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An SIS model for cultural trait transmission with conformity bias

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Abstract

Epidemiological models have been applied to human health-related behaviors that are affected by social interaction. Typically these models have not considered conformity bias, that is the exaggerated propensity to adopt commonly observed behaviors or opinions, or content biases, where the content of the learned trait affects the probability of adoption. Here we consider an interaction of these two effects, presenting an SIS-type model for the spread and persistence of a behavior which is transmitted via social learning. Uptake is controlled by a nonlinear dependence on the proportion of individuals demonstrating the behavior in a population. Three equilibrium solutions are found, their linear stability analyzed and the results compared with a model for unbiased social learning. Our analysis focuses on the effects of the strength of conformity bias and the effects of content biases which alter a conformity threshold frequency of the behavior, above which there is an exaggerated propensity for adoption. The strength of the conformity bias is found to qualitatively alter the predictions regarding whether the trait becomes endemic within the population, and the proportion of individuals who display the trait when it is endemic. As the conformity strength increases, the number of feasible equilibrium solutions increases from two to three, leading to a situation where the stable equilibrium attained is dependent upon the initial state. Varying the conformity threshold frequency directionally alters the behavior invasion threshold. Finally we discuss the possible application of this model to binge drinking behavior.

Keywords: conformity; cultural evolution; social learning; SIS; binge drinking

1 Introduction

Epidemiological models for the spread of infectious diseases, known as SIR models, have been widely researched since the work of Kermack and McKendrick (1927). The name derives from the assumed model structure, classifying individuals as either susceptible, infected or recovered. Many variations of SIR models exist (Murray, 1993; Hethcote, 2000; McCallum et al., 2001; Keeling and Rohani, 2008), including SIS models where individuals can be either susceptible or infected. An SIS model for infectious disease spread considers how the subpopulations of susceptible and infected individuals change in time, represented mathematically by two ordinary differential equations (ODEs). It is assumed that all individuals entering the population are susceptible. They may become infected through contact with infected individuals at a rate proportional to the frequency of infected individuals in the population. Infected individuals recover to the susceptible state at a constant rate.

The assumption that infection is spread through contact has led to the application of SIS and similar models to be applied to a range of human health-related behaviors where social interaction affects the spread of the behavior. Examples include models of addictive behaviors, such as smoking (Sharomi and Gumel, 2008), drug use (Song et al., 2006; White and Comiskey, 2007; Mulone and Straughan, 2009), drinking (Sanchez et al., 2007; Mubayi et al., 2010; Mulone and Straughan, 2011; Walters et al., 2012), the spread of happiness (Hill et al., 2010a) and the development of eating disorders (Gonzalez et al., 2003) or obesity (Hill et al., 2010b). Such models assume that the rate at which susceptible individuals adopt a behavior is proportional to the prevalence of the behavior in the population. However, we see from cultural evolutionary theory that this assumption may be oversimplifying the mechanisms involved in behavior transmission, and that biases in transmission can result in qualitatively distinct model predictions.

Cultural evolutionary theory considers the spread and persistence of socially transmitted traits, including ideas, beliefs, behaviors and material culture (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Mesoudi, 2011). A cultural trait is typically acquired by some form of social learning. If social learning is unbiased (random copying) then the probability that an individual adopts a cultural trait is equal to the trait's frequency in the population. The assumption that transmission is linearly frequency-dependent, i.e. unbiased, is commonly applied in the SIS model literature; cultural trait transmission, however, may be subject to a variety of content or contextual biases (Henrich and McElreath, 2003) which affect the transmission rate. Content dependent biases arise from some intrinsic property of the cultural trait. Such biases make it, for example, easier to remember or intrinsically more attractive than other competing traits (Richerson and Boyd, 2005; Mesoudi, 2011). Context dependent biases can be split into model-based and frequency-dependent biases (Henrich and McElreath, 2003; Richerson and Boyd, 2005; Mesoudi, 2011). The former is where the choice of a trait is affected by observable attributes of the

53 cultural parent, for example copying individuals that are perceived to be successful. The latter is typically where
54 the frequency of the trait in the population affects its uptake in a nonlinear fashion, such as a disproportionate
55 tendency to adopt the most common trait. This is termed as a conformist bias whereas a disproportionate tendency
56 to follow the minority is often known as anticonformist bias (Efferson et al., 2008; Eriksson and Coultas, 2009;
57 Kendal et al., 2009; Morgan et al., 2011).

58 A variety of empirical studies examining the extent of conformist bias have been conducted, with one of the
59 earliest finding that participants would conform to the majority viewpoint expressed by confederates (Asch, 1956).
60 This has since been criticized as the results do not demonstrate a disproportionate inclination to follow the majority
61 and hence may reflect random copying (Efferson et al., 2008). By defining conformity as an exaggerated tendency
62 to follow the majority, modeled by a sigmoidal curve, Efferson et al. (2008) conducted an experiment where players
63 repeatedly chose between two technologies with different expected, but randomly distributed, payoffs. A subset
64 of participants that indicated a conformist bias in their answers to questionnaires copied the technology choice of
65 asocial learners with an S-shaped probability distribution, indicating conformist behavior.

66 Later work by Eriksson and Coultas (2009) offers an alternative theoretical model of conformity. The authors
67 argue that the S-shaped probability curve originally used by Boyd and Richerson (1985) is unrealistic. Particularly,
68 the endpoints of the curve mean that a naïve individual cannot acquire a trait which is not being displayed in
69 the population, nor can they reject a trait which is universally expressed by the population. Furthermore, the
70 conformity threshold frequency, which we define to be the intermediate point where the nonlinear frequency
71 dependence curve meets the linear curve, need not occur when exactly half of the population display the trait.
72 Allowing the endpoints and the conformity threshold frequency to vary produces a model which can account for
73 content-dependent biases, such that the attraction of the trait itself may interact with a nonlinear frequency-
74 dependent probability of adoption. In applying their model to an experiment testing frequency-dependent effects
75 on opinion formation, they found evidence for anticonformist bias, suggesting that any expression of conformity
76 bias may be conditional (also see Morgan et al. (2011)). Results from a series of experiments conducted by Morgan
77 et al. (2011) suggest that subjects used conformist biased social learning. This, however, required a large number
78 of demonstrators and for the individuals to have low confidence in their ability to complete the task independently.
79 By contrast, a high magnitude of asocial influence resulted in a conformity bias where the conformity threshold
80 frequency was greater than a half.

