Research

Evolution of culture-dependent discriminate sociality: a gene–culture coevolutionary model

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Animals behave cooperatively towards certain conspecifics while being indifferent or even hostile to others. The distinction is made primarily according to kinship as predicted by the kin selection theory. With regards to humans, however, this is not always the case; in particular, humans sometimes exhibit a discriminate sociality on the basis of culturally transmitted traits, such as personal ornaments, languages, rituals, etc. This paper explores the possibility that the human faculty of cultural transmission and resultant cultural variation among individuals may have facilitated the evolution of discriminate sociality in humans. To this end, a gene–culture coevolutionary model is developed focusing on competition over control of resource as a context in which discriminate sociality may have evolved. Specifically, two types of culture-dependent discriminate sociality are considered: ingroup favouritism, with ingroup and outgroup being distinguished by the presence or absence of a cultural trait; and prestige hierarchies, with the prestige being conferred on the bearer of a cultural trait. The model specifies the conditions under which emergence and evolutionary stability of the two types of discriminate sociality are promoted by the presence of cultural variation among individuals.

Keywords: cultural niche construction; Hawk–Dove game; ingroup favouritism; Middle/Upper Palaeolithic transition; prestige; tag-based cooperation

1. INTRODUCTION

Cooperative behaviours in most animals are primarily directed towards close kin. Kin selection is believed to have shaped the innate predispositions in these animals to behave cooperatively to certain individuals but not to others [1]. Human individuals can also establish a strong emotional tie with certain individuals and behave cooperatively towards them while at the same time being indifferent or even hostile to others. In contrast to most non-human animals, however, human decisions regarding whether or not to behave cooperatively towards certain individuals are not necessarily based on kinship. Indeed, the flexibility in the choice of allies to whom cooperation is offered may be a salient feature of human sociality [2,3].

Evolution of cooperative behaviour among unrelated individuals has been studied extensively within the framework of Prisoner's Dilemma (PD) [4–6]. In a two-person PD, two individuals behave either cooperatively or uncooperatively towards each other and obtain a benefit from mutual cooperation, while each individual gains most from unilateral cooperation by the partner and loses most by cooperating unilaterally. Evolution of cooperation in groups has also been investigated by using *n*-person PD [7–9].

Resource-sharing is a form of cooperative behaviour. It is not hard to imagine that during the history of human evolution, there were times of resource scarcity owing to climate change, excessive exploitation, dispersal into an unfamiliar environment, and so on. Scarcity of critical resources leads to intraspecific competition, in which individuals may either try to monopolize the available resources or share them with others. Although each individual gains most when it successfully monopolizes the resources, others may also try to do the same, in which case aggressive fights may result. In species such as humans, aggressive fight over control of resource can be extremely costly, especially during the time of resource scarcity, so that individuals may be better off sharing the resource with others rather than running the risk of deadly conflict.

Dyadic competition over control of resource can be investigated using Hawk–Dove games [10,11]. In the conventional terminology, a Hawk–Dove game represents a contest between two players, each of whom either escalates the contest (Hawk) or displays first but retreats if the opponent escalates the contest (Dove). In the present context, the contest is rephrased as a dyadic interaction in which each individual either tries to monopolize a resource or is willing to share it with the opponent. Key assumptions are as follows: first, if both individuals contend for the resource, the winner of an aggressive fight takes it and the loser suffers injury; second, if one contends for the resource

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One contribution of 13 to a Theme Issue 'Human niche construction'.

and the other is willing to share, the former takes the resource without aggressive fight; and third, if both individuals are willing to share, the resource is shared equally.

It is certainly not a good idea to always try to share the resource because then those who are not willing to share will take all the resource. In Hawk–Dove games, a population of individuals who always try to share is evolutionarily unstable, being vulnerable to invasion by those who always contend for the resource. On the other hand, it may not be a good idea either to always try to monopolize the resource since in that case one will be frequently involved in dangerous fights. In Hawk–Dove games, a population of individuals who always contend for the resource is evolutionarily unstable if the cost of injury is substantial relative to the value of the resource. Note that if the cost of injury is sufficiently small that an aggressive fight on average pays for individuals, resource-sharing as described here can be formulated as a two-person PD.

When the cost of injury is substantial, contingent strategies that modify the behaviour according to with whom they are interacting can be evolutionarily stable. For strategies with such discriminate sociality to be possible, individuals need to differ in some ways. For example, the strategy called Assessor evaluates the relative fighting abilities, or resource-holding powers (RHPs), of individuals and tries to monopolize resources if it has a greater RHP than its opponent [10,11]. In addition, natural selection can also favour discriminate sociality for individual variations that are not correlated with RHP. For example, the strategy called Bourgeois, which contends for resources only if it is the ‘owner’ of them, can be evolutionarily stable [10,11].

Among humans, there exists an abundance of individual variations apparently uncorrelated with RHP. Human faculty of cultural transmission seems to play an essential role in creating such variations [12–15]. If solving a problem as represented by a Hawk–Dove game has been crucial in survival and reproduction of human individuals, especially during the times of resource scarcity, it is theoretically plausible that natural selection may have shaped a culture-dependent discriminate sociality in humans, that is, a predisposition to choose certain unrelated individuals on the basis of cultural variations and behave cooperatively only to them. Since natural selection would not have worked in this way without the human faculty of cultural transmission, this scenario is coherent with the niche construction perspective, which emphasizes the capability of humans (and other organisms) to modify their environment and consequently alter the selective pressure acting on them [16,17] (see also Gintis [18] for gene–culture coevolution of human sociality). Theoretical models have been developed to investigate possible effects of cultural transmission on human niche construction [19–21].

Humans have been suggested to have a distinct set of psychological mechanisms designed by natural selection causing them to exhibit discriminate sociality [22]. More specifically, Kurzban & Leary [22] argued that stigmatization, or exclusion of individuals with certain characteristics from social exchanges, may be caused

by a set of psychological mechanisms that has played a role in avoiding poor social exchange partners, forming dominant social groups, and keeping distance from infectious diseases through the history of human evolution. Another possibility is that discriminate sociality and the underlying psychological mechanisms may have been selectively favoured even though the distinction is based on arbitrary cultural variations that have nothing to do with the quality or health conditions of individuals.

