Tanaka *et al.* (2002) show how the cultural transmission of ‘careful’ or ‘risky’ behavior can act as a cultural background influencing the rate of disease transmission.

In a second example, the preference, or not, for sons over daughters may provide a cultural background, influencing the preference for sex-selective abortion and also the sex ratio at birth (SRB) in China (Laland *et al.*, 1995; Li, N., M. W. Feldman, and S. Tuljapurkar, 1999; Li, N., M. W. Feldman, and S. Li, 1999, 2000). Components of the cultural background for a particular trait may themselves be subject to evolution that is influenced by other cultural traits. For example, the preference for sons over daughters is typically associated with high fertility and the prevalence of virilocal over uxori-local marriage (Li, N. *et al.*, 2000; Li, S. *et al.*, 2000, 2003). Furthermore, the evolution of the virilocal over uxori-local marriage systems is thought to be associated with cultural factors such as a patriarchal family system and economic factors including high bride-cost and

dowry, high labour demand, the reliability of old-age support and earning potential of a son versus that of a son-in-law (Li, N. *et al.*, 2000).

Optimality models have often been used to analyse the evolution of fertility-reducing behaviors (Rogers, 1990, 1995; Kaplan *et al.*, 1995; Mace, 1996, 2000). However, recent models and reviews of fertility control have acknowledged that rather than individuals making entirely rational, optimal decisions, limited only by budget constraints, fertility control can also be affected by socially learned information and also by social influence (Cleland and Wilson, 1987; Pollak and Watkins, 1993; Bongaarts and Watkins, 1996; Montgomery and Casterline, 1996; Borgerhoff Mulder, 1998; Montgomery *et al.*, 2001; Behrman *et al.*, 2002). The term social influence is commonly used to define social processes such as conformity that can affect an individual's behavioral preferences and does not necessitate the acquisition of generic information (Montgomery and Casterline, 1996).

Gene-culture coevolutionary theory and cultural evolutionary theory (Cavalli-Sforza and Feldman, 1973, 1976, 1981), derived from classical population genetics theory, provides a suitable framework to study fertility control. It considers evolutionary dynamics as processes of frequency change, necessary to capture the effects of social learning and social influence, while defining transmission mechanisms and selection coefficients to incorporate any economic constraints. Unlike most optimality models, this approach has the advantage that the fitness of a trait is an outcome of frequency change rather than a maximization of functions chosen *a priori* by the investigator (Feldman, 2001).

Ihara and Feldman (2004) developed cultural evolutionary theory to consider the effect of cultural niche construction on the mode of transmission of a second cultural trait. In particular, they focused on the effects of a preference for a high or low level of education (i.e. 'background predisposition') on the evolution of small family size (i.e. 'fertility-reducing preference'). Here, niche construction affects the selective environment of the latter trait by influencing its mode of transmission. In particular, they assume that the average level of education may affect the degree to which traits are transmitted obliquely rather than vertically, for example, from teachers to pupils. They find that a preference for small family size can evolve if individuals with few offspring

are more likely to transmit their fertility preference to the offspring generation than individuals with a high number of offspring. This difference in the probability of transmission may result from parents with fewer offspring allocating more time and resources to achieving high status social roles (Richerson and Boyd, 1989; Nakajima and Aoki, 2002).

Here, we develop this area of research by considering the effect of cultural niche construction on the rate of *horizontal* transmission of a cultural trait, such as the preference for using some form of fertility control or contraceptive. These traits may be transmitted largely through horizontal transmission, for example, through peer groups or social networks (Montgomery and Casterline, 1996; Montgomery *et al.*, 2001; Behrman *et al.*, 2002). In addition, we investigate the effects of conformity to the norm on the evolution of a novel trait, as it is commonly observed that conformity constrains the adoption of a rare trait but facilitates the adoption of popular traits (Boyd and Richerson, 1985; Moscovici, 1985; Montgomery and Casterline, 1996). We also consider the evolution of traits that may have relatively low ‘Darwinian fitness’ (as defined by Cavalli-Sforza and Feldman, 1981). For example, parents who prefer to use contraceptives may typically have fewer offspring than those who prefer not to use contraceptives.

We consider a cultural background that consists of a vertically transmitted cultural trait, using the example of the preference for a high or low level of school education¹. While there may be many inter-related factors influencing the adoption of a high (or low) level of education, we focus on the effects of a cultural niche that is constructed through vertical transmission². Many hypotheses have been proposed to explain the well established negative relationship between level of education and fertility and also the positive relationship between the level of education and contraceptive use (Chaudhury, 1984; Heaton and Forste, 1998; Koc, 2000; Capo-chichi and Juarez, 2001; Basu, 2002; Murthi, 2002; McNay *et al.*, 2003). Here, we focus solely on the effect of education on the *rate* of horizontal transmission.

¹ ‘High’ and ‘low’ levels of education simply refer to the amount of formal school education received by the child.

² Note that some costs or economic constraints associated with the adoption of a high (or low) level of education may be assumed to be subsumed within the coefficient of vertical transmission.

Features of the cultural background, such as the average level of education in the population, are likely to influence the rate of horizontal transmission of traits in a number of ways. First, members of a social network may be more likely to be exposed to new ideas taught at school, including methods of contraception, if the average level of education is high rather than low (Cleland and Wilson, 1987). Second, education may enhance the fidelity of information transmission; for example, literacy may allow information to spread by written word with a lower mutation rate than by word of mouth. Third, the level of education is often positively related to wealth (Rogers, 1995; Mace, 2000). Wealthy, educated populations may be likely to enhance the rate of horizontal transmission of traits by using communication infrastructures such as a telephone network that cannot be afforded in poorer populations. Furthermore, the spread of traits such as the use of contraception may be facilitated in wealthy populations that have access to healthcare (Murthi, 2002), which can provide individuals with the option to use contraceptives. Healthcare may also reduce child mortality and thus increase the preference for the use of fertility control.

2. THE MODEL

The model considers two cultural traits. The first cultural trait, **E**, provides a cultural background or niche that may affect the evolution of the second cultural trait, **A**. There are two forms of each trait, *E* and *e* and *A* and *a*. The frequencies of individuals of the four cultural types *EA*, *Ea*, *eA* and *ea* are given by x_1 , x_2 , x_3 and x_4 , respectively. The frequencies of types *E* and *A* are given by $p = x_1 + x_2$ and $q = x_1 + x_3$, respectively.

The cultural niche, **E**, may represent the level of education in a human population. Thus *E* represents a high level of education and *e* represents a low level of education. Offspring inherit the *E* or *e* from their parents with the probabilities b_i and $1 - b_i$, respectively, as shown in the upper half of table 1 (where $0 \leq b_i \leq 1$ and $i=0, 1, 2$ and 3 distinguish the mating pair types (mother-father) *e-e*, *e-E*, *E-e* and *E-E*, respectively).

Table 1: Cultural transmission of E/e and A/a .