81 In light of these findings, we present a mathematical model to examine the dynamics of a cultural trait under
82 conformist biased transmission. Results are compared against the case of unbiased social transmission, before
83 considering the effect of a variable conformity threshold parameter. Our analysis focuses on the effect of the

84 strength of conformity on the existence and stability of equilibria. The formulation is equivalent to that of an SIS
 85 model, including a frequency-dependent rate of trait adoption and a constant rate of abandonment. The latter
 86 may reflect individual forgetting or the result of population-wide influences, such as mass media, or economic and
 87 environmental change. The formulation also approximates cases of frequency-dependent abandonment if this rate
 88 is very small. By way of an example, we discuss how the model may apply to the case of binge drinking within a
 89 population of young adults (see section 4).

90 2 Models for unbiased and conformist cultural trait transmission

91 We begin by assuming the existence of a cultural trait A within a population of N individuals where trait transmis-
 92 sion is frequency-dependent and abandonment of the trait is (approximately) frequency-independent. Individuals
 93 within the population can be categorized as type S, who do not display trait A, or type A, who do. The time-
 94 dependent variables $S(t)$ and $A(t)$ represent the number of type S and type A individuals respectively. We assume
 95 that all individuals enter the population as type S at a rate μ , however they may leave as either type at the same
 96 rate. Type S individuals can only acquire trait A through interactions with type A individuals, and we assume
 97 that the transmission rate is affected by the frequency of type A individuals in the population. We consider the
 98 transmission rate to be $\beta c(A/N)$ where β is the rate at which contact sufficient for transmission occurs. In the
 99 unbiased social learning model the function $c(A/N)$ represents the probability that contact is made with a type
 100 A individual. However, in the case of biased social learning, the function also includes a weighting which repre-
 101 sents the conformist influence. Type A individuals revert to type S at a constant rate, although this term also
 102 approximates the effect of a social influence when γ is very small. For a mathematical justification see appendix
 103 B.

104 From this we formulate the following equations

$$\begin{aligned} \dot{S}(t) &= \mu N - \beta S c(A/N) + \gamma A - \mu S, \\ \dot{A}(t) &= \beta S c(A/N) - (\gamma + \mu) A, \end{aligned} \tag{1}$$

105 where the total population $N = S + A$ is constant. Figure 1 represents these dynamics with arrows indicating the
 106 direction of flow through the system. The constant total population results from the entering and leaving rates (μ)
 107 being the same. This simplifying assumption is made so that the system may be reduced to one equation, which
 108 is non-dimensionalized by introducing the variables $s = S/N$ and $a = A/N$ to give

$$\dot{a}(t) = \beta(1 - a)c(a) - \rho a \tag{2}$$

109 where $\rho = \gamma + \mu$ has been introduced to simplify the mathematical analysis.

110 *Figure 1 here*

We must now consider the function $c(a)$. This determines the frequency-dependent relationship between the probability that type S individuals convert to type A and the frequency of type A individuals in the population. First we introduce a linear frequency-dependent function

$$\begin{aligned}c_L : [0, 1] &\rightarrow [0, 1] \\c_L(a) &= a,\end{aligned}$$

111 which gives us a model for unbiased trait transmission, resulting in the standard SIS model form. We then introduce
112 a nonlinear frequency-dependent function

$$\begin{aligned}c_1 : [0, 1] &\rightarrow [0, 1] \\c_1(a) &= a[1 + D(2a - 1)(1 - a)],\end{aligned}\tag{3}$$

113 which is the conformity function first proposed by Boyd and Richerson (1985). The conformity coefficient $D \in (0, 1]$
114 controls the strength of the bias. The value $D = 0$ is not considered as this would result in the linear function c_L . We
115 see from figure 2 that c_1 is an appropriate function to represent a conformity bias as its sigmodal shape ensures that
116 all individuals have a disproportionate tendency to follow the majority. When the frequency of type A individuals
117 in the population is less than a half, so $a < 1/2$, the probability of type S adopting trait A is $P(\text{adopting A}) < a$.
118 When the frequency of type A individuals is greater than a half then $a > 1/2$ and $P(\text{adopting A}) > a$. We refer
119 to $a_e = 1/2$ as the conformity threshold frequency as this is where $P(\text{adopting A}) = a$, i.e. where the linear and
120 nonlinear frequency-dependent curves meet.

121 The criteria for an appropriate conformity function are that exactly one saddle point and no local extrema
122 must exist in the region $(0, 1)$ and, initially, symmetry about the point $(1/2, 1/2)$. More complex real functions,
123 such as higher order polynomials or trigonometric functions, can also satisfy these criteria, however they may then
124 be locally approximated to a cubic polynomial function. As a result, the behavior of such systems pertaining to
125 existence and stability of equilibria will be qualitatively similar to the results presented here. Precise relationships
126 between the parameters and the conformity coefficient will, however, vary depending on the behavior of the chosen
127 conformity function with respect to the coefficient D .

128 *Figure 2 here*

129 We begin by analyzing the linear frequency-dependent SIS model which is constructed from equation (2) using
130 the linear function c_L to give

$$\dot{a}(t) = \beta a(1 - a) - \rho a.\tag{4}$$

131 As equation (4) is not analytically solvable we look for equilibrium solutions, which are values of a which satisfy
132 $\dot{a}(t) = 0$, and analyze their stability. Once a stable equilibrium is reached, the proportion of type A individuals
133 in the population remains constant in time and hence we can determine the prevalence of trait A within the
134 population. To ensure that the model provides realistic predictions we seek feasible solutions, characterized as
135 those which are unique and and lie in the interval $[0, 1]$. As we are interested in solutions for a we rewrite equation
136 (4) as a function of this variable giving

$$f_L(a) = a[\beta(1 - a) - \rho]. \quad (5)$$

137 Solving $f_L = 0$ results in two equilibrium solutions: $\bar{a}_0^L = 0$ which is feasible for all parameter values, and
138 $\bar{a}_1^L = (\beta - \rho)/\beta$ which is feasible for $\rho < \beta$.

