

A gene–culture coevolutionary model for brother–sister mating

(incest taboo/norm of reaction/evolutionarily stable strategies/cultural transmission/inbreeding depression)

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ABSTRACT We present a gene–culture coevolutionary model for brother–sister mating in the human. It is shown that cultural—as opposed to innate—determination of mate preference may evolve, provided the inbreeding depression is sufficiently high. At this coevolutionary equilibrium, sib mating is avoided because of cultural pressures.

Westermarck (1) proposed that “there is an *innate* aversion to sexual intercourse between persons living closely together from early youth” (italics added). In particular, sibs reared together are expected to avoid mating with one another. Studies on the Chinese custom of *sim-pua* (adoption of a future daughter-in-law) (2) and on marriage patterns among adults reared together as children in Israeli kibbutzim (3) seem to support Westermarck’s proposition.

Throughout the vertebrate, invertebrate, and plant kingdoms, the propensity to inbreed varies widely (4). In plants, both self-fertilization and self-incompatibility are widely represented. From simple population genetic models, an allele that increases the level of selfing may succeed if the depression of fitness that results from inbreeding is less than 50% (5–9). In animals and birds, experiments designed to detect inbreeding avoidance have produced mixed results (10). In Japanese quail, for example, females reared with siblings chose the company of first cousins over that of both sibs and third cousins (11). Such kin recognition mechanisms would permit inbreeding to be avoided without the necessity of dispersal, which is commonly evoked as a major means of inbreeding avoidance in many mammals.

An “innate” behavior is understood as one that has the same expression across the normal range of environments, so that within the species, there is little variation. Humans, however, are subject to an extraordinarily wide array of social environments, partly as a result of cultural differences among ethnic groups. Whereas sib mating has been banned in most societies that we know about, past and present, it was institutionalized in some (12, 13). Cousin mating, a milder form of inbreeding, is often preferred over complete outbreeding (14).

In the case of institutionalized sib mating in Roman Egypt, the innate avoidance mechanism postulated by Westermarck was readily overridden. Wolf’s studies (15, 16) of minor marriage in Taiwan are usually regarded as providing evidence for the Westermarck effect. But matings between the foster sibs did in fact occur.

Archaeological demonstration of lithic traditions suggests that cultural transmission has been an important determinant of behavior in hominids for more than two million years. In a cultural species, it is more appropriate to frame the discussion in terms of a “norm of reaction” rather than narrowly innate behavior. Thus, a genotype may respond quite differently

depending on the cultural pressures its carrier experiences. For example, whether the parents are sibs or unrelated may directly affect the probability that their offspring mate with one another.

Here we present a coevolutionary model in which the probability of sib mating is determined by an individual’s genotype and also by whether or not its parents were sibs. Analysis of this model yields the particularly interesting result that a wide norm of reaction may be evolutionarily stable (see qualification below). When gene–culture coevolution has resulted in fixation of a genotype with a wide norm of reaction, avoidance of sib mating will not be innate. Nevertheless, the evolved biases in cultural transmission and the selective disadvantage of inbred offspring will cause sib mating to be eliminated from the population. At this coevolutionary equilibrium, individuals are genetically capable of mating with sibs, but do not because of cultural pressure.

Model

With genetic determination of the inbreeding rate, it is well known that there is an evolutionary trade-off between the transmission of genes identical by descent to inbred offspring and the inbreeding depression suffered by those offspring. In the case of sib mating in an outbreeding population, the relatedness of a parent to inbred and outbred offspring is in the ratio of 3:2. Hence, using an inclusive fitness argument, if the inbreeding depression is d , sib mating will invade if $3(1-d) > 2$ or $d < 1/3$. This was also observed in a formal dynamical analysis (7). This argument holds under both diploidy and haploidy. For mathematical simplicity, we assume haploidy in what follows. Specifically, we posit two haploid genotypes A_1 and A_2 .

Experimental data suggest that mate choice is more strongly exercised by the female of a species. Therefore, we posit that the occurrence of sib mating is dependent on female choice. If she is of genotype A_i and her parents are sibs, the probability she will *want* to mate with her brother is b_{is} , whereas if her parents are unrelated, the corresponding probability is b_{ir} . In this context we should note, however, that marital dissatisfaction in the marriages studied by Wolf is not necessarily expressed more strongly in the *sim-pua* (i.e., wife).