Type of Mating Pair	Offspring	
	E	e
Mother - Father		
$E-E$	b_3	$(1-b_3)$
$E-e$	b_2	$(1-b_2)$
$e-E$	b_1	$(1-b_1)$
$e-e$	b_0	$(1-b_0)$
$A-A$	c_3	$(1-c_3)$
$A-a$	c_2	$(1-c_2)$
$a-A$	c_1	$(1-c_1)$
$a-a$	c_0	$(1-c_0)$

The second cultural trait, **A**, also has two alternative states, A and a , representing the respective use, or not, of contraception. The fertility of a mating pair decreases as the number of A individuals in the pair (i.e., 0, 1 or 2) increases. Specifically, the relative numbers of offspring for the four possible mother-father pairs $A-A$, $A-a$, $a-A$ and $a-a$, are $1-f$, $1-f/2$, $1-f/2$ and 1 , respectively (where $0 \leq f \leq 1$).

It is assumed that a preference for the use of contraception is transmitted horizontally within the offspring generation. However for this process to occur, trait **A** must be present in the offspring generation. Thus, prior to horizontal transmission, it is assumed that states A and a are vertically transmitted from parents to offspring with the probabilities, c_i and $1-c_i$, respectively (where $0 \leq c_i \leq 1$), as shown in the lower half of table 1. The frequencies x_1-x_4 after vertical transmission are shown in Appendix I.

After vertical transmission of trait **A**, type A is transmitted horizontally within the offspring generation (c). The probability that an individual acquires A through horizontal transmission, α , is dependent, in part, on a coefficient of horizontal transmission, h , and

the frequency of A in the offspring generation, q^c (see Eq. (1))³. α is also affected by the frequency of type E in the offspring generation, p^c , with a magnitude determined by the niche construction parameter, γ ⁴. Further, it is assumed that α is affected by conformity to the norm, represented by the function $1+\psi(2q^c-1)$. Thus, for positive values of the conformity coefficient, ψ , horizontal transmission of A is reduced when $q^c < 1/2$ and enhanced when $q^c > 1/2$. After horizontal transmission, the frequencies in the offspring generation (indicated by primes) are given by

$$x_i' = \mathbf{H}x_i^c, \quad (1)$$

$$\text{where } \mathbf{H} = \begin{pmatrix} 1 & \alpha & 0 & 0 \\ 0 & 1-\alpha & 0 & 0 \\ 0 & 0 & 1 & \alpha \\ 0 & 0 & 0 & 1-\alpha \end{pmatrix}, \quad \alpha = hq^c(1+\gamma p^c)(1+\psi(2q^c-1)),$$

$$0 \leq h \leq 1, \quad 0 \leq \psi \leq 1 \quad \text{and} \quad h(1+\gamma)(1+\psi) \leq 1.$$

For simplicity, we focus on the case where $b_3=1$, $b_0=0$, $c_3=1$ and $c_0=0$. Overall, the change in the frequency of E and A between generations is given by

$$\Delta p = p(1-p)(b_1+b_2-1) - \frac{D}{W} f \left[\frac{b_1+b_2}{2} - (b_1+b_2-1)p \right] \quad (2)$$

and

$$\Delta q = (1-\alpha) \frac{q(1-q)}{W} \left[(c_1+c_2) \left(1 - \frac{f}{2} \right) - 1 \right] + \alpha(1-q), \quad (3)$$

respectively, where the statistical association between the two traits is $D = x_1x_4 - x_2x_3$, the mean fitness of the population is $W = 1 - fq$, and the rate that an individual acquires A by horizontal transmission is $\alpha = hq^c(1+\gamma p^c)(1+\psi(2q^c-1))$. We have not shown the change in the statistical association between the two traits, D , as it is lengthy.

³We assume that the probability of a type A individual acquiring trait a is negligible.

⁴Note that we focus on the niche constructive effects of the mean level of education in the population rather than effects of the level of education adopted by each individual.

3. RESULTS

3.1. Rate of Change of Contraceptive Use

The first term of (3) represents the change in the frequency of contraceptive users that results from vertical transmission and fertility selection. In the absence of other processes, vertical transmission from parents to offspring is unbiased if $c_1+c_2=1$, biased to favour the transmission of A over a if $c_1+c_2>1$, but biased to favour the transmission of a over A if $c_1+c_2<1$. The second term of (3) represents the change in the frequency of contraceptive users that results from horizontal transmission. There is no change in the frequency of A if $q=0$ or $q=1$, since

$$q^c = q \left\{ \frac{1-q}{W} \left[(c_1 + c_2) \left(1 - \frac{f}{2} \right) - 1 \right] + 1 \right\}. \quad (4)$$

Partial differentials were taken to clarify the impact of each of the parameters (f , h , γ , ψ and $c_{tot}=c_1+c_2$) on the rate of change in the frequency of A (see Appendix II). Fertility selection, f , has a negative impact on the rate of change of the frequency of A , as shown by its influence in (3). The rate of change in the frequency of A is positively related to the fidelity of vertical transmission, $c_{tot}=c_1+c_2$, the coefficient of horizontal transmission, h , and the niche construction coefficient, γ . The model assumes that individuals only conform to A if it is more frequent than a in the population. Thus, the conformity coefficient, ψ , is positively related to the rate of change in the frequency of A when $q^c>1/2$ and negatively related when $q^c<1/2$. Figure 1 shows an example where conformity for a when A is rare delays the initial increase in the frequency of A .

We have not shown the impact of each of the parameters on the statistical association between the two traits, D , but numerical analysis suggests that typically D is extremely small.