Ingroup favouritism, or the tendency of human individuals to treat ingroup members more favourably than outgroup members, is an example of discriminate sociality. Tajfel *et al.* [23] conducted experiments on intergroup behaviour in which subjects were told that they were divided into two groups on the basis of a nominal criterion, such as whether they overestimated or underestimated numbers of dots projected on a screen or whether they preferred abstract paintings by one or the other painters. When asked to allocate rewards, the subjects transferred larger amounts of money to ingroup members than to outgroup members although there was no personal advantage in doing so and the group membership was completely anonymous. This and other studies have suggested that ingroup favouritism can emerge in the laboratory from mere categorization even if it is based on trivial and arbitrary criteria (see also [24]; reviewed in Yamagishi *et al.* [25]).

Another example of discriminate sociality arises from social hierarchy; that is, individuals sometimes behave discriminately in favour of those who occupy higher social status [26]. Henrich & Gil-White [27] highlighted the distinction between two types of social status: dominance and prestige. According to their definitions, dominance hierarchies are supported predominantly by force or force threat, while prestige hierarchies involve non-coerced deference by subordinates. In the context of the present study, dominance and prestige hierarchies may be regarded as consequences of RHP-dependent and RHP-independent discriminate sociality, respectively. Furthermore, Henrich & Gil-White [27] postulated a distinct set of psychological mechanisms through which prestige hierarchies emerge, advocating the view that these psychological mechanisms have been favoured by natural selection since subordinates have been able to acquire fitness-inducing skills and knowledge by conferring deference to those who have such useful cultural traits. Alternatively, but not incompatible with this view, prestige hierarchies may have been advantageous for subordinates in which such hierarchies facilitate avoidance of aggressive fights when difference in RHP is not clearly observable.

Variations among individuals in cultural traits (such as personal ornaments, languages, rituals, etc.) may have played a role in the evolution of human behaviour by promoting the emergence of discriminate sociality and underlying psychological mechanisms. In this paper, I explore this possibility using a simple gene–culture coevolutionary model (see [28]). A related issue is the evolution of ‘tag-based’ cooperation, in which cooperation is established among individuals sharing the same arbitrary trait [29–34]. In contrast

to the previous studies, this paper explicitly incorporates the vertical and horizontal transmission of a cultural trait [12] and focuses on the competition between two unrelated individuals over control of resources as a context in which the evolution may have taken place. Analysis of simple models such as PD and Hawk–Dove games has played a crucial role in studies of human behaviour. If used appropriately, simple models have the merits of clarifying the logical coherence of a hypothesis that is very complicated for verbal arguments, elucidating minimal assumptions required to explain complex phenomena, and providing qualitative predictions to be tested empirically.

In the following sections, I first introduce a general modelling framework in which genetic inheritance of behavioural strategies and cultural transmission of an arbitrary trait are considered. Secondly, I introduce competition over control of resource into the general framework and specify two competing strategies, one of which exhibits culture-dependent discriminate sociality. Finally, I examine whether culture-dependent discriminate sociality can emerge in a population without it and whether it can be evolutionarily stable. Through the analysis, I suggest that cultural variation among individuals can facilitate the evolution of discriminate sociality, which in turn may stimulate the spread of culturally transmitted traits.

2. MODEL

(a) *The general framework*

We examine whether a mutant strategy can invade a population of a resident strategy assuming that the fitness of a strategy depends on cultural variation among individuals. To this end, let us first introduce a gene–culture coevolutionary model that includes vertical and horizontal transmission of a cultural trait [12] and differential reproduction owing to culture-dependent fitness difference. Consider a population of asexually reproducing individuals with discrete generations. Suppose that each individual has either strategy A or B . Individuals are also dichotomized for the presence or absence of a cultural trait. Thus, there are four phenogenotypes in the population: strategy A without the cultural trait ($A0$), strategy A with the cultural trait ($A1$), strategy B without the cultural trait ($B0$) and strategy B with the cultural trait ($B1$) (table 1).

Population dynamics are modelled by assuming the following life cycles. First, individuals are born. Second, individuals may acquire the cultural trait via cultural transmission from their parents (vertical transmission). Third, the cultural trait may be transmitted within the offspring generation (horizontal transmission). Fourth, viability and/or fertility selection act on individuals through fitness difference, where an individual's fitness depends on cultural variation among individuals. Fifth, individuals give birth and die after the phase of cultural transmission to their offspring. Further details of the population dynamics are described in appendix A.

(b) *Competition over control of resource*

Suppose that individuals compete over control of a resource that affects their fitness. Competition occurs

Table 1. The four phenogenotypes.

phenogenotype	strategy	cultural trait	frequency	fitness
$A0$	A	absent	u_{A0}	W_{A0}
$A1$	A	present	u_{A1}	W_{A1}
$B0$	B	absent	u_{B0}	W_{B0}
$B1$	B	present	u_{B1}	W_{B1}

Table 2. The expected payoff to the self according to behaviours of the interacting individuals. $b > 0$, $c > 0$.

behaviour (self)	behaviour (opponent)	
	peaceful	aggressive
peaceful	b	0
aggressive	$2b$	$b - c$

as a dyadic interaction in which each individual is either aggressive or peaceful. When aggressive, an individual contends with the opponent for the resource and is prepared for an aggressive fight, whereas a peaceful individual is willing to share the resource with the opponent but will abandon it if necessary to avoid fighting. If both individuals are peaceful, the resource is shared equally and each of them gains a payoff b ($b > 0$). If both individuals are aggressive, an aggressive fight occurs, and one of them eventually wins the resource gaining a payoff $2b$, while the loser pays a cost $2c$ from injury ($c > 0$). If one individual is aggressive and the other peaceful, the former monopolizes the resource, which results in a payoff $2b$, while the payoff to the latter is 0 . Assume that two interacting individuals always differ in RHP and the one with a greater RHP wins an aggressive fight with the probability d ($1/2 < d < 1$). Following previous studies, assume further that each individual is equally likely to have a greater RHP than its opponent [10,11]. Table 2 shows the expected payoffs from an interaction.

Fitness of an individual is determined by a baseline value, w ($w > 0$), the frequencies of the phenogenotypes, u_{A0} , u_{A1} , u_{B0} and u_{B1} ($u_{A0} + u_{A1} + u_{B0} + u_{B1} = 1$; see table 1) and the expected payoffs from the competition over resource, W_{A0} , W_{A1} , W_{B0} and W_{B1} (see table 1):

$$W_{A0} = w + u_{A0}V(A0|A0) + u_{A1}V(A0|A1) + u_{B0}V(A0|B0) + u_{B1}V(A0|B1), \quad (2.1)$$

$$W_{A1} = w + u_{A0}V(A1|A0) + u_{A1}V(A1|A1) + u_{B0}V(A1|B0) + u_{B1}V(A1|B1), \quad (2.2)$$

$$W_{B0} = w + u_{A0}V(B0|A0) + u_{A1}V(B0|A1) + u_{B0}V(B0|B0) + u_{B1}V(B0|B1) \quad (2.3)$$

$$\text{and } W_{B1} = w + u_{A0}V(B1|A0) + u_{A1}V(B1|A1) + u_{B0}V(B1|B0) + u_{B1}V(B1|B1), \quad (2.4)$$

where $V(X|Y)$ denotes the expected payoff to phenogenotype X when interacting with phenogenotype Y .