139 We now look at equation (2) with conformity function c_1 which gives

$$\dot{a}(t) = \beta a(1 - a)[1 + D(2a - 1)(1 - a)] - \rho a. \quad (6)$$

140 This can be written as $\dot{a} = a f_1(a)$ where we see that $\bar{a}_0^1 = 0$ is an equilibrium solution which always exists,
141 independent of the values of β , ρ and D . The remaining equilibrium solutions are the roots of

$$f_1(a) = \beta(1 - a)[1 + D(2a - 1)(1 - a)] - \rho \quad (7)$$

which can be found explicitly, but their complexity makes further analysis difficult. By using properties of the
function f_1 it is possible to determine the number and nature of equilibrium points under certain conditions. The
cubic polynomial f_1 has leading coefficient $2\beta D > 0$, so it always has one real root, and $f_1(a) \rightarrow \pm\infty$ as $a \rightarrow \pm\infty$.
The roots of $f_1'(a) = \beta(6Da^2 - 10Da + 4D - 1)$ give the local maximum and local minimum of f_1 which are

$$a_-^1 = \frac{5}{6} - \frac{1}{6}\sqrt{\frac{D+6}{D}} \quad \text{and} \quad a_+^1 = \frac{5}{6} + \frac{1}{6}\sqrt{\frac{D+6}{D}}$$

142 respectively. The vertical intercept occurs at $f_1(0) = \beta(1 - D) - \rho$.

143 The parameter ρ only occurs in the constant term of equation (7) so serves to shift the graph of f_1 down the
144 vertical axis as it increases, thus we know that the limiting case of $\rho = 0$ maximizes the function. This observation
145 leads us to introduce

$$g_1(a) = \beta(1 - a)[1 + D(2a - 1)(1 - a)] \quad (8)$$

which is equal to the function f_1 in the limiting case of $\rho = 0$ and hence has the same turning points as f_1 . Direct
calculation of the turning points reveals $g_1(a_-^1) > 0$ and $g_1(a_+^1) < 0$, where $a_-^1 < 1 < a_+^1$, so g_1 has three real
roots which are $a = 1$, $a \in (-\infty, a_-^1]$ and $a \in [a_+^1, \infty)$. Consequently $f_1(a_+^1) < 0$ and f_1 has three real roots for
sufficiently small ρ , however the root lying in $[a_+^1, \infty)$ is never feasible as $a_+^1 > 1$ and is therefore disregarded. For

the remaining two roots to exist and be unique we require $\rho < g_1(a_-^1)$, shown by the shaded region in figure 3a, where

$$g_1(a_-^1) = \frac{\beta}{54} \left[9 + D + (6 + D) \sqrt{\frac{6 + D}{D}} \right].$$

146 This existence condition allows us to determine the form of the actual solutions, which are shown in appendix A.

147 The feasibility of the remaining solutions, defined as $\bar{a}_1^1 \in (-\infty, a_-^1)$ and $\bar{a}_2^1 \in (a_-^1, 1)$, must be determined
 148 when they exist. As we already have the equilibrium solution $\bar{a}_0^1 = 0$ we require \bar{a}_1^1 and \bar{a}_2^1 to lie in $(0, 1]$ for
 149 the equilibrium points to be unique. By considering the sign of a_-^1 , which determines the location of the local
 150 maximum of f_1 , we construct two cases: $D \in (0, 1/4]$ and $D \in (1/4, 1]$, corresponding to $a_-^1 \leq 0$ and $a_-^1 > 0$
 151 respectively. In the first case \bar{a}_2^1 can be feasible, which occurs when the vertical intercept is positive. This provides
 152 the condition $\rho < \beta(1 - D)$. For the second case, \bar{a}_2^1 is feasible for $\rho < g_1(a_-^1)$ (i.e. for when it exists), and \bar{a}_1^1
 153 is feasible for $\beta(1 - D) < \rho < g_1(a_-^1)$ which is where the vertical intercept is negative and the turning point is
 154 positive. These cases are shown in figure 3.

155 *Figure 3 here*

156 2.1 Stability Analysis

To determine the local stability of an equilibrium solution we consider the system close to the equilibrium point and linearize around this point. For a function $F(a)$ and equilibrium point \bar{a} we consider $F(\bar{a} + a)$ where a is small.

Linearizing around the point \bar{a} gives

$$F(a) = aF'(\bar{a}) + \mathcal{O}(a^2)$$

157 as $F(\bar{a}) = 0$, so close to the equilibrium point we have $F(a) = ka$ for $k \in \mathbb{R}$ constant. In our system linearizing
 158 results in an ODE of the form $\dot{a} = ka$ which has solutions $a(t) = Ke^{kt}$ for $K \in \mathbb{R}$ constant. For asymptotic
 159 stability we require $k < 0$ as this ensures that the solution decays with time.

For the unbiased social learning model, equation (5), linearizing gives

$$f_L = (\beta - \rho - 2\beta\bar{a})a$$

so \bar{a}_0^L and \bar{a}_1^L are asymptotically stable for $\rho > \beta$ and $\rho < \beta$ respectively. For the conformist biased model, equation (6), the condition for asymptotic stability is $f_1(\bar{a}) + \bar{a}f_1'(\bar{a}) < 0$ where $f_1(\bar{a}) = 0$ for $\bar{a} \neq 0$ and

$$\bar{a}f_1'(\bar{a}) = \beta\bar{a}(6D\bar{a}^2 - 10D\bar{a} + 4D - 1).$$

160 From this we know that \bar{a}_0^1 is asymptotically stable for $\rho > \beta(1 - D)$. Asymptotic stability of the remaining

161 feasible solutions requires $f'_1(\bar{a}) < 0$ which is true provided $\bar{a} \in (a_-^1, a_+^1)$, so \bar{a}_1^1 is never stable and \bar{a}_2^1 is always
 162 asymptotically stable. These results are summarized in table 1.