Figure 1

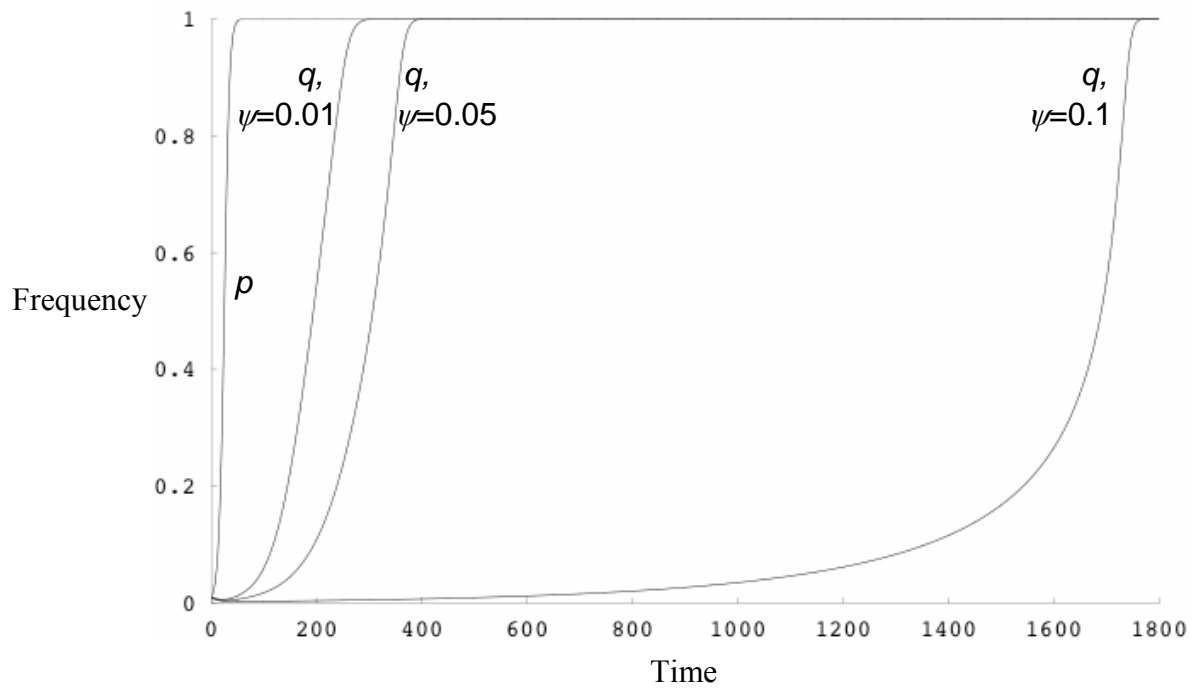


Figure 1: The graph shows the frequency of E (dashed line) and A (solid lines) with different values of the conformity coefficient, ψ , where $b_1=b_2=0.6$, $c_1=c_2=0.5$, $h=0.4$, $f=0.6$ and $\gamma=0.2$. When q is small, larger values of ψ increase conformity to a which delays the increase in q .

3.2. Local Stability of the Corner Equilibrium States

This analysis considers the local stability of the four ‘corner’ equilibrium states for (\hat{p}, \hat{q}) , namely $E_0(0,0)$, $E_1(1,0)$, $E_2(0,1)$ and $E_3(1,1)$, corresponding to $x_4=1$, $x_2=1$, $x_3=1$ and $x_1=1$, respectively.

If vertical transmission bias favours e over E ($b_1+b_2 < 1$), the equilibrium $E_0(0,0)$ is unstable and invaded by A only if

$$(c_1 + c_2) \left(1 - \frac{f}{2}\right) > \frac{1}{1 + h(1 - \psi)}, \quad (5)$$

while the equilibrium $E_2(0,1)$ is unstable if

$$(c_1 + c_2) \left(1 - \frac{f}{2}\right) < 1 - \frac{(1 - f)h(1 + \psi)}{1 - h(1 + \psi)}, \quad (6)$$

and stable otherwise. If $b_1+b_2 > 1$, both $E_0(0,0)$ and $E_2(0,1)$ are unstable.

Figure 2

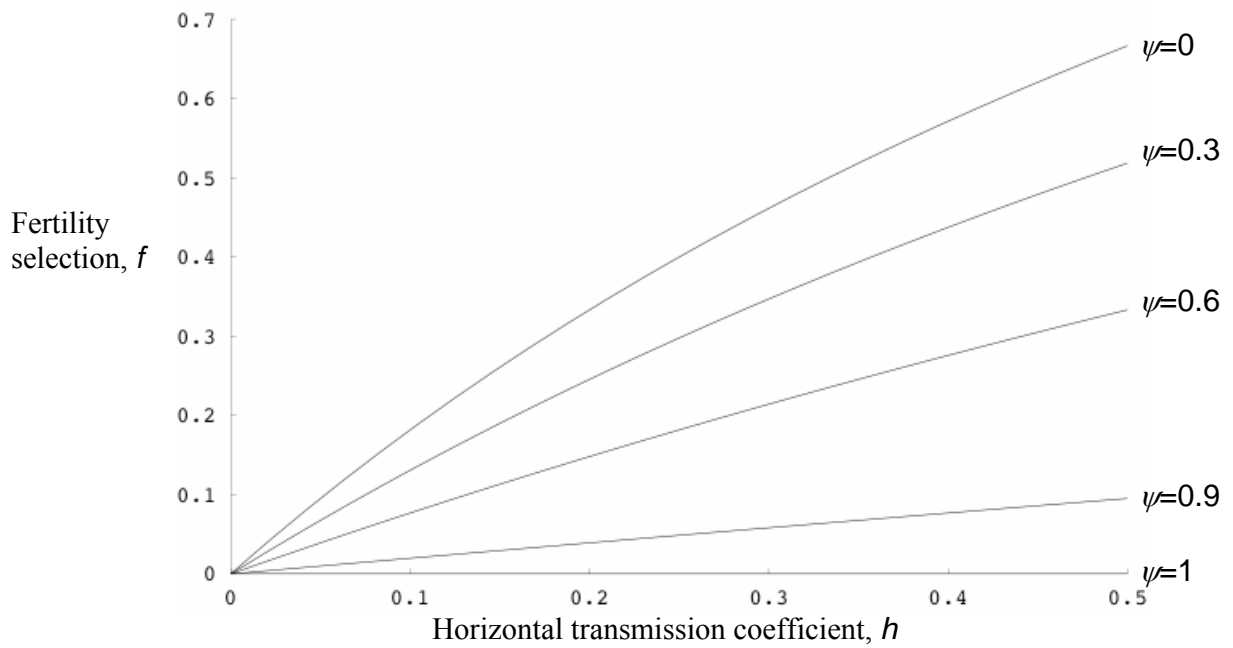


Figure 2: $E_0(0,0)$ is unstable in the regions under the lines given by Eq. (7) for the given conformity coefficient, ψ , across the given values of fertility selection, f , and horizontal transmission coefficients, h , where $c_1+c_2=1$, $\gamma=0$, and for any values of b_1 and b_2 where $b_1+b_2 < 1$.

Assuming that the vertical transmission of A is unbiased ($c_1+c_2=1$), (5) can be rearranged to derive the line

$$f = 2\left(1 - \frac{1}{1+h(1-\psi)}\right), \quad (7)$$

which specifies values of f below which A invades as a result of horizontal transmission (see Figure 2). Figure 2 shows that invasion of A can occur at high fertility selection, f , if the coefficient of horizontal transmission, h , is also high and conformity, ψ , is low.

When A is rare, conformity to a constrains the invasion of A . Thus invasion is only possible at particularly low values of fertility selection, f , but is impossible when the conformity coefficient, $\psi=1$. Note that in this case, niche construction does not influence invasion by A as $\hat{p} = 0$.

The equilibria $E_1(1,0)$ and $E_3(1,1)$ are both unstable if $b_1+b_2 < 1$. If $b_1+b_2 > 1$, $E_1(1,0)$ is unstable and invaded by A if

$$(c_1 + c_2)\left(1 - \frac{f}{2}\right) > \frac{1}{1+h(1-\psi)(1+\gamma)}, \quad (8)$$

while $E_3(1,1)$ is unstable if

$$(c_1 + c_2)\left(1 - \frac{f}{2}\right) < 1 - \frac{(1-f)h(1+\psi)(1+\gamma)}{1-h(1+\psi)(1+\gamma)}, \quad (9)$$

and is locally stable otherwise.