(c) The strategies

The following two strategies are considered. First, Assessor is a strategy that evaluates the relative RHPs of interacting individuals and behaves aggressively if and only if its RHP is perceived to be greater than the opponent's [10,11]. Roughly speaking, Assessor is peaceful to the stronger and aggressive to the weaker. In addition, assume that RHP is not always evaluated accurately: Assessor's evaluation is incorrect in the proportion e of all cases ($0 < e < 1/2$). Note that Assessor's behaviour is not affected by cultural variation among individuals.

Second, consider a strategy that alters the behaviour based on the presence or absence of the cultural trait in interacting individuals. The strategy, which is called Culture-dependent discriminator (CDD), is aggressive against its opponent with the probability f_{ij} , where i signifies the presence ($i = 1$) or absence ($i = 0$) of the cultural trait in the self, and j signifies the presence ($j = 1$) or absence ($j = 0$) of the same trait in the opponent ($0 \leq f_{ij} \leq 1$) (table 3). Assume that the cultural trait is so conspicuous that its presence or absence is clearly observable and always recognized accurately. Table 4 shows the expected payoffs, $V(X|Y)$, under these assumptions (appendix B).

3. ANALYSIS

Let strategies A and B be Assessor and CDD, respectively (see appendix C for a more general treatment). A special emphasis is on the following two behaviour rules for CDD. The first rule is specified by $f_{00} = f_{11} = 0$ and $f_{01} = f_{10} = 1$ (rule I), in which CDD is always peaceful towards someone who is concordant with itself for the presence or absence of the cultural trait while always aggressive against someone who is discordant in this respect. When following rule I, CDD can be regarded as exhibiting an ingroup favouritism, with ingroup and outgroup being defined by the cultural variation among individuals. The second rule is given by $f_{01} = f_{11} = 0$ and $f_{00} = f_{10} = 1$ (rule II); that is, CDD is always peaceful towards those with the cultural trait and always aggressive against those without it. Rule II may apply if the cultural trait is perceived by CDD as indicative of prestige. In other words, CDD with rule II can be regarded as following a prestige hierarchy, with the prestige being defined by the cultural variation among individuals.

When the cultural trait is newly introduced into a population consisting only of Assessors by invention or transmission from other populations, the frequency of individuals having the trait may either increase or decrease in succeeding generations. The frequency decreases and eventually becomes 0 if

$$v_A < \frac{1}{(1 + h_A)}, \quad (3.1)$$

where v_A and h_A represent, respectively, the rates of vertical and horizontal transmission for Assessor ($0 < v_A < 1$, $0 < h_A < 1$; see appendix A). Intuitively, when (3.1) holds, the rates of vertical and/or horizontal transmission are not sufficiently high to allow the cultural trait to spread; hence, cultural trait is absent in the equilibrium population of Assessor. In contrast,

Table 3. CDD's probability of aggression (f_{ij}) according to the presence or absence of the cultural trait in the interacting individuals.

cultural trait (self)	cultural trait (opponent)	
	absent	present
absent	f_{00}	f_{01}
present	f_{10}	f_{11}

the frequency of the cultural trait increases and eventually converges to y_2^* if the inequality in (3.1) is reversed, where $y_2^* = [(1 + h_A)v_A - 1]/(h_A v_A^2)$. Note that y_2^* increases as either v_A or h_A increases. Thus, there are some individuals with the trait in the equilibrium population of Assessor when the inequality in (3.1) is reversed.

Suppose that a small frequency of CDD is introduced, by mutation of immigration, into the equilibrium population of Assessor. If the frequency of CDD increases in the succeeding generations, CDD is said to invade the population. On the contrary, if the frequency can never increase and always converges to 0, the population of Assessor is referred to as stable against invasion by CDD. Whether CDD can invade the equilibrium population of Assessor is examined for each of the two behaviour rules for CDD (rules I and II) (see appendix D for details).

Similarly, a population consisting only of CDDs will converge either to an equilibrium state in which the cultural trait is absent or to another in which some individuals possess the trait. Whether the equilibrium population of CDD can be stable against invasion by Assessor is examined for each of the behaviour rules (see appendix E for details).

(a) Rule I: ingroup favouritism

Suppose that CDD follows rule I ($f_{00} = f_{11} = 0$, $f_{01} = f_{10} = 1$). Whether CDD with Rule I can invade the equilibrium population of Assessor is examined as follows. First, consider the case when the ratio of the benefit from resource acquisition to the cost from injury, b/c , is low, specifically,

$$\frac{b}{c} < 2e(1 - e). \quad (3.2)$$

In this case, CDD with rule I can invade the equilibrium population of Assessor in which the cultural trait is absent. This is consistent with intuition since when the cultural trait is absent, CDD with rule I is always peaceful, and this behaviour pays off given that b/c is sufficiently low. When the inequality in (3.1) is reversed and thus the cultural trait is present in the equilibrium population of Assessor, invasion by CDD with rule I is possible if either of the following two conditions is met:

$$v_A < v_A^* \quad \text{and} \quad v_B < v_B^*, \quad (3.3)$$

$$v_A > v_A^* \quad \text{and} \quad v_B > v_B^*, \quad (3.4)$$

where v_B is the rate of vertical transmission for CDD ($0 < v_B < 1$; see appendix A) and the threshold rates of vertical transmission, v_A^* , v_A^{**} and v_B^* are given in

Figure 1. Regions on the $v_A v_B$ -plane for which CDD with rule I can invade the population of Assessor (the shaded regions) and combinations of parameter values for which the population of CDD with rule I is stable (the filled circles) or unstable (the empty circles) against invasion by Assessor, where v_A and v_B denote the rates of vertical transmission for Assessor and CDD, respectively. The dashed lines represent $v_A = 1/(1 + h_A)$. (a) $b = 4$; (b) $b = 5$; (c) $b = 9$; and (d) $b = 15$. Other parameter values are: $w = 20$, $c = 10$, $d = 0.6$, $e = 0.4$, $h_A = 0.5$ and $h_B = 0.8$.