163 *Table 1 here*

164 2.1.1 Model comparison

165 We now identify how a conformity bias affects the persistence of trait A in the population compared with the
 166 linear case. Recall that $\rho = \mu + \gamma$ was introduced to simplify the analysis, so any interpretation of ρ requires
 167 an understanding of how μ and γ behave. As we are interested in the proportion of type A individuals in the
 168 population we consider the flow to and from this subpopulation, shown in figure 1.

169 Flow into A is only affected by the parameter β and flow out of A happens at rate $\mu + \gamma$, so ρ is the rate
 170 that individuals leave A. By considering ρ fixed across both the linear and nonlinear frequency-dependent models
 171 we can define threshold values of β required for type A individuals to persist in the population. In the linear
 172 frequency-dependent model the threshold value is $\beta_L = \rho$. In the nonlinear model the threshold is different as it
 173 depends upon the strength of the conformist tendency. The threshold value is $\beta_N^1 = \rho/(1 - D)$ so, for very small
 174 D , the linear and nonlinear threshold values are approximately equal. As the strength of conformity increases
 175 so does the threshold value, thus $\beta_N^1 > \beta_L$. This indicates that when there is a conformity bias acting within a
 176 population, the contact rate β must be greater than in the linear case for trait A to become endemic within the
 177 population. This is demonstrated by simulation results, summarized in table 2 (section A), where increasing the
 178 value of β results in the endemic equilibrium solution becoming feasible and stable for a linear frequency-dependent
 179 relationship, but not with a nonlinear one. Section B of table 2 shows that, as the conformity strength increases,
 180 a larger value of β is required for the endemic equilibrium solution to become feasible.

When $D > 1/4$, there exists a second threshold value. For trait A to persist in the population without any
 dependence on the initial frequency of type A individuals then the threshold value remains as $\beta_N^1 > \beta_L$. This
 corresponds to when the equilibrium solution \bar{a}_2^1 is feasible and stable whereas \bar{a}_1^1 is not feasible. As D increases so
 does the threshold value, though it is undefined at $D = 1$. This indicates that when conformity strength is at its
 maximum, it is not possible to have a contact rate which is sufficiently large to overcome the propensity to conform.
 Trait A, therefore, cannot become endemic in this scenario. By introducing a second threshold, $\beta_M^1 = \rho/k_1(D)$
 where

$$k_1(D) = \frac{1}{54} \left[9 + D + (6 + D) \sqrt{\frac{6 + D}{D}} \right],$$

181 trait A may become endemic. Using the extreme values of D we can bound $k_1(D)$ from above by $k_1(D) < 45/54 < 1$

182 and therefore $\beta_M^1 > \beta_L$, so again the threshold value for the conformity model is greater than that of the unbiased
183 social learning model. We also see from figure 3a that $\beta(1 - D) < g_1(a_\perp^1) = \beta k_1(D)$ and therefore $1/k_1(D) <$
184 $1/(1 - D)$ so $\beta_M^1 < \beta_N^1$. This lower nonlinear threshold value means that trait A can become endemic in the
185 population even when $D = 1$, dependent upon the initial state. We know from our stability analysis (section 2.1)
186 that the system can have two asymptotically stable solutions, \bar{a}_0^1 and \bar{a}_2^1 , so the solution that is reached depends
187 on the initial frequency of type A individuals in the population. By defining $t_0 = 0$ then for $a(t_0) < \bar{a}_1^1$ trait A
188 cannot persist in the population and for $a(t_0) > \bar{a}_1^1$ it becomes endemic. This shows that beginning with very few
189 type A individuals means it is likely that trait A will die out in the population. If at t_0 there was, for example,
190 some major environmental change leading to a sufficiently large number of individuals becoming type A, then trait
191 A would persist in the population. Table 2, section C, gives an example of where the two equilibrium solutions
192 are feasible and stable for sufficiently large conformity strength, compared to the model with a weaker conformity
193 strength.

194 *Table 2 here*

195 **3 Model for conformist cultural trait transmission with varying con-** 196 **formity threshold**

197 We now generalize our model further by allowing the threshold value a_e to vary away from $1/2$, which could
198 indicate a content bias acting in the population. We use the conformity function

$$c_2(a) = a[1 + D(2a - \eta)(1 - a)] \quad (9)$$

which produces an asymmetric sigmodial curve. The threshold value is $a_e = \eta/2$ where $\eta \in (0, 2)$, but restrictions
must be placed on the conformity coefficient D to ensure that c_2 is monotone increasing on $[0, 1]$. This is achieved
by considering the local minimum and local maximum of c_2 ,

$$\tilde{a}_- = \frac{2 + \eta}{6} - \frac{\sqrt{D^2\eta^2 - 2D^2\eta + 4D^2 + 6D}}{6D} \quad \text{and} \quad \tilde{a}_+ = \frac{2 + \eta}{6} + \frac{\sqrt{D^2\eta^2 - 2D^2\eta + 4D^2 + 6D}}{6D}$$

199 respectively, where we require $\tilde{a}_- \leq 0$ and $\tilde{a}_+ \geq 1$. This gives conditions $D \leq 1/\eta$ and $D \leq 1/(2 - \eta)$. As
200 $\text{Max}\{D\} = 1$, the first condition does not always hold for $\eta \in (1, 2)$ and the second for $\eta \in (0, 1)$. For example,
201 when $\eta = 1/2$ then $D \leq 2/3$ which is a stricter condition on D than we desire. To eliminate this problem we
202 restrict D so that $D \in (0, 1/(2 - \eta))$ for $\eta \in (0, 1]$ and $D \in (0, 1/\eta)$ for $\eta \in (1, 2)$.

203 Figure 4a shows the function for $\eta \in (0, 1]$ where the intersection point a_e lies in the interval $(0, 1/2]$. This
 204 represents a situation where less than half of the population displaying trait A is sufficient for a naïve individual
 205 to be more likely to take up trait A than in the linear case. Figure 4b shows the function for $\eta \in (1, 2)$ and
 206 $a_e \in (1/2, 1)$. Here, more than half the population must display trait A in order for the probability of behavior
 207 uptake to be greater than in the linear case. An increase in the value of η represents an increased aversion to
 208 adopting trait A. As with the previous conformity function c_1 , an increase in the conformity strength D increases
 209 the concavity of conformity function c_2 .