Mating is conditional on survival to reproductive age. Each individual, male or female, whose parents are sibs has a viability of $1-d$ relative to an individual with unrelated parents. One girl and one boy are born in each family, and deaths occur independently. A surviving female may want to mate with her brother, but can only do so if he also survives. If he dies, she mates with an unrelated male with probability h . The remaining fraction $1-h$ of incestuous females who have lost their brothers refrain from mating.

Define S_{ij} to be the frequency of ordered sib matings between an A_i female and an A_j male, with R_{ij} the corresponding frequency of random matings between an A_i female and an

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A_j male. Among the newborns of the next generation, let X_{ij} be the frequency of ordered sibships, comprising an A_i sister and an A_j brother and derived from a sib mating. Similarly, Y_{ij} is the frequency of ordered sibships of the same composition but derived from unrelated parents. In this haploid model,

$$\begin{aligned} X_{11} &= S_{11} + \frac{S_{12} + S_{21}}{4}, & Y_{11} &= R_{11} + \frac{R_{12} + R_{21}}{4} \\ X_{12} &= X_{21} = \frac{S_{12} + S_{21}}{4}, & Y_{12} &= Y_{21} = \frac{R_{12} + R_{21}}{4} \\ X_{22} &= S_{22} + \frac{S_{12} + S_{21}}{4}, & Y_{22} &= R_{22} + \frac{R_{12} + R_{21}}{4}. \end{aligned} \quad [1]$$

Finally, let z_i be the frequency of genotype A_i among the random mating males. We assume that all males, whether mated to their sisters or not, compete equally for random mating females. Hence

$$\begin{aligned} Wz'_1 &= (1-d) \left(S_{11} + \frac{S_{12} + S_{21}}{2} \right) + R_{11} + \frac{R_{12} + R_{21}}{2}, \\ Wz'_2 &= (1-d) \left(S_{22} + \frac{S_{12} + S_{21}}{2} \right) + R_{22} + \frac{R_{12} + R_{21}}{2}, \end{aligned} \quad [2]$$

where a prime indicates adults of the next generation and

$$W = (1-d) \sum_i \sum_j S_{ij} + \sum_i \sum_j R_{ij}. \quad [3]$$

Our assumptions imply the following recursions in the basic variables S_{ij} and R_{ij} , where all summations are over 1 and 2:

$$TS'_{ij} = (1-d)^2 X_{ij} b_{is} + Y_{ij} b_{ir}, \quad [4a]$$

$$\begin{aligned} TR'_{ij} &= \sum_k (1-d) X_{ik} (b_{is} dh + 1 - b_{is}) z'_k \\ &+ \sum_k Y_{ik} (1 - b_{ir}) z'_k, \end{aligned} \quad [4b]$$

where

$$T = (1-d) \sum_i \sum_j X_{ij} [1 - b_{is} d(1-h)] + \sum_i \sum_j Y_{ij}. \quad [4c]$$

Genetic Monomorphism in A_1

Assume that the genotype A_1 is fixed. Dynamics of the frequency of sib matings, S_{11} (and of random matings, $R_{11} = 1 - S_{11}$) are then determined by the vertical transmission rates, b_{1s} and b_{1r} , and by natural selection against inbred offspring, d .

The equilibrium frequency of sib matings, \hat{S}_{11} , satisfies

$$\begin{aligned} 0 &= f(S_{11}) = d[1 + (1-d)(1-h)b_{1s}]S_{11}^2 \\ &- [1 + b_{1r} - (1-d)^2 b_{1s}]S_{11} + b_{1r}. \end{aligned} \quad [5]$$

Because $b_{1r} \geq 0$ and $f(1) = -(1-d)[1 - (1-hd)b_{1s}] \leq 0$, there is only one valid equilibrium if $1 - (1-hd)b_{1s} > 0$ ($d > 0$ is assumed). If $1 - (1-hd)b_{1s} = 0$, Eq. 5 factors to yield

$$f(S_{11}) = (S_{11} - 1)\{[1 - (1-d)^2 b_{1s}]S_{11} - b_{1r}\}. \quad [6]$$

Hence, two valid equilibria, $\hat{S}_{11} = b_{1r}/[1 - (1-d)^2 b_{1s}]$ and $\hat{S}_{11} = 1$, exist if $b_{1r} < 1 - (1-d)^2 b_{1s}$, but $\hat{S}_{11} = 1$ is the only valid equilibrium when this inequality is reversed.