Table 4. The expected payoff to the self according to the strategies (Assessor or CDD) and the cultural trait (present or absent) in the interacting individuals. $\alpha = b/2 - ce(1 - e)$, $\beta = 3b/2 - (b + c)(e + d - 2ed)$, $\gamma = b/2 + (b + c)(1 - e - d + 2ed)$.

self	opponent			
	Assessor (absent)	Assessor (present)	CDD (absent)	CDD (present)
Assessor (absent)	$b/2 + \alpha$	$b/2 + \alpha$	$3b/2 - f_{00}\gamma$	$3b/2 - f_{10}\gamma$
Assessor (present)	$b/2 + \alpha$	$b/2 + \alpha$	$3b/2 - f_{01}\gamma$	$3b/2 - f_{11}\gamma$
CDD (absent)	$b/2 + f_{00}\beta$	$b/2 + f_{01}\beta$	$b - cf_{00}^2$	$b(1 + f_{01} - f_{10}) - cf_{01}f_{10}$
CDD (present)	$b/2 + f_{10}\beta$	$b/2 + f_{11}\beta$	$b(1 - f_{01} + f_{10}) - cf_{01}f_{10}$	$b - cf_{11}^2$

appendix D. Note that $1/(1 + h_A) < v_A^{**} < v_A^*$ in this case. Figure 1a illustrates the regions on the $v_A v_B$ -plane in which CDD with rule I can invade the equilibrium population of Assessor (the shaded regions) when (3.2) holds.

Second, when the benefit-to-cost ratio is intermediate so that

$$2e(1 - e) < \frac{b}{c} < \frac{e + d - 2ed - e(1 - e)}{1 - e - d + 2ed}, \quad (3.5)$$

CDD with rule I can never invade the equilibrium population of Assessor whether or not individuals having the cultural trait exist (figure 1b).

Third, consider the case when the benefit-to-cost ratio is high, specifically,

$$\frac{b}{c} > \frac{e + d - 2ed - e(1 - e)}{1 - e - d + 2ed}. \quad (3.6)$$

When (3.1) holds so that the cultural trait is absent in the equilibrium population of Assessor, CDD with rule I cannot invade the population. Nevertheless, if both CDD and the cultural trait are introduced simultaneously into the population, their frequencies may increase in a coevolutionary manner, even though either one of them cannot increase in the absence of the other (given that (3.1) and (3.6) hold). This type of gene-culture coevolution is possible if CDD's rate

Figure 2. Sample trajectories of changes in the frequencies of CDD with rule I ($u_{B0} + u_{B1}$) and the cultural trait ($u_{A1} + u_{B1}$). The arrows indicate directions of changes. The filled and empty circles represent locally stable and unstable equilibrium states, respectively. (a) $b = 5$, $v_A = 0.2$, $v_B = 0.8$; (b) $b = 9$, $v_A = 0.2$, $v_B = 0.95$. Other parameter values are: $w = 20$, $c = 10$, $d = 0.6$, $e = 0.4$, $h_A = 0.5$ and $h_B = 0.8$.

of vertical transmission is sufficiently high, namely,

$$v_B > \frac{w + b/2 + \alpha}{w + b/2 + \beta}, \quad (3.7)$$

where $\alpha = b/2 - ce(1 - e)$ and $\beta = 3b/2 - (b + c)(e + d - 2ed)$. When the inequality in (3.1) is reversed so that a proportion, y_2^* , of individuals possess the cultural trait in the equilibrium population of Assessor, invasion by CDD with rule I is possible if either of the following two conditions is met:

$$v_A < v_A^* \quad \text{and} \quad v_B > v_B^*, \quad (3.8)$$

$$v_A > v_A^* \quad \text{and} \quad v_B < v_B^*, \quad (3.9)$$

where $1/(1 + h_A) < v_A^* < v_A^{**}$ in this case. Figure 1c,d shows the parameter region in which CDD with rule I can invade the equilibrium population of Assessor when (3.6) holds (parameter combinations satisfying (3.9) do not exist in these examples). Inequality (3.8) means that invasion by CDD with rule I is possible if the rate of vertical transmission for Assessor is low and the corresponding rate for CDD is high. This is explained as follows: when (3.8) is met, the cultural trait will become statistically associated with CDD, and consequently, CDD's ingroup favouritism induces aggressive behaviour against Assessor, which gives a fitness advantage to CDD as the benefit-to-cost ratio of aggressive fight is high (i.e. (3.6)). Similarly, according to (3.9), invasion by CDD with rule I is also possible if v_A is large and v_B is small. This is because though in this case the cultural trait will become associated with Assessor, CDD's ingroup favouritism still promotes aggression against Assessor.

Let us now turn to the stability of the population of CDD. Assessor can always invade the equilibrium population of CDD with rule I if no-one has the cultural trait. However, when some individuals have the trait at the equilibrium state, the population of CDD with rule I can be stable for some combinations of parameter values satisfying either (3.2), (3.5) or (3.6) as shown in figure 1 (the filled circles). Figure 2 shows sample trajectories of changes in the frequencies of CDD with rule I and the cultural

trait for parameter values satisfying (3.5) (figure 2a) or (3.6) (figure 2b).

(b) Rule II: prestige hierarchies

Suppose that CDD follows rule II ($f_{01} = f_{11} = 0$, $f_{00} = f_{10} = 1$). Whether CDD with rule II can invade the equilibrium population of Assessor is examined as follows. First, consider the case when the benefit-to-cost ratio, b/c , is low so that (3.2) holds. In this case, CDD with rule II cannot invade the equilibrium population of Assessor in which the cultural trait is absent. When the inequality in (3.1) is reversed and thus the proportion y_2^* of individuals have the cultural trait at the equilibrium state, invasion by CDD with rule II is possible if

$$v_A > v_A^*. \quad (3.10)$$

Thus, the presence of the cultural trait can also facilitate the invasion by CDD with rule II, which is never possible in the absence of the trait. Figure 3a illustrates the parameter region in which CDD with rule II can invade the equilibrium population of Assessor (the shaded region) when (3.2) holds. It is worth mentioning that (3.10) does not depend on v_B or h_B , the rates of vertical and horizontal transmission for CDD. This is explained as follows. CDD with rule II perceives others as prestigious and thus behaves peacefully towards them whenever they possess the cultural trait. Hence, when CDD is rare, an individual CDD's fitness does not vary depending on whether or not the individual has the trait, although it does vary depending on the prevalence of the trait among Assessors. As the benefit-to-cost ratio of aggressive fight is low, CDD with rule II gains a greater payoff when the trait is more common (recall that y_2^* increases with v_A).