Figure 3

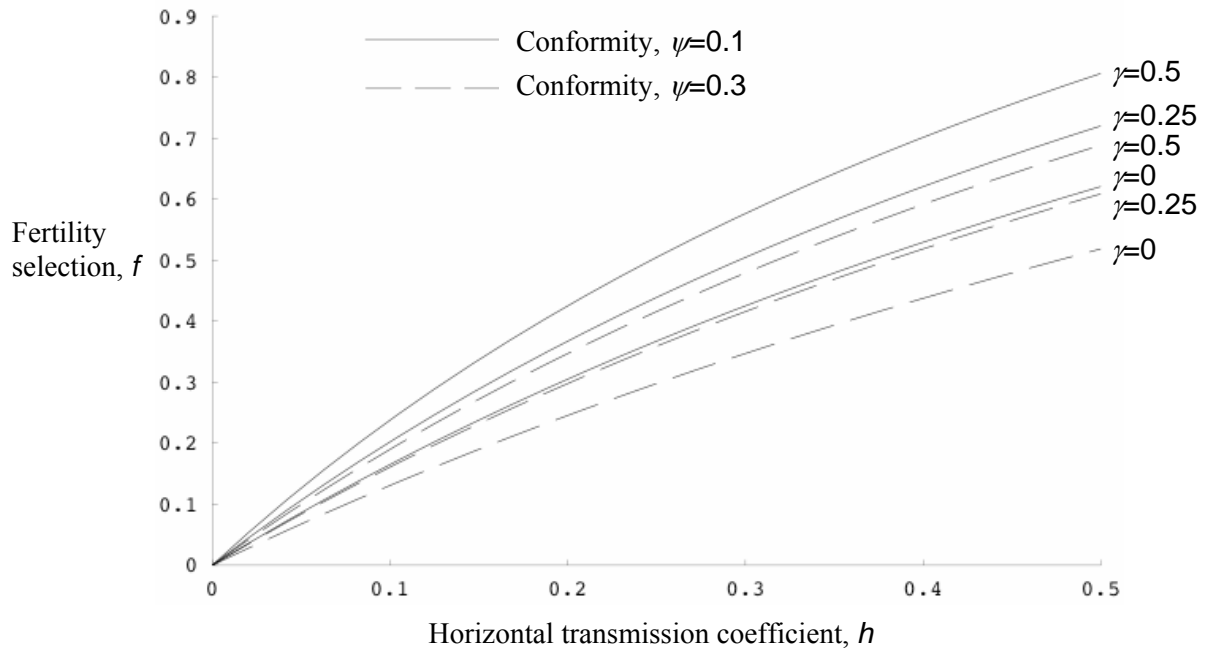


Figure 3: $E_I(1,0)$ is unstable in the regions under the lines given by Eq. (10) for the given conformity coefficient, ψ , across the given values of fertility selection, f , and horizontal transmission coefficients, h , where $c_1+c_2=1$, $\gamma=0$, and for any values of b_1 and b_2 where $b_1+b_2 < 1$.

Assuming that the vertical transmission of A is unbiased ($c_1+c_2=1$), (8) can be rearranged to derive the line

$$f = 2 \left(1 - \frac{1}{1 + h(1 - \psi)(1 + \gamma)} \right), \quad (10)$$

which specifies values of f below which A invades as a result of horizontal transmission (see Figure 3). In the absence of niche construction ($\gamma=0$) (10) is identical to (7) (also see Figure 2). However, at $E_I(1,0)$, $\hat{p} = 1$, and thus positive values of the niche construction coefficient ($\gamma > 0$) increase the region of parameter space (f , h and ψ) under which A is predicted to invade the population. In particular, figure 3 shows that in the presence of niche construction, A is predicted to invade under a lower coefficient of horizontal transmission for a given level of fertility selection than in the absence of niche construction. As in the absence of niche construction, the invasion of A is constrained by the level of conformity to a .

3.3. Global Stability Analysis

Numerical analysis shows that if there is vertical transmission bias favouring e over E (i.e. $b_1+b_2 < 1$), E always goes extinct ($\hat{p} = 0$), while if vertical transmission bias favours E over e (i.e. $b_1+b_2 > 1$), E always spreads to fixation ($\hat{p} = 1$).

The evolution of A in the absence of conformity, $\psi=0$

In this case, (3) can be rearranged to give

$$\Delta q = \frac{q(1-q)}{W^2} F(q), \quad (11)$$

where $F(q)$ is given by the following quadratic

$$F(q) = q^2 \phi_2^2 h(1 + \gamma^c) + q[\phi_1(\phi_1 + \phi_2) + \phi_2 h(2 + \phi_1)(1 + \gamma^c)] + \phi_1 + (1 + \phi_1)h(1 + \gamma^c),$$

where $\phi_1 = (c_1 + c_2) \left(1 - \frac{f}{2} \right) - 1$ and $\phi_2 = (2 - c_1 - c_2) \left(1 - \frac{f}{2} \right) - 1$.

In addition to the four corner equilibria ($E_0(0,0)$, $E_I(1,0)$, $E_2(0,1)$ and $E_3(1,1)$), the system may approach the edge equilibrium $E_4(0, \hat{q}_0)$, where $0 < \hat{q}_0 < 1$, if $b_1+b_2 < 1$, and

the edge equilibrium $E_5(1, \hat{q}_1)$, where $0 < \hat{q}_1 < 1$, if $b_1+b_2 > 1$. The roots of $F(q)$ may give equilibria of type $E_4(0, \hat{q}_0)$ if $b_1+b_2 < 1$ and of type $E_5(1, \hat{q}_1)$ if $b_1+b_2 > 1$. Next, we outline the conditions under which the equilibria are locally stable. Here, we consider $b_1+b_2 > 1$, in which case E becomes fixed in the population ($\hat{p} = 1$ and thus $p^c = 1$). Note that at equilibrium, there is no effect of niche construction on A if $b_1+b_2 < 1$. Thus, the equivalent conditions satisfying equilibrium stability can be found by setting $\gamma=0$.

If $0 < q < 1$, the sign of Δq is equivalent to that of $F(q)$. We find that

$$F(0) = (c_1 + c_2) \left(1 - \frac{f}{2}\right) [1 + h(1 + \gamma)] - 1, \quad (12)$$

and thus, from (8), $E_I(1,0)$ is locally stable if $F(0) < 0$ and unstable when $F(0) > 0$.

We also find that

$$F(1) = (1 - f) \left\{ 1 - f - (2 - c_1 - c_2) \left(1 - \frac{f}{2}\right) [1 - h(1 + \gamma)] \right\}, \quad (13)$$

and thus, from (9), $E_3(1,1)$ is locally stable if $F(1) > 0$ and unstable if $F(1) < 0$.

Figure 4 (following page): Sample trajectories and equilibria when $\psi = 0$. The trajectories are from various initial values of p and q (initial value for D is always zero). The arrows indicate directions of change. The filled circles represent locally stable equilibria while the empty circles are unstable equilibria. (a) $c_2 = c_1 = 0.5$, $\gamma = 0.2$; (b) $c_2 = c_1 = 0.4$, $\gamma = 2$; (c) $c_2 = c_1 = 0.59$, $\gamma = 0.2$; (d) $c_2 = c_1 = 0.5$, $\gamma = 1.25$; and (e) $c_2 = c_1 = 0.5$, $\gamma = 2$. Other parameter values are $b_2 = b_1 = 0.6$, $f = 0.6$, and $h = 0.2$.