For small perturbations from the equilibrium, \hat{S}_{11} , stability is governed by the eigenvalue

$$\begin{aligned} \lambda &= \frac{\{1 - (1-d)[1 - b_{1s}d(1-h)]\}\hat{S}_{11} + (1-d)^2 b_{1s} - b_{1r}}{1 - \{1 - (1-d)[1 - b_{1s}d(1-h)]\}\hat{S}_{11}} \\ &= 1 + f'(\hat{S}_{11})/\hat{T}. \end{aligned} \quad [7]$$

(Here we are still assuming fixation on the genotype A_1 . Stability to introduction of the allele A_2 will be considered later.) Clearly, $\lambda > -1$. Hence, the equilibrium \hat{S}_{11} is stable if $f'(\hat{S}_{11}) < 0$ —i.e., when \hat{S}_{11} is the smaller root of $f(S_{11}) = 0$, and \hat{S}_{11} is unstable when $f'(\hat{S}_{11}) > 0$. Thus, when there is only one valid equilibrium, it is always stable, and when there are two, the smaller is stable.

Stability to Introduction of New Allele A_2

We next consider stability of the genetic monomorphism in A_1 derived above to introduction of a new allele A_2 . Standard linear stability analysis shows that the nonzero eigenvalues are given by the roots of the characteristic polynomial

$$\begin{aligned} \Phi(\lambda) &= [(1-d)^2(b_{1s} + b_{2s})/(4\hat{T}) - \lambda][(1-d)^2 b_{2s}/\hat{T} - \lambda] \\ &\cdot (m^* - \lambda) + (m/8\hat{T})\{(b_{1r} + 3b_{2r})\lambda - (1-d)^2/(2\hat{T})\} \\ &\cdot [b_{2r}(b_{1s} + b_{2s}) + b_{2s}(b_{1r} + b_{2r})], \end{aligned} \quad [8a]$$

where

$$\begin{aligned} m &= (1-d)\{(1-d)[2 - (b_{1s} + b_{2s})(1-dh)]\hat{S}_{11} \\ &+ [2 - b_{1r} - b_{2s}(1-dh)]\hat{R}_{11}\}/(\hat{T}\hat{W}), \end{aligned} \quad [8b]$$

$$\begin{aligned} m^* &= \{(1-d)[2 - b_{1s}(1-dh) - b_{2r}]\hat{S}_{11} \\ &+ (2 - b_{1r} - b_{2r})\hat{R}_{11}\}/(2\hat{T}\hat{W}), \end{aligned} \quad [8c]$$

$$\hat{T} = (1-d)[1 - b_{1s}d(1-h)]\hat{S}_{11} + \hat{R}_{11},$$

$$\hat{W} = (1-d)\hat{S}_{11} + \hat{R}_{11}. \quad [8d]$$

$\Phi(\lambda)$ is a cubic of the form

$$\Phi(\lambda) = (\lambda_1 - \lambda)(\lambda_2 - \lambda)(\lambda_3 - \lambda) + k(\lambda - \lambda^*), \quad [9]$$

where we may assume $\lambda_1 \leq \lambda_2 \leq \lambda_3$. In Appendix 1 we show that, provided $\lambda^* \leq \lambda_3$, the monomorphic equilibrium is locally stable if $\Phi(1) < 0$ and locally unstable if $\Phi(1) > 0$.

Norms of Reaction and Evolutionarily Stable Strategies (ESS)

Each genotype A_i is defined by its norm of reaction specified by b_{ir} , b_{is} . A genetic monomorphism in A_1 will be evolutionarily stable (17, 18) if the parameters b_{1r} and b_{1s} are such that A_2 cannot invade whatever the values of b_{2r} and b_{2s} .

Our first major result is that a fully internal norm of reaction—i.e., $0 < b_{1r}, b_{1s} < 1$ —cannot be an ESS. The proof, which is detailed in Appendix 2, relies on small perturbations of the parameters. Set $b_{2r} = b_{1r} + \xi$ and $b_{2s} = b_{1s} + \eta$, where ξ and η are small. Then $\lambda^* < \lambda_3$ in which case linear stability is assured if and only if $\Phi(1) < 0$. In general, the expansion of $\Phi(1)$ will take the form

$$\Phi(1) = c_{\xi\xi}\xi + c_{\eta\eta}\eta + c_{\xi\xi\xi}\xi^2 + c_{\xi\eta\xi}\xi\eta + c_{\eta\eta\eta}\eta^2 + \text{third order terms}. \quad [10]$$

For a fully internal norm of reaction to be an ESS, we require the linear terms $c_{\xi\xi} = c_{\eta\eta} = 0$ and the quadratic form to be negative definite. However, as shown in Appendix 2, $c_{\xi\xi} = 0$, whence $c_{\xi\xi}c_{\eta\eta} - (c_{\xi\eta})^2 \leq 0$ and, even if $c_{\xi\xi} = c_{\eta\eta} = 0$, the quadratic form is not negative definite.