Second, when the benefit-to-cost ratio is intermediate so that (3.5) is satisfied, CDD with rule II can never invade the equilibrium population of Assessor, irrespective of the presence or absence of the cultural trait in the population (figure 3b).

Third, consider the case when the benefit-to-cost ratio is high so that (3.6) holds. CDD with rule II can invade the equilibrium population of Assessor in which the cultural trait does not exist. This is

Figure 3. Regions on the $v_A v_B$ -plane for which CDD with rule II can invade the population of Assessor (the shaded regions) and combinations of parameter values for which the population of CDD with rule II is stable (the filled circles) or unstable (the empty circles) against invasion by Assessor, where v_A and v_B denote the rates of vertical transmission for Assessor and CDD, respectively. The dashed lines represent $v_A = 1/(1 + h_A)$. (a) $b = 4$; (b) $b = 5$; (c) $b = 9$; and (d) $b = 15$. Other parameter values are: $w = 20$, $c = 10$, $d = 0.6$, $e = 0.4$, $h_A = 0.5$ and $h_B = 0.8$.

because CDD with rule II is always aggressive when no one has the cultural trait, and behaving in this way pays off given that b/c is sufficiently high. When the inequality in (3.1) is reversed so that the cultural trait exists in the equilibrium population of Assessor, invasion by CDD with rule II is possible if

$$v_A < v_A^*. \quad (3.11)$$

Figure 3c,d shows the parameter regions in which CDD with rule II can invade the equilibrium population of Assessor when (3.6) is satisfied.

Let us now examine the stability of the population of CDD. Assessor can invade the equilibrium population of CDD with rule II in which the cultural trait is absent if

$$\frac{b}{c} < \frac{e + d - 2ed}{1 - e - d + 2ed}. \quad (3.12)$$

On the contrary, when some individuals have the trait at the equilibrium state, the population of CDD with rule II can be stable against invasion by Assessor, even for parameter combinations satisfying (3.12) (the filled circles in figure 3). Figure 4 shows sample trajectories of the population dynamics for parameter combinations satisfying (3.2) (figure 4a) or (3.5) (figure 4b).

4. DISCUSSION

Evolution of culture-dependent discriminate sociality is explored by analysing a gene–culture coevolutionary model in which competition over control of resource is assumed to have a significant impact on the fitness of individuals. The competition is formulated as a Hawk–Dove game (table 2), in which two strategies, CDD and Assessor, are considered. CDD alters its behaviour depending on the presence or absence of a culturally transmitted trait among individuals (table 3), while Assessor's behaviour depends not on the cultural variation, but on the relative RHPs of individuals. Two behaviour rules, rules I and II, that determine how CDD responds to given patterns of cultural variation are examined. When behaving under rule I, CDD is regarded as exercising ingroup favouritism, with ingroup and outgroup being categorized based on the cultural variation. When rule II is assumed, on the other hand, CDD is regarded as following a prestige hierarchy, with the prestige being identified based on the cultural variation.

An aggressive fight over control of resource results in a benefit of resource acquisition, b , to the winner and a cost of injury, c , to the loser. Whether CDD can invade the population of Assessor is investigated for each of the three ranges of the benefit-to-cost ratio, b/c , specified by (3.2), (3.5) and (3.6). When b/c is low so that (3.2) holds, aggressive fighting is extremely costly and hence a strategy that is always peaceful would

Figure 4. Sample trajectories of changes in the frequencies of CDD with rule II ($u_{B0} + u_{B1}$) and the cultural trait ($u_{A1} + u_{B1}$). The arrows indicate directions of changes. The filled and empty circles represent locally stable and unstable equilibrium states, respectively. (a) $b = 4$, $v_A = 0.9$, $v_B = 0.6$; (b) $b = 5$, $v_A = 0.6$, $v_B = 0.6$. Other parameter values are: $w = 20$, $c = 10$, $d = 0.6$, $e = 0.4$, $h_A = 0.5$ and $h_B = 0.8$.

invade the population of Assessor. Similarly, CDD with rule I can invade the population of Assessor without the cultural trait since this strategy is always peaceful in the absence of cultural variation (figure 1a). In contrast, CDD with rule II cannot invade the population of Assessor without the cultural trait as this strategy is always aggressive in the absence of cultural variation. Nonetheless, CDD with Rule II may invade the population of Assessor if more than a threshold proportion of the resident individuals have the cultural trait (figure 3a). That is, the presence of the cultural trait can facilitate the invasion by CDD with rule II.

When b/c is intermediate so that (3.5) is satisfied, the population of Assessor is not invaded by a strategy that is always peaceful or one that is always aggressive. Accordingly, neither CDD with rules I nor II can invade the population of Assessor without the cultural trait. Thus, if CDD could invade the population of Assessor in the presence of the cultural trait, that would be an even stronger support for the claim that the presence of the cultural trait facilitates the evolution of discriminate sociality. This turns out, however, not to be the case: invasion by CDD is not possible even if the cultural trait exists in the equilibrium population of Assessor (figures 1b and 3b).

When b/c is high so that (3.6) holds, aggressive fighting is relatively less costly (though $b < c$ may still hold) and thus a strategy that is always aggressive can invade the population of Assessor. Hence, CDD with rule II can also invade the population of Assessor without the cultural trait (figure 3c,d). On the other hand, CDD with rule I cannot invade the population of Assessor if the cultural trait does not exist at all. Nonetheless, the frequencies of CDD with rule I and the cultural trait may increase in a coevolutionary manner if both are introduced into the population (figure 1c,d). In other words, ingroup favouritism and cultural variation on which it depends can emerge, through gene–culture coevolution, where none of them initially exists. The coevolutionary process takes place when Assessor's rate of vertical transmission is low and CDD's rate is high (see (3.1), (3.7) and (3.8)). This might be possible if individuals are strongly motivated to acquire the cultural

trait through vertical transmission only if they have the innate predisposition to culture-dependent ingroup favouritism; that is to say, while individuals without the predisposition are indifferent to having or not having the cultural trait, those with the predisposition may be more sensitive about and thus inclined to display what they regard as their group identity.