Figure 4

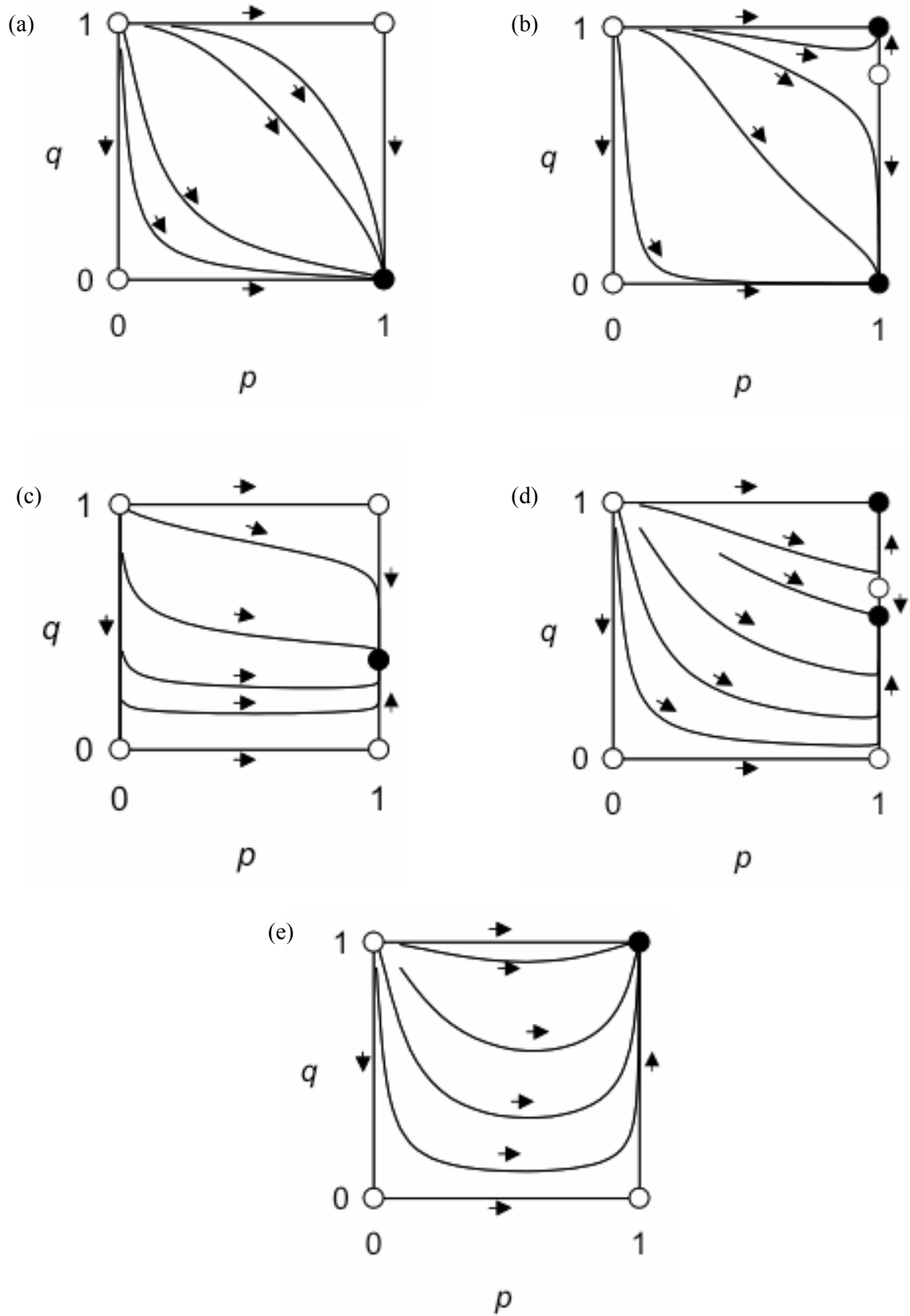


Figure 4a shows that if $E_I(1,0)$ is locally stable ($F(0)<0$) and $E_3(1,1)$ is unstable ($F(1)<0$), the frequency of A always decreases to the equilibrium $E_I(1,0)$. There is no edge equilibrium as both the roots of the quadratic function, $F(q)=0$, lie outside the range $0 \leq q \leq 1$. Thus, the equilibrium $E_I(1,0)$ is globally stable.

If $E_3(1,1)$ is stable ($F(1)>0$), since we can express $F(0)$ as

$$F(0) = \frac{F(1)}{1-f} + (2-f)(c_1 + c_2 - 1)h(1 + \gamma p^c), \quad (14)$$

for $F(0)<0$, it is necessary that $c_1 + c_2 < 1$. When $F(0) < 0$ and $F(1) > 0$, $E_I(1,0)$ is also stable and there is one unstable edge equilibrium ($E_5(1, \hat{q}_1)$), where \hat{q}_1 is the larger of the two roots of the quadratic, $F(q)=0$. Figure 4b shows that A approaches one of the fixation points, $E_3(1,1)$ or $E_I(1,0)$, depending on the initial state.

If $E_I(1,0)$ is unstable ($F(0)>0$), since we can express $F(1)$ as

$$F(1) = (1-f) \left[F(0) - (2-f)(c_1 + c_2 - 1)h(1 + \gamma p^c) \right], \quad (15)$$

for $F(1)<0$, it is necessary that $c_1 + c_2 > 1$. When $F(0) > 0$ and $F(1) < 0$, both $E_I(1,0)$ and $E_3(1,1)$ are unstable and the frequency of A moves to a globally stable equilibrium, $E_5(1, \hat{q}_1)$, where \hat{q}_1 is the smaller solution of the quadratic $F(q)=0$ (Figure 4c).

If $E_I(1,0)$ is unstable ($F(0)>0$) and $E_3(1,1)$ is stable ($F(1)>1$), numerical analysis reveals that there may either be zero or two edge equilibria within the range $0 < \hat{q}_1 < 1$, depending on the parameter values. Figure 4d shows that if there are two such edge equilibria, the lower frequency edge equilibrium is always stable while the higher frequency edge equilibrium is always unstable. The frequency of A moves to either $E_5(1, \hat{q}_1)$ or $E_3(1,1)$, depending on the initial state. Figure 4e shows that $E_3(1,1)$ is globally stable if there is no edge equilibrium.

The evolution of A with conformity, $\psi>0$

We were unable to solve $\Delta q = 0$ in (3) to derive explicit conditions for the various equilibrium states. However, numerical analysis reveals that the conditions under which $E_2(0,1)$ (or $E_3(1,1)$) is locally stable do not always preclude stability of $E_0(0,0)$ (or $E_I(1,0)$). In other words, the local stability of either $E_2(0,1)$ or $E_3(1,1)$ does not guarantee

their global stability. Hence, initial increase of A when it is rare, may not always entail that it goes to fixation.