210 The nonlinear frequency-dependent SIS model with variable threshold point η is

$$\dot{a}(t) = \beta a(1-a)[1 + D(2a - \eta)(1-a)] - \rho a, \quad (10)$$

formed from equation (2) and the conformity function c_2 . We analyze this model by proceeding as in section 2,
 beginning by defining $f_2(a)$, where $\dot{a} = a f_2(a)$, so that the equilibrium solutions are $\bar{a}_0^2 = 0$ and the roots of

$$f_2(a) = \beta(1-a)[1 + D(2a - \eta)(1-a)] - \rho.$$

The function f_2 has distinct turning points

$$a_-^2 = \frac{4+\eta}{6} - \frac{1}{6}\sqrt{(2-\eta)^2 + \frac{6}{D}} \quad \text{and} \quad a_+^2 = \frac{4+\eta}{6} + \frac{1}{6}\sqrt{(2-\eta)^2 + \frac{6}{D}}$$

and vertical intercept $f_2(0) = \beta(1 - \eta D) - \rho$. Taking the limiting case of $\rho = 0$ we introduce the function

$$g_2(a) = \beta(1-a)[1 + D(2a - \eta)(1-a)]$$

and direct calculation reveals that $g_2(a_-^2) > 0$ and $g_2(a_+^2) < 0$ where $a_-^2 < 1$ and $a_+^2 > 1$. Hence g_2 has roots
 $a \in (-\infty, a_-^2)$, $a = 1$ and $a \in (a_+^2, \infty)$ so f_2 has three roots for sufficiently small ρ . One of the roots is never
 feasible so we ignore it. For the three solutions to exist the condition $\rho < g_2(a_-^2)$ must hold where

$$g_2(a_-^2) = \frac{\beta}{54} \left[9(2-\eta) + D(2-\eta)^3 + (6 + D(2-\eta)^2) \sqrt{\frac{6 + D(2-\eta)^2}{D}} \right].$$

211 As before, we can now determine the form of the exact solutions, shown in appendix A.

212 To determine the feasibility of the two roots $\bar{a}_1^2 \in (-\infty, a_-^2)$ and $\bar{a}_2^2 \in (a_+^2, 1)$, the sign of a_-^2 must be considered,
 213 where $a_-^2 \leq 0$ gives the case $D \leq 1/(2+2\eta)$. Only \bar{a}_2^2 is ever feasible given $\rho < g_2(0)$, where $g_2(0) = \beta(1 - \eta D)$ is the
 214 vertical intercept. When $D > 1/(2+2\eta)$ both solutions can be feasible if $\rho < g_2(a_-^2)$ for \bar{a}_2^2 and $g_2(0) < \rho < g_2(a_-^2)$
 215 for \bar{a}_1^2 .

216 *Figure 4 here*

217 **3.0.2 Stability Analysis**

218 Following the method of linearization from section 2.1 we find that the condition for asymptotic stability of an
 219 equilibrium solution of equation (10) is $f_2(\bar{a}) + \bar{a}f_2'(\bar{a}) < 0$. The equilibrium solution \bar{a}_0^2 is asymptotically stable
 220 for $\rho < g_2(0)$ and the stability of the remaining two solutions requires $f_2'(\bar{a}) < 0$, which corresponds to solutions
 221 lying in the interval (a_-^2, a_+^2) . Hence we find that a feasible \bar{a}_2^2 is always asymptotically stable and a feasible \bar{a}_1^2 is
 222 never stable. The feasibility and stability conditions for the equilibrium solutions are summarized in table 3.

223 *Table 3 here*

224 **3.0.3 Model comparison**

As in section 2.1.1, we can define threshold values of β for which the stable equilibrium changes from being trait-
 A-free to the trait persisting in the population. We first consider $D \leq 1/(2 + 2\eta)$ and define the threshold value
 to be $\beta_N^2 = \rho/(1 - \eta D)$ so $\beta_N^2 > \beta_L$. For $\eta < 1$ we have $\beta_N^2 < \beta_N^1$, which is an intuitive result when comparing the
 curves c_1 and c_2 . Defining the distance between these two curves as

$$d(a) = c_1 - c_2 = D(\eta - 1)a(1 - a)$$

225 then $d < 0$ for $\eta < 1$ which signifies that $P(\text{adopting A} | c_2) > P(\text{adopting A} | c_1)$. Hence, for some fixed a value,
 226 the probability of adopting trait A is greater when we take conformity function c_2 . The threshold value β_N^2 is
 227 lower than β_N^1 as, for each individual contact, the probability of transmission is greater than with c_1 and hence
 228 fewer contacts are required for trait A to become endemic. For $\eta > 1$ the converse is true, whereby $d > 0$ and
 229 hence $P(\text{adopting A} | c_2) < P(\text{adopting A} | c_1)$. The effect of η is shown in table 2, section D, where the other
 230 parameter values are fixed. When $\eta = 0.7$ the endemic solution is feasible so type A individuals will persist in the
 231 population. Comparing this with the previous model (which is equivalent to $\eta = 1$) we see that the persistence of
 232 type A individuals is not certain but depends on the initial state. A further increase to $\eta = 1.2$ results in trait
 233 A dying out within the population, owing to the change in the conformity bias effect.

When $D > 1/(2 + 2\eta)$ the threshold β_N^2 is defined for $\eta D \neq 1$. As with the previous conformity model, a
 second threshold exists where trait A persisting in the population is dependent upon initial state. This threshold
 is $\beta_M^2 = \rho/k_2(D)$ where

$$k_2(D) = \frac{1}{54} \left[9(2 - \eta) + D(2 - \eta)^3 + (6 + D(2 - \eta)^2) \sqrt{\frac{6 + D(2 - \eta)^2}{D}} \right]$$

234 and $\beta_M^2 < \beta_N^2$. Again this threshold value increases with η so $\beta_M^2 < \beta_M^1$ when $\eta < 1$ and $\beta_M^2 > \beta_M^1$ for $\eta > 1$.

4 Discussion

Our analysis reveals that varying the conformity threshold frequency a_e affects the β value required for cultural trait A to become endemic in the population, where β represents the average rate of contacts sufficient for transmission of cultural trait A. Lowering a_e results in an increased probability of adopting trait A for some fixed a value, and hence lowers the threshold value of β which is required for the trait to persist. By contrast, β must be large for this to occur when a_e is high.