Whether the population of CDD can be stable against invasion by Assessor is also examined. The population of CDD in which no one has the cultural trait can never be stable when rule I is assumed, and cannot be stable unless (3.12) is violated when rule II is assumed. However, the population of CDD with either rules I or II can be stable in the presence of cultural variation among CDDs. Combination of parameter values are found for which the population of CDD is stable within each of the three ranges of the benefit-to-cost ratio (figures 1 and 3). The presence of cultural variation, therefore, can always stabilize the population of individuals possessing discriminate sociality.

Two things about the model assumptions are worth mentioning. First, I intend to keep the model as simple as possible primarily for logical clarity and mathematical tractability. More realistic but less simple assumptions are also possible; for example, one can assume that each individual has a constant RHP rather than a constant probability of having a greater RHP than its opponent. In this sense, the model presented in this paper can serve as a basis for future studies that incorporate more realistic assumptions. Second, although I assume throughout this paper that the strategies (i.e. Assessor and CDD) are genetically transmitted, the model is consistent with the interpretation that they are culturally transmitted. In the latter case, the transmission of the strategies follows replicator dynamics where the probability with which the strategy of a given individual is imitated is proportional to its 'fitness' (see [35]).

(a) *Evolution of discriminate sociality*

Evolution of discriminate sociality for phenotypic similarity has been studied in the recent literature on

tag-based cooperation [29–34]. Riolo *et al.* [29], using agent-based computer simulations, suggested that evolution of cooperation is facilitated if each agent discriminates other agents to make costly donations only to those that are similar to itself in an arbitrary tag. Axelrod *et al.* [30] conducted another series of simulations, in which coevolution of an arbitrary tag and behavioural strategy in a two-person PD was considered. They found that a tag-based discriminate altruism can emerge through the coevolutionary process, but only if there is a spatial structure (or, viscosity) (see also [31]). Throughout this paper, the population is assumed to be well-mixed and no spatial structure is considered. Since spatial structure can favour the evolution of cooperation by promoting non-random interactions [36,37], future study may find that cultural variation plays an even greater role in facilitating the evolution of discriminate sociality in structured populations.

Efferson *et al.* [38] showed that cultural groups can emerge endogenously among subjects in laboratory while initially meaningless arbitrary symbols play a role as cultural markers, becoming associated with either of the groups. Each subject of the experiment chose a behaviour (A or B) and an arbitrary symbol (circle or triangle) and played a coordination game with another subject (in a coordination game, the players gain the maximum payoff when they choose the same behaviour). Though behaviours of other subjects were unknown before interaction, each subject could choose her partner on the basis of the symbols assigned to them. As sessions proceeded, statistical association between behaviour and symbol built up and the subjects showed a preference for partners having the same symbol. Efferson *et al.* [38] interpreted this preference as a form of ingroup favouritism in the choice of partners, which is slightly different from ingroup favouritism in the choice of behaviours as considered in the present study. Effects of ingroup favouritism in the choice of partners on the maintenance of cultural diversity have been examined theoretically by McElreath *et al.* [39], also assuming a coordination game. Castro & Toro [40,41] analysed mathematical models to study the evolution of ingroup favouritism in the choice of partners based on arbitrary tags.

(b) *The Middle/Upper Palaeolithic transition*

If the mechanism proposed in this paper has indeed played a role in the evolution of human discriminate sociality, when and where did it take place? Let me finish with an attempt to situate the model in the history of human evolution.

Various lines of evidence suggest that Cro-Magnons (*Homo sapiens*), or early modern humans, replaced Neanderthals (*Homo neanderthalensis*) in Europe by 30 000 years ago (possibly with some level of hybridization; see [42,43]). It is reasonable to speculate that extinction of the Neanderthals may have been caused by difference in behaviour between the two species. Behavioural difference is partially inferred from difference in artefacts: artefacts created by Neanderthals, which are usually assigned to Mousterian Industry or Middle Palaeolithic, are rather uniform through time

and space, while Cro-Magnons manufactured a much wider variety of artefacts using specialized techniques (Aurignacian Industry or Upper Palaeolithic). Furthermore, there is little unequivocal evidence of art and personal ornaments among Mousterian people [44,45], whereas thousands have been known from Upper Palaeolithic.

On the one hand, the Middle/Upper Palaeolithic transition may be attributable to a new cognitive (neurological) capability acquired by modern humans around 50 000 years ago, not long before the beginning of Upper Palaeolithic [45]. An obstacle to this hypothesis is Châtelperronian Industry, which is associated with Neanderthals in a certain area of Western Europe, but includes such artefacts as bone tools and personal ornaments exhibiting Upper Palaeolithic characteristics [46]. Châtelperronian Industry indicates that the Neanderthals were cognitively capable of creating those artefacts at least by imitating Aurignacian people. Moreover, the hypothesis does not explain the presence of art and ornamentation in African Middle Stone Age about 75 000 years ago [47–49] (see [50]). Alternatively, on the other hand, the cognitive capability may have existed both in early modern humans and the Neanderthals, though it was fully manifested only in early modern humans and a small minority of the Neanderthals. Proponents of this view regard the Middle/Upper Palaeolithic transition as having been stimulated by social and demographic changes [44,51].

The present study demonstrates the logical coherence of a third possibility: the Neanderthals and early modern humans alike were equipped with the cognitive capability required to produce art and personal ornamentation, possibly as a part of more general cognitive adaptation, while early modern humans were far more highly motivated to use the capability for creating those artefacts. My suggestion is that the enhanced level of motivation might have been due to a discriminate sociality that emerged through a gene–culture coevolutionary process as proposed above in *Homo sapiens* after their appearance in Africa. To put it in another way, while the Neanderthals were not concerned much about their personal or group identity, the Cro-Magnons were innately sensitive about cultural variation among individuals and as a result more motivated to display their social identity. According to this view, the Neanderthals could have created art and ornaments if motivated exogenously, perhaps through contact with early modern humans. It also explains why anatomically modern humans did not exhibit fully modern behaviour until the beginning of Upper Palaeolithic, if the gene–culture coevolution can be regarded as a gradual process. My hypothesis is partially in line with the claim that genetic difference between the Neanderthals and early modern humans played a role in the Middle/Upper Palaeolithic transition (e.g. [45]), and partially with the argument that art and ornaments became commonplace in Upper Palaeolithic because of the increasing importance of displaying individual or personal identity (e.g. [52]).