Numerical analysis also reveals that if $b_1+b_2 < 1$, the population will converge to one of $E_0(0,0)$, $E_2(0,1)$ or a locally stable edge equilibrium, $E_4^L(0, \hat{q}_0)$. In addition, there can be up to two unstable edge equilibria. We represent an unstable edge equilibrium by $E_4^U(0, \hat{q}_0)$. If neither $E_0(0,0)$ nor $E_2(0,1)$ is locally stable, the population always converges to $E_4^L(0, \hat{q}_0)$. We are able to determine (see Appendix III) that for this to occur it is necessary that

$$c_1 + c_2 > 1 + \psi . \tag{16}$$

Thus, an edge equilibrium may be attained if there is a bias in vertical transmission favouring A and the bias exceeds the strength of conformity, preventing A from going extinct when A is rare and conformity favours type a . If one of $E_0(0,0)$ or $E_2(0,1)$ is locally stable, then an unstable edge equilibrium, $E_4^U(0, \hat{q}_0)$, and a locally stable edge equilibrium, $E_4^L(0, \hat{q}_0)$, exist under certain parameter conditions. If $E_0(0,0)$ and $E_2(0,1)$ are both locally stable, there exists either one unstable edge equilibrium, $E_4^U(0, \hat{q}_0)$, or under a highly restricted set of parameter conditions, a locally stable edge equilibrium of intermediate frequency between two unstable edge equilibria.

Similarly, if $b_1+b_2 > 1$, the population will converge to one of $E_1(1,0)$, $E_3(1,1)$ or $E_5^L(0, \hat{q}_0)$ and there can be up to two unstable edge equilibria. If neither $E_1(1,0)$ nor $E_3(1,1)$ is locally stable, the population always converges to $E_5^L(0, \hat{q}_0)$ also requiring (16) to be satisfied. However, if one of $E_1(1,0)$ or $E_3(1,1)$ is locally stable, then an unstable edge equilibrium, $E_5^U(0, \hat{q}_0)$, and a locally stable edge equilibrium, $E_5^L(0, \hat{q}_0)$, exist under certain parameter conditions. If $E_1(1,0)$ and $E_3(1,1)$ are both locally stable, there exists either one unstable edge equilibrium, $E_5^U(0, \hat{q}_0)$, or under a highly restricted set of parameter conditions, a locally stable edge equilibrium of intermediate frequency between two unstable edge equilibria.

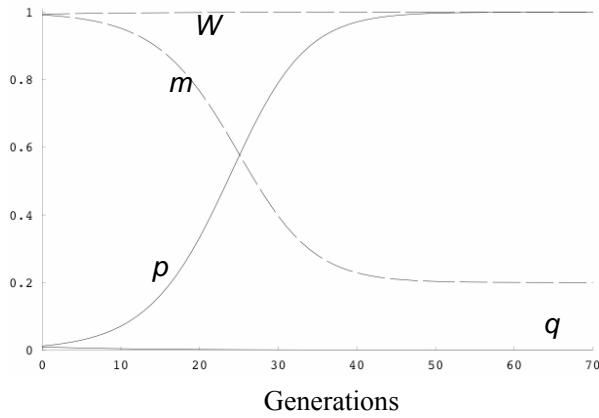
3.4. The Effect of the Cultural Background on the Viability of Individuals

Often, the average level of education is positively correlated with other measures of development, including income and life expectancy (U. N. D. P. , 1990; Bongaarts and Watkins, 1996). In this section, we consider the case where the cultural background, determined by the frequency of E individuals, affects not only the rate of horizontal transmission but also the viability of individuals. Following Ihara and Feldman (2003), we assume that a proportion, $1 - v_0(1 + v_1 p)$, of juveniles die before maturity (where $0 < v_1 < 1$ and $0 < v_0 < 1/(1 + v_1)$). Thus the relative mortality of the population, m , is given by

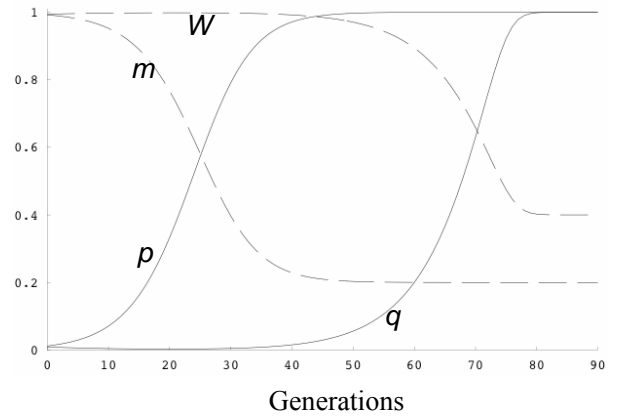
$$m = \frac{1 - v_0(1 + v_1 p)}{1 - v_0}, \quad (17)$$

and is a decreasing function of p ($0 < m < 1$).

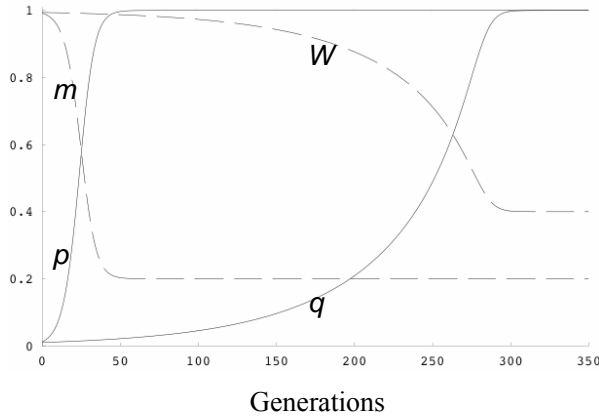
(a) No niche construction, $\gamma = 0$, and fidelity of horizontal transmission, $h = 0.35$.



(b) Niche construction, $\gamma = 1$, and fidelity of horizontal transmission, $h = 0.35$.



(c) No niche construction, $\gamma = 0$, and high fidelity of horizontal transmission, $h = 0.5$.



(d) Niche construction, $\gamma = 0.8$, and high fidelity of horizontal transmission, $h = 0.5$.

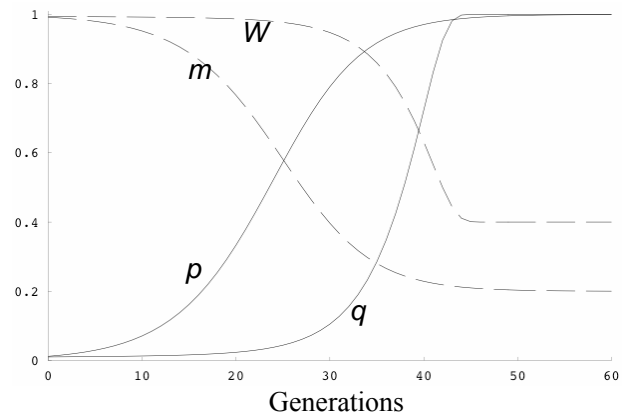


Figure 5: Changes in the frequency of the cultural background, p , the frequency of contraceptive use, q , the average relative mortality, m , and the average relative fertility, W , across generations, where $v_0=0.5$, $v_1=0.8$, $b_1=b_2=0.6$, $c_1=c_2=0.5$, $f=0.6$ and $\psi=0.1$. Niche construction, determined by γ , occurs in parts (b) and (d) but not parts (a) and (c). The coefficient of horizontal transmission is higher in parts (c) and (d) than in parts (a) and (b).