Thus, for any norm of reaction with $0 < b_{1r}, b_{1s} < 1$, there is always another norm of reaction b_{2r}, b_{2s} that can invade. Under the reasonable assumption that $b_{1r} \leq b_{1s}$, an evolutionarily stable norm of reaction entails $b_{1r} = 0$ and/or $b_{1s} = 1$.

Norms of Reaction with $b_{1r} = 0$

In view of the often-made claim that avoidance of sib mating is innate, the case $b_{1r} = 0$ deserves special attention. When $b_{1r} = 0$, we have $\hat{S}_{11} = 0$ and $\hat{T} = \hat{W} = 1$ at the genetic monomorphism. (If, in addition, $h = 0$ and $b_{1s} = 1$, the unstable equilibrium $\hat{S}_{11} = 1$ also exists.) From Eqs. 8a and 8c, because $\lambda^* = (1 - d)^2(b_{1s} + 2b_{2s})/6 < 1/2$ and $m^* = (2 - b_{2r})/2 \geq 1/2$, we have $\lambda^* < \lambda_3$. Hence, linear stability of $\hat{S}_{11} = 0$ to invasion by A_2 is determined by the sign of

$$\begin{aligned} \Phi(1) = & - (b_{2r}/8)\{4[1 - (1 - d)^2(b_{1s} + b_{2s})/4] \\ & \cdot [1 - (1 - d)^2b_{2s}] - (1 - d)[2 - b_{2s}(1 - dh)] \\ & \cdot [3 - (1 - d)^2(b_{1s} + 2b_{2s})/2]\}. \end{aligned} \quad [11]$$

Notice first that b_{2r} does not affect stability provided it is positive. Here we assume $b_{2r} > 0$, reserving the analysis of the case $b_{2r} = 0$ for the next section. Second, a norm of reaction of the form $b_{1r} = 0, b_{1s} \geq 0$ will be an ESS only if $\Phi(1) < 0$ for all b_{2s} . Rewrite Eq. 11 as

$$\Phi(1) = - (b_{2r}/8)\Psi(b_{2s}), \quad [12a]$$

where

$$\begin{aligned} \Psi(b_{2s}) = & 6(d - 1/3) - d(1 - d)^2b_{1s} + d(1 - d)[-2(1 - d) \\ & + 3(1 - h)]b_{2s} + (1 - d)^3[1 - d - d(1 - h)] \\ & \cdot b_{1s}b_{2s}/2 - d(1 - d)^3(1 - h)b_{2s}^2. \end{aligned} \quad [12b]$$

Hence, $\Psi(b_{2s})$ is linear in b_{2s} , if $h = 1$ and takes the form of a quadratic that is convex upward if $0 \leq h < 1$. In either case, $\Psi(b_{2s}) > 0$ [$\Phi(1) < 0$] for $0 \leq b_{2s} \leq 1$ if and only if $\Psi(0) > 0$ and $\Psi(1) > 0$.

In particular, from the requirement that $\Psi(0) > 0$, a necessary condition for evolutionary stability of $b_{1r} = 0$ is

$$6(d - 1/3) - d(1 - d)^2b_{1s} > 0. \quad [13]$$

Hence, for a given value of $d > 1/3$, inequality 13 is more likely to be satisfied the smaller is the value of b_{1s} , i.e., the narrower is the norm of reaction.

In Fig. 1 we graph the minimum values for d for which the two extreme cases, $b_{1r} = b_{1s} = 0$ and $b_{1r} = 0$ with $b_{1s} = 1$, will be evolutionarily stable (subject to the condition $b_{2r} > 0$). The horizontal axis measures h . For intermediate values of b_{1s} we have a family of nonintersecting curves that lie between these two curves. The dependence on h and b_{1s} is not pronounced, and we see that the norm of reaction $b_{1r} = 0$ with $b_{1s} = 1$ can be an ESS if $d > 0.4$. If the inbreeding depression from sib matings in humans has consistently exceeded 40%, then a wide norm of reaction, i.e., a large difference ($b_{1s} - b_{1r}$), may have evolved. Based on Seemanová's study (19) of nuclear family incest, Durham (20) estimates the inbreeding depression resulting from death plus major defect to be about 45%.