Morgan et al. (2011) found that an increased conformity threshold frequency was consistent with strong confidence in information acquired asocially. Here we have a similar asymmetric conformity function, but without requiring asocial learning. Instead, the value of the conformity threshold frequency coefficient η may capture the interaction of a content bias with conformity bias. For instance, the conformity threshold frequency for an attractive cultural trait may be smaller than that of a trait that does not hold the same intrinsic appeal. Our analysis shows that the value of η can affect the conditions for trait A extinction.

The effect of a content bias on social transmission may, however, be more complex than simply altering the conformity threshold. A content bias may also affect the value of the adoption and abandonment rates, β and γ . For example, a trait that is highly attractive or salient would have a high rate β at which contact sufficient for transmission occurs. From the results of our conformity model, we can see that content bias affecting β will alter the feasibility of an endemic equilibrium for a given conformity bias strength D .

Evidence from Efferson et al. (2008) and Morgan et al. (2011) suggests that some individuals will exhibit conformist bias under certain circumstances whereas others will not. An extension to the work here would be to consider the spontaneous uptake of trait A to account for some of this variation. This development would remove the trait-free equilibrium and affect the initial trait frequency which, we have shown in our current model, can have important consequences, such as when conformity bias is strong and the system is bistable.

The general models presented here can be applied to health-related behaviors and thus provide an extension to the existing epidemiological literature, some of which was discussed in section 1. One possible application could be to model the drinking habits of young people in the U.K. Alcohol consumption within this age group is predominantly binge drinking (Institute of Alcohol Studies, 2010, 2013), which is defined as drinking 8+ units for men and 6+ units for women in one drinking session (Deacon et al., 2007). Evidence suggests that peer group influence is a major contributor to an individual choosing to binge drink (French and Cooke, 2012; Institute of Alcohol Studies, 2013), so such behavior could be considered to be driven by social learning with a likely conformist bias. Our model does not assume differential mortality as the long term health effects of alcohol misuse are unlikely to develop within the modeled timescale. Instead, young adults are likely to leave the modeled population at rate

266 μ as a result of lifestyle changes such as movement out of a student community, or starting a family. For example,
267 Seaman and Ikegwonu (2010) found that young adults in the U.K. were more likely to moderate their drinking
268 when becoming parents.

269 The frequency-independent term γ may represent reversion resulting from exposure to governmental or mass
270 media campaigns to abstain from binge drinking, while assuming any frequency-dependent influence of susceptible
271 individuals on binge drinkers is small by comparison. The effect of top-down impositions, such as alcohol minimum
272 pricing or the reduction of sweet or otherwise attractive- tasting alcoholic drinks, on binge drinking may be
273 predicted. Such scenarios may be modeled by altering the reversion rate γ and the value of the conformity
274 threshold through η to introduce a content bias into the system. This may provide an initial indicator as to
275 the potential success of proposed strategies to reduce the prevalence of binge drinking within the young adult
276 population.

277 In conclusion, we have developed a model for cultural trait transmission within an SIS framework by introducing
278 a nonlinear frequency-dependent relationship with a variable conformity threshold frequency, which could account
279 for the interaction of conformity and content biases acting within the population. Hence, the analysis of the
280 conformity threshold frequency advances cultural evolutionary theory in line with empirical evidence, suggesting
281 that individuals may employ multiple non-independent learning biases.

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285 **A Exact solutions to $f_1(a) = 0$ and $f_1(a) = 0$**

Following the method described by Murray (1993, appendix 2.3), let

$$x = \frac{D+6}{36D}, \quad y = \frac{\beta(D+9) - 54\rho}{108\beta D}, \quad z = -\frac{5}{6}.$$

286 Then, for $\rho < g_1(a_-^1)$, the exact solutions to $f_1(a) = 0$ are

$$a = 2x^{\frac{1}{2}} \sin \phi - z, \quad a = -2x^{\frac{1}{2}} \sin\left(\frac{\pi}{3} + \phi\right) - z, \quad a = 2x^{\frac{1}{2}} \sin\left(\frac{\pi}{3} - \phi\right) - z, \quad (11)$$

for $\phi = \frac{1}{3} \sin^{-1}\left[\frac{y}{2x^{\frac{3}{2}}}\right]$, $|\phi| \leq \frac{\pi}{6}$. For the model with varying conformity threshold frequency the solutions to $f_2(a) = 0$, for $\rho < g_2(a_-^2)$, are given by equations (11) with

$$x = \frac{6 + D(2 - \eta)^2}{36D} \quad y = \frac{\beta(9(2 - \eta) + D(2 - \eta)^3) - 54\rho}{108\beta D} \quad z = -\frac{4 + \eta}{6}.$$

287 **B Justification of the linear reversion term γA for small γ**

Consider the two functions

$$r_1 = \gamma a,$$

$$r_2 = \gamma a s [1 + \hat{D}(2s - 1)(1 - s)],$$

representing reversion from type A back to type S. The function r_1 assumes no social influence, whereas r_2 assumes a conformist influence of the same form as c_1 (used in section 2) with conformity coefficient \hat{D} . The difference between these two functions can be calculated by subtracting r_2 from r_1 , resulting in

$$d_\gamma(a) = \gamma a^2 (-2\hat{D}a^2 + 3\hat{D}a + 1 - \hat{D}).$$

The turning points of this function occur at $a = 0$ and

$$a = \frac{9}{16} \pm \frac{1}{16} \sqrt{17 + \frac{64}{\hat{D}}}.$$

288 By considering these points as $\hat{D} \rightarrow 0$ it can be determined that for all values of \hat{D} the function d_γ is strictly
 289 monotonically increasing on $(0, 1)$, therefore attains its maximum within $[0, 1]$ at $a = 1$. By direct calculation,
 290 $d_\gamma(1) = \gamma$ so the maximum error magnitude which can arise from using the linear function r_1 over the conformity
 291 function r_2 is γ . As stated in section 2 we assume γ to be very small, and much smaller than β , therefore using r_1
 292 is appropriate owing to the small magnitude of the error.