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APPENDIX A. THE POPULATION DYNAMICS

Let u_{A0} , u_{A1} , u_{B0} and u_{B1} denote the frequencies ($u_{A0} + u_{A1} + u_{B0} + u_{B1} = 1$) of the four phenotypes, $A0$, $A1$, $B0$ and $B1$, respectively, in the parental generation after horizontal transmission. Also, let W_{A0} , W_{A1} , W_{B0} and W_{B1} represent the fitness of the four phenotypes (table 1). The frequencies of the phenotypes in the offspring generation after vertical transmission, u'_{A0} , u'_{A1} , u'_{B0} and u'_{B1} , are given by

$$\overline{W}u'_{A0} = W_{A0}u_{A0} + (1 - v_A)W_{A1}u_{A1}, \quad (\text{A } 1)$$

$$\overline{W}u'_{A1} = v_A W_{A1}u_{A1}, \quad (\text{A } 2)$$

$$\overline{W}u'_{B0} = W_{B0}u_{B0} + (1 - v_B)W_{B1}u_{B1} \quad (\text{A } 3)$$

$$\text{and } \overline{W}u'_{B1} = v_B W_{B1}u_{B1}, \quad (\text{A } 4)$$

where v_A and v_B represent the rates of vertical transmission for strategies A and B , respectively ($0 < v_A < 1$, $0 < v_B < 1$), and $\overline{W} = W_{A0}u_{A0} + W_{A1}u_{A1} + W_{B0}u_{B0} + W_{B1}u_{B1}$ is the mean fitness.

The frequencies of the phenotypes in the offspring generation after horizontal transmission, u''_{A1} , u''_{A1} , u''_{B0} and u''_{B1} , are given by

$$u''_{A0} = [1 - h_A(u'_{A1} + u'_{B1})]u'_{A0}, \quad (\text{A } 5)$$

$$u''_{A1} = u'_{A1} + h_A(u'_{A1} + u'_{B1})u'_{A0}, \quad (\text{A } 6)$$

$$u''_{B0} = [1 - h_B(u'_{A1} + u'_{B1})]u'_{B0} \quad (\text{A } 7)$$

$$\text{and } u''_{B1} = u'_{B1} + h_B(u'_{A1} + u'_{B1})u'_{B0}, \quad (\text{A } 8)$$

where h_A and h_B are the rates of horizontal transmission for strategies A and B , respectively ($0 < h_A < 1$, $0 < h_B < 1$).

APPENDIX B. HOW TO CONSTRUCT TABLE 4

First, when an Assessor interacts with another Assessor, the expected payoff does not depend on the presence or absence of the cultural trait. For example, the expected payoff to an Assessor without the cultural trait when interacting with another Assessor without the trait is given by:

$$\begin{aligned} & \{(1 - e)^2 2b + (1 - e)e[d2b - (1 - d)2c] + e(1 - e)b\}/2 \\ & + \{(1 - e)eb + e(1 - e)[(1 - d)2b - d2c] \\ & + e^2 2b\}/2, \end{aligned} \quad (\text{B } 1)$$

which simplifies to the corresponding expression in table 4. The first term of (B 1) represents the case when the self has the greater RHP than the opponent and the second term represents the opposite case. Secondly, when an Assessor interacts with a CDD, the expected payoff depends on the cultural trait. For example, the expected payoff gained by an Assessor without the cultural trait from an interaction of the CDD with the trait is

$$\begin{aligned} & \{(1 - e)(1 - f_{10})2b + (1 - e)f_{10}[d2b - (1 - d)2c] \\ & + e(1 - f_{10})b\}/2 + \{(1 - e)(1 - f_{10})b \\ & + e(1 - f_{10})2b + ef_{10}[(1 - d)2b \\ & - d2c]\}/2. \end{aligned} \quad (\text{B } 2)$$

Thirdly, when a CDD interacts with another CDD, the expected payoff again depends on the cultural trait; for example, the expected payoff to a CDD without the cultural trait when interacting with a CDD with the trait is

$$(1 - f_{01})(1 - f_{10})b + f_{01}(1 - f_{10})2b + f_{01}f_{10}(b - c). \quad (\text{B } 3)$$

Other expressions in table 4 are obtained similarly.

APPENDIX C. LOCAL STABILITY OF A POPULATION FIXED WITH STRATEGY A

We ask whether a population fixed with strategy A can be invaded by strategy B . Suppose that the population dynamics have an equilibrium state given by $(u_{A0}, u_{A1}, u_{B0}, u_{B1}) = (1 - \hat{y}, \hat{y}, 0, 0)$, where $0 \leq \hat{y} \leq 1$. An equilibrium state is regarded as locally stable if and only if the Jacobian matrix around that state has the leading eigenvalue that is larger than -1 and smaller than 1 . One of the eigenvalues of the 3×3 Jacobian matrix obtained from (A 1)–(A 8) is

$$\begin{aligned} \lambda = & v_A \left(F(\hat{y})\hat{y} + \frac{\hat{W}_{A1}}{\hat{W}} \right) \\ & \times \left[1 + h_A \left(1 - 2v_A \hat{y} \frac{\hat{W}_{A1}}{\hat{W}} \right) \right], \end{aligned} \quad (\text{C } 1)$$

where $F(\hat{y})$ is the partial derivative of $W_{A1}/\overline{W}$ with respect to u_{A1} evaluated at the equilibrium state. Hence,

$$|\lambda| < 1 \quad (\text{C } 2)$$

is a necessary condition for the equilibrium state to be locally stable. Note that eigenvalue λ has the corresponding eigenvector given by $(u_{A1}, u_{B0}, u_{B1}) = (1, 0, 0)$, which means that if the inequality in (C 2) is reversed, the rare cultural trait spreads in the population in the absence of individuals with strategy B .

The two other eigenvalues are identical with those of the following matrix:

$$\mathbf{J} = \begin{pmatrix} \left(1 - h_B v_A \hat{y} \frac{\hat{W}_{A1}}{\hat{W}}\right) \frac{\hat{W}_{B0}}{\hat{W}} & (1 - v_B) \left(1 - h_B v_A \hat{y} \frac{\hat{W}_{A1}}{\hat{W}}\right) \frac{\hat{W}_{B1}}{\hat{W}} \\ h_B v_A \hat{y} \frac{\hat{W}_{A1}}{\hat{W}} \frac{\hat{W}_{B0}}{\hat{W}} & \left[v_B + (1 - v_B) h_B v_A \hat{y} \frac{\hat{W}_{A1}}{\hat{W}}\right] \frac{\hat{W}_{B1}}{\hat{W}} \end{pmatrix}. \quad (\text{C } 3)$$

It is shown that the absolute value of the leading eigenvalue of $\mathbf{J}$ is smaller than unity if and only if both of the following conditions are met:

$$\begin{aligned} \frac{\hat{W}_{B0}}{\hat{W}} & < 1 + \frac{h_B v_A \hat{y} \hat{W}_{A1} / \hat{W}}{v_B [1 - h_B v_A \hat{y} \hat{W}_{A1} / \hat{W}]} \\ & \times \left(1 - \frac{1 - v_B}{1 - v_B \hat{W}_{B1} / \hat{W}} \right), \end{aligned} \quad (\text{C } 4)$$

$$\text{and } \frac{\hat{W}_{B1}}{\hat{W}} < \frac{1}{v_B}. \quad (\text{C } 5)$$

Taken together, the equilibrium state is locally stable if and only if (C 2), (C 4) and (C 5) are satisfied.