Case of $b_{1r} = b_{2r} = 0$

Recall that the norm of reaction we consider in this paper is defined by the pair of probabilities, b_{1r} and b_{1s} . We showed in the previous section that any norm of reaction with $b_{1r} = 0$ can be stable against all alternatives that satisfy the restriction $b_{2r} > 0$. To complete the analysis, let us consider the fate of mutants with $b_{2r} = 0$. In other words, when two strategies are

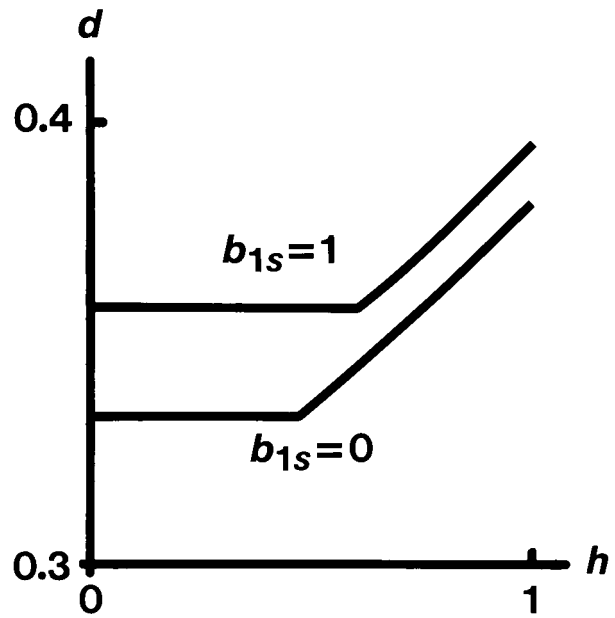


FIG. 1. The curves labeled $b_{1s} = 0$ and $b_{1s} = 1$ give the minimum values of the inbreeding depression, d , for which the two norms of reaction $b_{1r} = b_{1s} = 0$ and $b_{1r} = 0$ with $b_{1s} = 1$ will be evolutionarily stable against all alternatives that satisfy $b_{2r} > 0$. The horizontal axis measures the probability, h , that an incestuous female mates with an unrelated male when her brother dies. For intermediate values of b_{1s} , there is a family of nonintersecting curves that lie between these two curves. The curve labeled $b_{1s} = 0$ meets the d axis at $1/3$.

both characterized by $b_{1r} = 0$ differing only in b_{1s} , which will do better?

From Eq. 11 we expect that the dominant eigenvalue will be one, necessitating a second order analysis. This is outlined in Appendix 3. Applying the method of Nagylaki (21), we obtain the interesting result that, even to second order, the genetic monomorphism in A_1 is neutrally stable. Hence, natural selection on the alternative norms will be very weak, and transitions may occur by random drift. In particular, a wide norm of reaction is just as likely to evolve as a narrow one.

Norms of Reaction with $b_{1s} = 1$

A norm of reaction with $b_{1r} = 0$ implies no sib matings at equilibrium. However, sibling incest is in fact observed at low, but nonnegligible, frequencies in modern human societies. Because sibling incest is rare, we should consider the evolutionary stability of norms of reaction with b_{1r} small. To this end, expand the characteristic polynomial Eq. 8b evaluated at $\lambda = 1$ in powers of b_{1r} , giving

$$\begin{aligned} \Phi(1) = & - (b_{2r}/8)\tilde{\Psi}(b_{2s}) + (b_{1r}/8)[\tilde{\Psi}(b_{2s}) + c_1(1 - b_{2s}) \\ & + c_2b_{2r}] + o(b_{1r}), \end{aligned} \quad [14]$$

where $\tilde{\Psi}(b_{2s})$ is given by Eq. 12b with b_{1s} set equal to 1, and c_1 and c_2 are functions of the parameters.

Evolutionarily stability obtains when $\Phi(1) < 0$ for all b_{2r} and b_{2s} . However, from Eq. 14 this cannot occur: If $\tilde{\Psi}(b_{2s}) < 0$ for some b_{2s} , then $\Phi(1) > 0$ for sufficiently large b_{2r} . If $\tilde{\Psi}(b_{2s}) > 0$ for all b_{2s} , then $\Phi(1) > 0$ when $b_{2r} = 0$ and $b_{2s} = 1$. From Eq. 12b, we see that $\Psi(b_{2s})$ can vanish at most twice for b_{2s} in $[0,1]$. Hence, we conclude that a strategy with b_{1r} small and $b_{1s} = 1$ cannot be an ESS.