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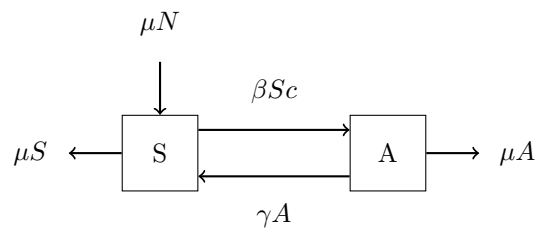


Figure 1: Pictorial representation of the SAS model for cultural trait transmission, relating to equations (1). The nodes S and A represent the subpopulations of type S and type A individuals respectively. The labeled arrows indicate the rate and direction of movement through the system.

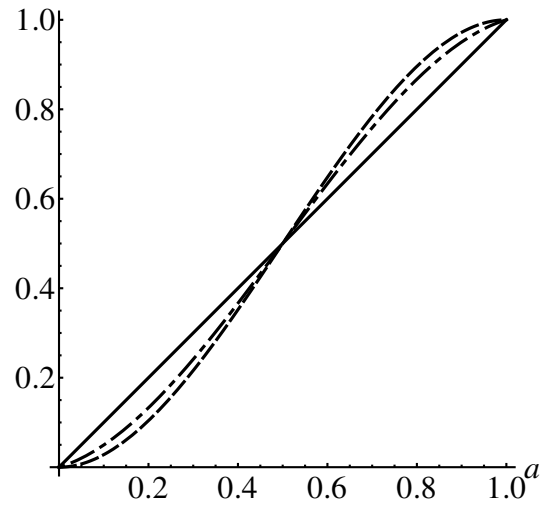


Figure 2: Plot of the functions c_L (dot-dashed) and c_1 , given by equations (2) and (3) respectively, with conformity strength values $D = 0.7$ (dashed) and $D = 1$ (bold). As the strength of the conformist tendency (D) increases, so does the concavity of the conformity curve c_1 . Consequently, as D increases, the probability of adopting trait A decreases for $a < 1/2$ and increases for $a > 1/2$.

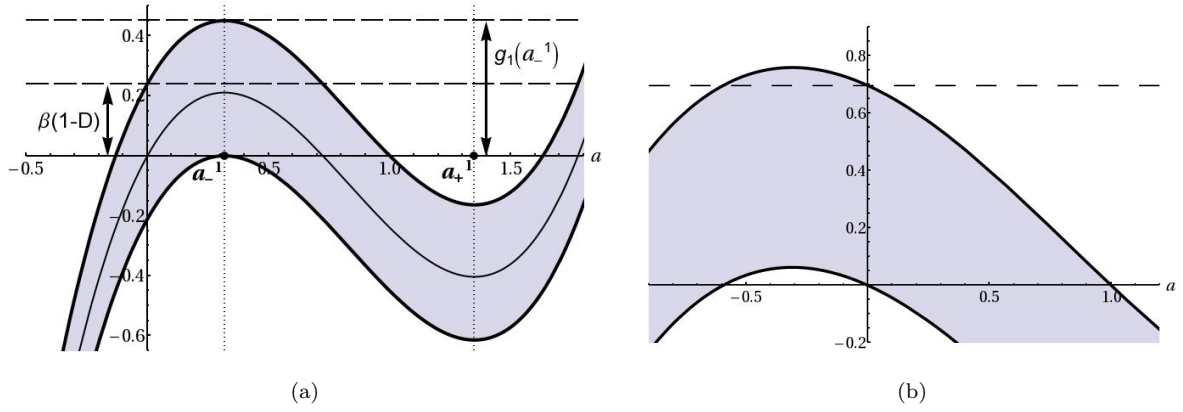


Figure 3: (a) The shaded region is the area bounded above and below by the curves $g_1(a)$ (equation (7)) and $f_1(a)$ (equation (8)) respectively, where $\beta = 0.8$, $D = 0.7$ and $\rho = g_1(a_-^1) = 0.451$. For f_1 in the limiting case of $\rho = 0$ (equivalent to curve g_1) only one root is feasible ($a = 1$, which is independent of β and D). As the value of ρ increases the two leftmost roots tend towards $a = a_-^1 = 0.318$. The central curve, with $\rho = \beta(1 - D) = 0.24$, highlights where two equilibria become feasible. Eventually, when $\rho = g_1(a_-^1)$, both of these equilibria cease to exist.

(b) the shaded region is bounded by the curves $g_1(a)$ and $f_1(a)$ with $\beta = 0.8$, $D = 0.13$ and $\rho = \beta(1 - D) = 0.696$. As the value of ρ increases, the only feasible solution decreases away from $a = 1$ towards $a = 0$, at which point it becomes unfeasible. This situation where only one equilibria is feasible arises for $D \in (0, 1/4]$, unlike the scenario of (a) where two feasible solutions may exist and $D \in [1/4, 1)$.

		<i>Feasible</i>	<i>Asymptotically Stable</i>	<i>Unstable</i>	
Linear	\bar{a}_0^L	Always	$\rho > \beta$	$\rho < \beta$	
	\bar{a}_1^L	$\rho < \beta$	$\rho < \beta$	—	
		\bar{a}_0^1	Always	$\rho > \beta(1 - D)$	$\rho < \beta(1 - D)$
$D \in (0, 1/4]$	\bar{a}_1^1	Never	—	—	
	\bar{a}_2^1	$\rho < \beta(1 - D)$	$\rho < \beta(1 - D)$	—	
		\bar{a}_0^1	Always	$\rho > \beta(1 - D)$	$\rho < \beta(1 - D)$
$D \in (1/4, 1]$	\bar{a}_1^1	$\beta(1 - D) < \rho < g_1(a_-^1)$	—	$\beta(1 - D) < \rho < g_1(a_-^1)$	
	\bar{a}_2^1	$\rho < g_1(a_-^1)$	$\rho < g_1(a_-^1)$	—	

Table 1: For the linear frequency-dependent model the stability of the equilibria switches when the rate of transmission (β) is equal to the rate of leaving the type A class (ρ). When the leaving rate is greater, $\rho > \beta$, trait A dies out. When $\rho < \beta$ however, trait A persists. For a conformity strength $D \in (0, 1/4]$ the stability of the zero solution and endemic solution switches when $\rho = \beta(1 - D)$, that is where the rate of leaving A is equal to the transmission rate, subject to a conformity effect. This threshold is greater than the linear case so a larger transmission rate β is required for trait A to become endemic. For an increased conformity strength ($D > 1/4$) a bistable state exists where the stable equilibria is dependent upon the initial frequency of type A individuals.