Figure 5 shows examples of changes in p , q , m and W across generations. As in Ihara and Feldman (2004), we find that under conditions where both E and A increase from low values to fixation, the increase in E is accompanied by a decrease in mortality while the increase in A is accompanied by a decline in fertility. Parts (a) and (b) of figure 5 compare the dynamics under conditions where niche construction is required for the fixation of A . In the absence of niche construction (Figure 5a) the decline in mortality is not followed by a decline in fertility. Figure 5c shows an example where A becomes fixed in the absence of niche construction because the coefficient of horizontal transmission, h , is particularly high. However, in such cases the time taken for the fixation of A is always slower than in the presence of niche construction (Figure 5d).

It is worth noting that there can be large variation in the time lag between the change in frequency of E accompanied by m , and A accompanied by W , depending on the parameter values. Indeed, A can even spread to fixation faster than E if the rate of horizontal transmission is sufficiently high and fertility selection is sufficiently low. Finally, in all cases where A increases in frequency in the absence of niche construction, both mortality and fertility decline simultaneously (i.e. starting at generation zero) (e.g. Figures 5c-d). However, if niche construction is required for A to spread, there is a time-lag between the decline in mortality and fertility, lasting until the average level of education is sufficient to drive an increase in the frequency of A (e.g. Figure 5b).

4. DISCUSSION

A bias in the vertical transmission of a cultural background favouring a high level of education over a low level of education may facilitate the horizontal transmission of a trait such as the use of contraception. This type of niche construction can be a critical factor in allowing the preference for contraceptive use to spread either to a polymorphic equilibrium or to fixation, despite fertility selection favouring a over A and conformity to a when A is rare. Thus cultural niche construction can facilitate the spread of traits with low Darwinian fitness and can provide an environment that counteracts conformity to norms.

The model predicts that for contraceptive use to spread through a population, the rate of horizontal transmission must be sufficient to counteract any reduction in the trait

frequency that results from fertility selection. If these processes balance one another, it is possible for the trait to reach a polymorphic equilibrium. Under such circumstances, promotion of fertility control by the media or by institutional changes may be necessary for the rate of horizontal transmission to be enhanced so that fertility control spreads to fixation.

Montgomery and Casterline (1996) suggest that “social effects may help to explain ... the curious lags in the response of fertility to changes in underlying determinants and, conversely, sudden bursts of change in fertility”. Our model shows how conformity can suppress the response of a preference for fertility control to changes in the average level of education. Conversely, the model shows that once the majority of the population have adopted fertility control, the rate of change in its adoption is positively related to the coefficient of conformity.

The spread of the use of contraception may contribute to the ‘demographic transition’, characterized by a reduction in fertility often found in societies undergoing industrialization (Vining, 1986). A demographic transition is typically associated with an increase in the level of education and a decrease in mortality, followed by a reduction in fertility. There are at least three evolutionary hypotheses for the demographic transition (reviewed in Borgerhoff Mulder, 1998). First, small family size may be evolutionarily advantageous in conditions where parental investment is critical for offspring reproduction. Second, the decrease in fertility may be a maladaptive response to the modern environment, which has changed drastically from those in which human psychological and physiological mechanisms evolved. Third, the decrease in fertility may be a result of Darwinian cultural evolution, which may not necessarily maximize biological fitness.

Our model is in accordance with the third hypothesis (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). The model shows that an increase in the level of education may provide a cultural background that facilitates a subsequent reduction in fertility by increasing the rate of horizontal transmission of traits such as the use of contraception. From our model, a time lag between the decline in mortality and fertility suggests that such cultural niche construction is critical to the spread of the latter.

The model also predicts that the length of the time lag is inversely related to the magnitude of the cultural niche construction.

We have assumed an unstructured population. However the cultural niche may also affect the rate of horizontal transmission between populations, within a metapopulation. For example, Bongaarts and Watkins (1996) note that the earliest countries to undergo the demographic transition were those that were most highly developed, measured as a linear combination of literacy, life expectancy and real GDP per capita. However, with time, the onset of the transition in different countries occurred at ever lower levels of development. Moreover, they found that the pace of fertility decline is related to the level of development when the transition begins and not the pace of development. They suggest that the decline in fertility is affected by a nested set of social interactions: within social networks, between social networks within a country, and between countries within the global community. Thus, niche construction may have affected patterns of fertility control between social networks and also between countries.

Our analysis shows how education may influence the evolution of a fertility-reducing trait by enhancing the rate of horizontal transmission. Ihara and Feldman (2004) show that education may also influence the evolution of a fertility-reducing trait as a function of the mode of transmission by assuming that high education facilitates the rate of oblique transmission relative to vertical transmission. As in the current model, their model generates dynamics that are consistent with a demographic transition. In both Ihara and Feldman (2004) and the current study, the common influence of the average level of education on the evolution of a low-fertility trait is for the former to enhance the rate with which the latter is transmitted. An interesting difference between the outcome of the models is that Ihara and Feldman's oblique transmission model always generates a single globally stable equilibrium, while for our horizontal transmission model, in the absence of conformity, two equilibria can be locally stable under a single set of parameter values (see Figure 4b and d). The various assumptions and predictions of our model can be tested using established methods to estimate the rate of vertical and horizontal transmission of traits (Hewlett and Cavalli-Sforza, 1986; Guglielmino *et al.*, 1995; Li *et al.*, 2000; Hewlett *et al.*, 2002).

Using the simple ‘two locus’ modelling paradigm, both Ihara and Feldman (2004) and the current study show that an increase in the level of education may contribute to a demographic transition by affecting the rate at which fertility-reducing traits are adopted. However, many other factors must be considered to explain a demographic transition completely (Watkins, 1990; Kaplan *et al.*, 1995; Borgerhoff Mulder, 1998; Basu, 2002; Murthi, 2002). For example, influences on fertility control may include the cost of education, changes in child-mortality, women’s education in particular, the mass media and institutional changes, parental investment and the inheritance of wealth (Borgerhoff Mulder, 1998; Mace, 2000; Basu, 2002; Murthi, 2002).

There may be a wide range of cases for which similar models could be developed to predict the influence of a vertically transmitted trait on the evolution of a horizontally transmitted trait. For example, a vertically transmitted preference for sons over daughters may influence the horizontal transmission of information about availability of ultrasound B for foetal sex detection or the behavioral act of carrying out sex-selective abortion (Li, N., M. W. Feldman, and S. Tuljapurkar, 1999; Li, N., M. W. Feldman, and S. Li, 1999, 2000; Feldman, 2003). Traits that are vertically transmitted in many societies, for example, religious beliefs and preferences for particular social stratification may influence the horizontal transmission of traits concerning political change, sexual equality and gender orientation. The mechanism of the interaction between the two traits, however, may differ between each of these cases. Indeed, horizontally transmitted traits may sometimes provide a cultural niche that affects the persistence of vertically transmitted traits. For instance, the horizontal transmission of technological innovations may influence vertically transmitted division of labour between sexes for skills such as food gathering, farming and manual labour.