On the other hand, numerical work suggests that a norm of reaction where b_{1r} is large can be evolutionarily stable to all alternative strategies that satisfy $b_{2s} < 1$. When $b_{2s} = 1$, this norm of reaction is neutrally stable to second order. An

example of such a norm of reaction is $b_{1r} = 0.5$ and $b_{1s} = 1$ when $d = 0.2$ and $h = 0$. However, in this case the frequency of sib matings at equilibrium is predicted to be one, which is unrealistically high.

Discussion

In our model, if $b_{1r} = b_{1s}$ the female's mating preference is completely determined by her genotype. The particular case $b_{1r} = b_{1s} = 0$ corresponds to innate avoidance of brother-sister mating. On the other hand, if $b_{1r} < b_{1s}$ parental mating behavior directly affects mate choice by their daughter. In particular, if $b_{1r} = 0$ and $b_{1s} = 1$ then we can say that mate choice is culturally determined.

A norm of reaction provides for phenotypic plasticity of a genotype in a range of environments. Sensitivity to variation in parental mating type may then be regarded as a norm of reaction mediated by cultural transmission. In our model the norm of reaction for genotype A_1 is defined by the pair b_{1r}, b_{1s} . It is natural to refer to the difference $b_{1s} - b_{1r}$ as the width of this norm.

We have attempted to identify parameter sets b_{1r}, b_{1s} that are unbeatable by any alternative set b_{2r}, b_{2s} . Although there are no norms of reaction that are truly evolutionarily stable, the approach has proved informative. First we showed that a fully internal norm of reaction $0 < b_{1r}, b_{1s} < 1$ cannot be an ESS. On the reasonable assumption $b_{1r} \leq b_{1s}$ (otherwise a daughter is more likely to be incestuous when her parents are unrelated than when they are themselves incestuous), evolutionary stability entails $b_{1r} = 0$ and/or $b_{1s} = 1$. Next we showed that a norm of reaction where b_{1r} is positive and small with $b_{1s} = 1$ can also be rejected. Hence, the remaining candidates for an unbeatable parameter set are (i) $b_{1r} = 0$ with b_{1s} arbitrary; and (ii) b_{1r} positive and large with $b_{1s} = 1$.

Concerning alternative ii, numerical work suggests that the norm of reaction b_{1r} positive and large with $b_{1s} = 1$ may be evolutionarily stable. However, the only cases we have been able to identify entail an equilibrium frequency of one for sib matings. Even if we introduce forms of cultural transmission other than the vertical (parent-offspring) assumed here (22), it would seem difficult to reduce the predicted frequency to the low levels observed in most societies past and present.

A norm of reaction where $b_{1r} = 0$ may be evolutionarily stable against all alternatives that satisfy $b_{2r} > 0$. Here, the other parameter defining the norm, b_{1s} , may take any value between 0 and 1. In Fig. 1 we graph the minimum values of the inbreeding depression, d , for which the two extreme cases, $b_{1r} = b_{1s} = 0$ and $b_{1r} = 0$ with $b_{1s} = 1$, are evolutionarily stable. For intermediate values of b_{1s} , we have a family of nonintersecting curves that lie between these two curves.

When d is sufficiently large and h is relatively small—e.g., if $d > 0.358$ and $h < 0.617$, any such norm of reaction will be evolutionarily stable (subject to the condition $b_{2r} > 0$). For smaller d or larger h , Fig. 1 shows that a small value of b_{1s} is more likely to produce evolutionary stability. Note that a norm of reaction where $b_{1r} = 0$ and b_{1s} is small involves relatively strong genetic determination of inbreeding avoidance, whereas if $b_{1r} = 0$ and b_{1s} is large, there is a significant cultural component in the determination of the daughter's preference. There is no theoretical reason to prefer one norm over the other on the basis of our model, although the latter norm seems more realistic because human mate choice is sensitive to cultural pressures. That the former will evolve in a larger region of the space of parameters d and h is consistent with the proposal of Cavalli-Sforza and Feldman (23) that genetic determination will usually prevail over the cultural.

With this norm of reaction, regardless of the value of b_{1s} , the frequency of sib mating will converge to zero at the gene-culture coevolutionary equilibrium. In particular, if $b_{1s} > 0$,

individuals are genetically capable of sib mating, but do not because of cultural pressures.

An interesting relation exists between the two norms of reaction b_{1r}, b_{1s} , and b_{2r}, b_{2s} , where $b_{1r} = b_{2r} = 0$ but b_{1s} and b_{2s} differ. Both are neutrally stable to second order to invasion by the other. In fact, numerical iteration of Eq. 4 reveals that the subspace $R_{11} + R_{12} + R_{21} + R_{22} = 1$ is neutrally stable. Hence, two such norms of reaction may coexist, implying a genetic polymorphism in the probability that a daughter from a brother-sister union will herself be incestuous. Moreover, in a finite population transitions between the two norms may occur by random drift.