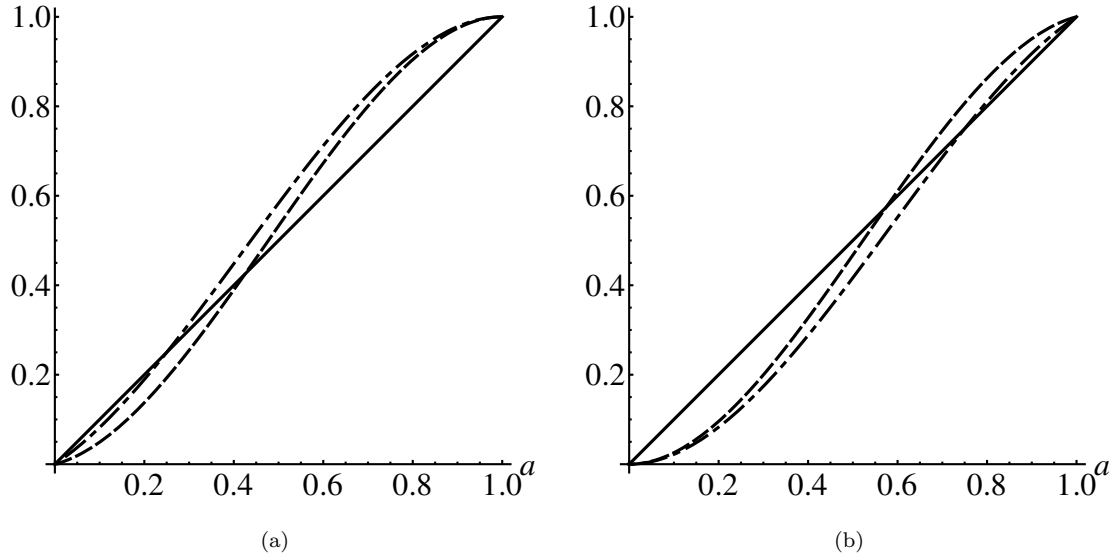


Figure 4: The figures show the functions c_L (equation (2), bold) and c_2 (equation (9)) with $D = 1$ and (a) $\eta = 0.5$ (dot-dashed), $\eta = 0.85$ (dashed) and (b) $\eta = 1.15$ (dashed), $\eta = 1.5$ (dot-dashed). When more than $\eta/2$ of the population display trait A, the probability of uptake is greater than that of the linear case. As the value of η increases, the probability of adopting trait A reduces, representing a content bias which dissuades individuals from adopting the trait. The probability of adopting trait A is (a) greater than for the function c_1 (equation (3), figure 2) when $\eta < 1$ and (b) less than c_1 when $\eta > 1$.

	<i>Function</i>	β	D	η	<i>Stable solution</i>
A	c_L	0.2	—	—	0
	c_L	0.27	—	—	0.741
	c_1	0.27	0.1	—	0
B	c_L	0.3	—	—	0.167
	c_1	0.3	0.1	—	0.103
	c_1	0.3	0.7	—	0
C	c_1	0.45	0.1	—	0.441
	c_1	0.45	0.7	—	0 or 0.380
D	c_2	0.45	0.7	0.6	0.515
	c_2	0.45	0.7	1	0 or 0.380
	c_2	0.45	0.7	0.2	0

Table 2: Table showing simulation results for different parameter values, with $\rho = 0.25$ fixed. The stable solution is the frequency of type A individuals in the population once the system has reached equilibrium where all values are to three significant figures.

A: Comparison between the linear frequency-dependent function c_L and the conformity function c_1 highlighting the effect of the transmission rate β on the stability of an endemic equilibrium ($a > 0$).

B: For a fixed transmission rate β the linear frequency-dependent model results in a higher frequency of type A individuals in the population than the conformity model. Provided the conformity strength D is large enough, an endemic equilibrium will not be reached and type A individuals will always die out.

C: For certain parameter values, an increase in the conformity strength will result in a bistable system. In the example given, a threshold exists at $a(0) = 0.258$. For an initial frequency of type A individuals greater than 0.258, trait A will become endemic within the population with approximately 38% displaying the trait at equilibrium. For an initial frequency of type A individuals less than 0.258 the trait will eventually die out.

D: The effect of a content bias, controlled by η in conformity function c_2 , is investigated. As the value of η increases, the persistence of type A individuals first becomes dependent on their initial frequency before becoming impossible.

		<i>Feasible</i>	<i>Asymptotically Stable</i>	<i>Unstable</i>
	\bar{a}_0^2	Always	$\rho > \beta(1 - \eta D)$	$\rho < \beta(1 - \eta D)$
$D \in (0, 1/4]$	\bar{a}_1^2	Never	—	—
	\bar{a}_2^2	$\rho < \beta(1 - \eta D)$	$\rho < \beta(1 - \eta D)$	—
	\bar{a}_0^2	Always	$\rho > \beta(1 - \eta D)$	$\rho < \beta(1 - \eta D)$
$D \in (1/4, 1]$	\bar{a}_1^2	$\beta(1 - \eta D) < \rho < g_2(a_-^2)$	—	$\beta(1 - \eta D) < \rho < g_2(a_-^2)$
	\bar{a}_2^2	$\rho < g_2(a_-^2)$	$\rho < g_2(a_-^2)$	—

Table 3: For $D \in (0, 1/4]$ the stability of the zero and endemic solutions switches at $\rho = \beta(1 - \eta D)$. This is where the leaving rate is equal to the transmission rate, modified by a combined conformity and content bias term. The value of η , representing a content bias, affects the magnitude of variation between this threshold and the threshold associated with conformity function c_1 (see table 1 for comparison). As with the previous conformity model (section 2), increasing the conformity strength ($D > 1/4$) allows for a bistable solution where the initial frequency of type A individuals affects their long-term survival.