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Appendix I – The Frequencies $x_1 - x_4$ after Vertical Transmission

$$\begin{aligned}
 Wx_1^c &= (1-f)c_3 \left[b_3 x_1^2 + (b_2 + b_1)x_1 x_3 + b_0 x_3^2 \right] \\
 &\quad + (1-f/2)c_2 (b_3 x_1 x_2 + b_2 x_1 x_4 + b_1 x_2 x_3 + b_0 x_3 x_4) \\
 &\quad + (1-f/2)c_1 (b_3 x_1 x_2 + b_2 x_2 x_3 + b_1 x_1 x_4 + b_0 x_3 x_4) \text{ ,} \\
 &\quad + c_0 \left[b_3 x_2^2 + (b_2 + b_1)x_2 x_4 + b_0 x_4^2 \right]
 \end{aligned} \tag{A1}$$

$$\begin{aligned}
 Wx_2^c &= (1-f)(1-c_3) \left[b_3 x_1^2 + (b_2 + b_1)x_1 x_3 + b_0 x_3^2 \right] \\
 &\quad + (1-f/2)(1-c_2) (b_3 x_1 x_2 + b_2 x_1 x_4 + b_1 x_2 x_3 + b_0 x_3 x_4) \\
 &\quad + (1-f/2)(1-c_1) (b_3 x_1 x_2 + b_2 x_2 x_3 + b_1 x_1 x_4 + b_0 x_3 x_4) \text{ ,} \\
 &\quad + (1-c_0) \left[b_3 x_2^2 + (b_2 + b_1)x_2 x_4 + b_0 x_4^2 \right]
 \end{aligned} \tag{A2}$$

$$\begin{aligned}
 Wx_3^c &= (1-f)c_3 \left[(1-b_3)x_1^2 + (2-b_2-b_1)x_1 x_3 + (1-b_0)x_3^2 \right] \\
 &\quad + (1-f/2)c_2 \left[(1-b_3)x_1 x_2 + (1-b_2)x_1 x_4 + (1-b_1)x_2 x_3 + (1-b_0)x_3 x_4 \right] \\
 &\quad + (1-f/2)c_1 \left[(1-b_3)x_1 x_2 + (1-b_2)x_2 x_3 + (1-b_1)x_1 x_4 + (1-b_0)x_3 x_4 \right] \text{ ,} \\
 &\quad + c_0 \left[(1-b_3)x_2^2 + (2-b_2-b_1)x_2 x_4 + (1-b_0)x_4^2 \right]
 \end{aligned} \tag{A3}$$

and

$$\begin{aligned}
 Wx_4^c &= (1-f)(1-c_3) \left[(1-b_3)x_1^2 + (2-b_2-b_1)x_1 x_3 + (1-b_0)x_3^2 \right] \\
 &\quad + (1-f/2)(1-c_2) \left[(1-b_3)x_1 x_2 + (1-b_2)x_1 x_4 + (1-b_1)x_2 x_3 + (1-b_0)x_3 x_4 \right] \\
 &\quad + (1-f/2)(1-c_1) \left[(1-b_3)x_1 x_2 + (1-b_2)x_2 x_3 + (1-b_1)x_1 x_4 + (1-b_0)x_3 x_4 \right] \text{ ,} \\
 &\quad + (1-c_0) \left[(1-b_3)x_2^2 + (2-b_2-b_1)x_2 x_4 + (1-b_0)x_4^2 \right]
 \end{aligned} \tag{A4}$$

where $W = 1 - f(x_1 + x_3) = 1 - fq$.

Appendix II – Partial Derivatives

$$\frac{\partial \Delta q}{\partial f} = -\frac{1-\alpha}{2W^2} q(1-q)[(c_1 + c_2)(1-q) + (2 - c_1 - c_2)q] \quad (\text{A5})$$

$$\frac{\partial \Delta q}{\partial h} = \frac{1-q}{W} \left[1-q + q \left(1 - \frac{f}{2} \right) (2 - c_1 - c_2) \right] q^c (1 + \eta p^c) [1 + \psi(2q^c - 1)] \quad (\text{A6})$$

$$\frac{\partial \Delta q}{\partial \gamma} = \frac{1-q}{W} \left[1-q + q \left(1 - \frac{f}{2} \right) (2 - c_1 - c_2) \right] h p^c q^c [1 + \psi(2q^c - 1)] \quad (\text{A7})$$

$$\frac{\partial \Delta q}{\partial c_{tot}} = \frac{1-q}{W} q(1-\alpha) \left(1 - \frac{f}{2} \right), \quad (\text{A8})$$

$$\frac{\partial \Delta q}{\partial \psi} = \frac{1-q}{W} \left[1-q + q \left(1 - \frac{f}{2} \right) (2 - c_1 - c_2) \right] h q^c (1 + \eta p^c) (2q^c - 1) \quad (\text{A9})$$

where $c_{tot} = c_1 + c_2$. The right hand side of A5 is negative, the right hand side of A6-A8 are positive and the sign of the right hand side of A9 depends on q^c (see main text).

Appendix III – Necessary Conditions for the Stability of Edge Equilibria where

$$\underline{0 < \hat{q} < 1}$$

First we consider $b_1+b_2 > 1$, in which case the population will converge to one of $E_1(1,0)$, $E_3(1,1)$ or $E_5(1, \hat{q}_0)$.

From (8) and (9), for both $E_1(1,0)$ and $E_3(1,1)$ to be unstable, it is necessary that

$$\frac{1}{1+h(1-\psi)(1+\gamma)} < 1 - \frac{(1-f)h(1+\psi)(1+\gamma)}{1-h(1+\psi)(1+\gamma)}, \quad (\text{A10})$$

or that

$$\frac{2h(1+\gamma)[(1-f/2)(1+\psi)(1+h(1+\gamma)(1-\psi))-1]}{[1+h(1+\gamma)(1-\psi)][1-h(1+\gamma)(1+\psi)]} < 0. \quad (\text{A11})$$

From the numerator of the left hand side of (A11), it is clear that (A10) is true if

$$1-f/2 < \frac{1}{(1+\psi)[1+h(1-\psi)(1+\gamma)]}. \quad (\text{A12})$$

If both $E_1(1,0)$ and $E_3(1,1)$ are unstable, inequalities (8), (9) and (A12) are satisfied simultaneously. Inequalities (8) and (A12) are satisfied if

$$c_1 + c_2 > 1 + \psi. \quad (\text{A13})$$

The same procedure reveals the same result (A13) where $b_1+b_2 < 1$ and the population converges to one of $E_0(0,0)$, $E_2(0,1)$ or $E_4(0, \hat{q}_0)$.