We now argue that the norm of reaction, $b_{1r} = 0$ with $b_{1s} > 0$, may be consistent with the known facts and suggest a way in which this may be tested. First, in apparent contradiction, sib matings are observed at low, but nonnegligible, frequencies in modern societies. However, nuclear family incest often involves the mentally retarded (19), so that this is unlikely to be an evolved response. Second, about one-sixth of all marriages in one region of Roman Egypt were between full sibs (13). These socially recognized unions were recorded in the census documents and persisted for several centuries before the custom eventually disappeared. Hence, the institution is best regarded a transient phenomenon, initiated by forces extraneous to our model. We may be able to test our prediction of $b_{1s} > 0$ (or, for example, that incest results from being homozygous for a recessive gene) if sufficient transgenerational data are available. If $b_{1s} > 0$, brother-sister marriages should occur recurrently in the descendants of an incestuous pair. What is transmitted vertically may not be an "inbreeding meme," but rather economic circumstances that favor sib mating. However, the result will be the same. If $b_{1s} = 0$, on the other hand, occurrence of sib mating should be sporadic. Third, the norm of reaction $b_{1r} = 0$ with $b_{1s} > 0$ cannot be an ESS unless the inbreeding depression, d , exceeds $1/3$. As noted above, Durham's (20) estimate of d based on Seemanová's (19) data is about 45%. However, this estimate combines the effects of mortality and morbidity, on the assumption that serious abnormalities are the equivalent of death. The inbreeding depression as computed from differential mortality alone is about 10%.

Ralls *et al.* (24) estimated inbreeding depression in 38 captive species of mammals. As measured by survivorship to a specified age, the average inbreeding depression for sib matings is 33%. They suggest that, under natural as opposed to captive conditions, the cost of inbreeding may be exacerbated. In the case of humans, it is arguable whether inbreeding depression would have been more severe without modern medical care. Although this seems likely, reproductive compensation coupled with selective infanticide of malformed children would partly reduce the disparity in the number of surviving children. We conclude that the inbreeding depression for sib matings may have been about 45% during most of history and prehistory, if serious congenital abnormalities resulted in death, infertility, or the inability to mate.

Finally, a few words on the incest taboo. Why sex and marriage within the nuclear family are prohibited by custom, rule, or law is a major conundrum that continues to puzzle anthropologists, and even some jurists (ref. 25; see also ref. 20 for a recent review). The present paper only scratches the surface of the problem, but we believe that it suggests one direction in which a solution may be sought. In the context of a gene-culture coevolutionary model, the establishment of an incest taboo may be equated with the spread of an "outbreeding meme." The meme spreads in our model because of evolved biases in cultural transmission and natural selection against inbred offspring. There is no need to invoke rational choice based on a realization of the deleterious consequences of inbreeding.

Appendix 1

Our demonstration assumes that in Eq. 9 we have the strict inequalities $0 < \lambda_1 < \lambda_2 < \lambda_3$, but the proof can be generalized. From Eq. 8e, $\hat{T} \geq (1 - d)^2$. Hence, two of the λ_i 's have the bounds

$$0 \leq (1 - d)^2(b_{1s} + b_{2s})/(4\hat{T}) \leq 1/2, \tag{A1-1}$$

$$0 \leq (1 - d)^2b_{2s}/\hat{T} \leq 1, \tag{A1-2}$$

and λ^* has the bounds

$$0 \leq (1 - d)^2[b_{1r}b_{2s} + b_{2r}(b_{1s} + 2b_{2s})]/[2\hat{T}(b_{1r} + 3b_{2r})] \leq 1/2. \tag{A1-3}$$

We wish to prove that the dominant eigenvalue, which is positive, is less than unity if $\Phi(1) < 0$, and is greater than unity if $\Phi(1) > 0$. Consider three cases. First assume $\lambda^* \leq \lambda_1$. Then $\Phi(\lambda) > 0$ in the interval $\lambda_2 \leq \lambda \leq \lambda_3$, where $\lambda_2 \leq 1$ from Eqs. A1-1 and A1-2. Moreover, $\Phi'(\lambda) = 2[(\lambda_1 - \lambda) + (\lambda_2 - \lambda) + (\lambda_3 - \lambda)] < 0$ for $\lambda \geq \lambda_3$. Hence, $\Phi(\lambda)$ intersects the λ -axis only once when $\lambda > \lambda_3$. Next, if $\lambda_1 < \lambda^* \leq \lambda_2$, then $\Phi(\lambda_1) < 0 \leq \Phi(\lambda_2)$ and we also have $\lambda_1 < \lambda_2 \leq 1$. Similarly, if $\lambda_2 < \lambda^* \leq \lambda_3$, then $\Phi(\lambda_1) < 0 \leq \Phi(\lambda^*)$ where $\lambda_1 < \lambda^* \leq 1/2$. In all cases, therefore, if $\lambda^* \leq \lambda_3$, then the largest root of $\Phi(\lambda)$ is less than unity if $\Phi(1) < 0$ and greater than unity if $\Phi(1) > 0$. It is clear that if $\lambda^* > \lambda_3$ and $\Phi(1) > 0$, the largest eigenvalue is greater than unity.

Appendix 2

Set

$$b_{2r} = b_{1r} + \xi, \quad b_{2s} = b_{1s} + \eta, \tag{A2-1}$$

where ξ and η are small. Then $\lambda^* \approx (1 - d)^2b_{1s}/(2\hat{T}) < (1 - d)^2b_{1s}/\hat{T} \approx (1 - d)^2b_{2s}/\hat{T}$, which implies $\lambda^* < \lambda_3$. Substitution of Eq. A2-1 and $\lambda = 1$ in Eq. 8b yields

$$\begin{aligned} \Phi(1) = & [(1 - d)^2b_{1s}/(2\hat{T}) - 1 + (1 - d)^2\eta/(4\hat{T})] \\ & \cdot [(1 - d)^2b_{1s}/\hat{T} - 1 + (1 - d)^2\eta/\hat{T}] \\ & \cdot \{(1 - d)[2 - b_{1s}(1 - dh) - b_{1r}]\hat{S}_{11} \\ & + 2(1 - b_{1r})\hat{R}_{11}\}/(2\hat{T}\hat{W}) - 1 - \xi/(2\hat{T}) \\ & + (1 - d)/(8\hat{T}^2)[\{2(1 - d)[1 - b_{1s}(1 - dh)]\hat{S}_{11} \\ & + [2 - b_{1r} - b_{1s}(1 - dh)]\hat{R}_{11}\}/\hat{W} \\ & - (1 - dh)\eta] \cdot \{4b_{1r}[1 - (1 - d)^2b_{1s}/(2\hat{T})] \\ & + 3[1 - (1 - d)^2b_{1s}/(2\hat{T})]\xi - [3(1 - d)^2b_{1r}/ \\ & \cdot (2\hat{T})]\eta - [(1 - d)^2/\hat{T}]\xi\eta\}. \tag{A2-2} \end{aligned}$$

Expanding Eq. A2-2 in ξ and η , there is no ξ^2 term. Hence, $c_{\xi\xi} = 0$ in Eq. 10.

Appendix 3

Expansion of Eq. 4 in the small variables $S_{11}, S_{12} + S_{21}, S_{12} - S_{21}, S_{22}, R_{12} + R_{21}, R_{12} - R_{21}$, and R_{22} yields the local stability matrix:

$$M = \begin{pmatrix} * & * & 0 & 0 & 0 & 0 & 0 \\ 0 & * & 0 & 0 & 0 & 0 & 0 \\ 0 & * & 0 & 0 & 0 & 0 & 0 \\ 0 & * & 0 & * & 0 & 0 & 0 \\ 0 & * & 0 & * & 1 & 0 & 2 \\ 0 & * & 0 & * & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}. \tag{A3-1}$$

The asterisks indicate nonnegative terms. In particular, the three diagonal asterisks are less than unity, whence the dominant eigenvalue one is nondegenerate.

The right eigenvector corresponding to this dominant eigenvalue $(0,0,0,0,1,0,0)^T$, where T denotes the transpose. Hence, according to the method of Nagylaki (21) we need consider only the terms in $(R_{12} + R_{21})^2$ among the second-order terms. Such terms appear in the expansions of $(R_{12} + R_{21})'$ and R_{22}' , where they contribute $-(R_{12} + R_{21})^2/2$ and $(R_{12} + R_{21})^2/4$, respectively.

Next, the left eigenvector corresponding to the eigenvalue one is

$$(0, *, 0, *, 1, 0, 2), \tag{A3-2}$$

where the asterisks here indicate positive terms. Then the product of the vector of second order terms and Eq. A3-2 vanishes. Thus, if $b_{1r} = b_{2r} = 0$, then to second order, the genetic monomorphism in A_1 is neutrally stable to the introduction of A_2 .

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