APPENDIX D. CAN CULTURE-DEPENDENT DISCRIMINATOR INVADE THE POPULATION OF ASSESSOR?

There always exists an equilibrium state, E_1 , given by $(u_{A0}, u_{A1}, u_{B0}, u_{B1}) = (1, 0, 0, 0)$, which represents a population consisting only of Assessor without the cultural trait. From (C 2), (C 4) and (C 5), the equilibrium state is locally stable if and only if all of the following are satisfied:

$$(1 + h_A)v_A < 1, \quad (\text{D } 1)$$

$$\alpha > f_{00}\beta \quad (\text{D } 2)$$

$$\text{and } v_B < \frac{w + b/2 + \alpha}{w + b/2 + f_{10}\beta}, \quad (\text{D } 3)$$

where $\alpha = b/2 - ce(1 - e)$ and $\beta = 3b/2 - (b + c)(e + d - 2ed)$. If the inequality in (D 1) is reversed, the rare cultural trait spreads in the absence of CDD. If the inequality in (D 2) is reversed, rare CDD increases in the absence of the cultural trait (since one of the eigenvalues of matrix **J** corresponds to the eigenvector given by $(u_{A1}, u_{B0}, u_{B1}) = (0, 1, 0)$, and (D 2) specifies the condition under which the absolute value of the eigenvalue is smaller than unity (see appendix C)). If the inequality in (D 3) is reversed, CDD and the cultural trait can increase when both are rare but not absent.

When the inequality in (D 1) is reversed, there exists another equilibrium state, E_2 , given by $(u_{A0}, u_{A1}, u_{B0}, u_{B1}) = (1 - y_2^*, y_2^*, 0, 0)$, where $y_2^* = [(1 + h_A)v_A - 1]/(h_A v_A^2)$. Equilibrium state E_2 represents a population in which everyone is CDD and some but not others have the cultural trait. Local stability of E_2 is analysed for each of rules I and II assuming that the inequality in (D 1) is reversed. First, suppose that CDD follows rule I ($f_{00} = f_{11} = 0, f_{01} = f_{10} = 1$). For E_2 to be unstable, it is necessary that either $\beta < \alpha < 0$ or $0 < \alpha < \beta$ is satisfied. When $\beta < \alpha < 0$, E_2 is unstable if and only if either (3.3) or (3.4) is satisfied, where the threshold rates of vertical transmission are given as follows: v_A^* is the smaller solution of a quadratic equation for v_A ,

$$h_A(\beta - \alpha)v_A^2 - (1 + h_A)\beta v_A + \beta = 0; \quad (\text{D } 4)$$

v_A^* is the smaller solution of another quadratic equation,

$$h_A\alpha v_A^2 - (1 + h_A)\beta v_A + \beta = 0, \quad (\text{D } 5)$$

and v_B^* is given by

$$v_B^* = \frac{w + b/2 + \alpha}{w + b/2 + (1 - y_2^*)\beta} \times \left(1 + \frac{h_B v_A y_2^*}{1 - h_B v_A y_2^*} \frac{(1 - y_2^*)\beta - \alpha}{y_2^* \beta - \alpha} \right). \quad (\text{D } 6)$$

When $0 < \alpha < \beta$, equilibrium state E_2 is unstable if and only if either (3.8) or (3.9) is satisfied. Second, when rule II ($f_{01} = f_{11} = 0, f_{00} = f_{10} = 1$) is assumed, either $\beta < \alpha < 0$ or $0 < \alpha < \beta$ is necessary for E_2 to be unstable. When $\beta < \alpha < 0$, E_2 is unstable if and only if (3.10) is met. When $0 < \alpha < \beta$, it is unstable if and only if (3.11) holds.

APPENDIX E. CAN ASSESSOR INVADE THE POPULATION OF CULTURE-DEPENDENT DISCRIMINATOR?

There always exists an equilibrium state, E_3 , given by $(u_{A0}, u_{A1}, u_{B0}, u_{B1}) = (0, 0, 1, 0)$, representing a population fixed with CDD without the cultural trait. The equilibrium state is locally stable if and only if all of the following are satisfied:

$$(1 + h_B)v_B < \frac{w + b - cf_{00}^2}{w + b(1 - f_{01} + f_{10}) - cf_{01}f_{10}}, \quad (\text{E } 1)$$

$$\frac{b}{2} - cf_{00}(1 - f_{00}) < f_{00}\beta \quad (\text{E } 2)$$

$$\text{and } v_A < \frac{w + b - cf_{00}^2}{w + 3b/2 - f_{01}\gamma}, \quad (\text{E } 3)$$

where $\lambda = b/2 + (b + c)(1 - e - d + 2ed)$. If the inequality in (E 1) is reversed, the rare cultural trait spreads in the absence of Assessor. If the inequality in (E 2) is reversed, Assessor can invade the population without the cultural trait. If the inequality in (E 3) is reversed, Assessor and the cultural trait can increase when both are rare but not absent.

Depending on parameter values, there may be other equilibrium states in which Assessor is absent. Such equilibrium states exist if the following equation for u_{B1} has one or more solutions satisfying $0 < u_{B1} < 1$:

$$G(u_{B1}) = v_B \frac{W_{B1}}{\overline{W}} \left[1 + h_B \left(1 - v_B u_{B1} \frac{W_{B1}}{\overline{W}} \right) \right] - 1 = 0, \quad (\text{E } 4)$$

where $W_{B1} = w + b[1 - u_{B0}(f_{01} - f_{10})] - c(u_{B0}f_{01}f_{10} + u_{B1}f_{11}^2)$ and $\overline{W} = w + b - c(u_{B0}^2f_{00}^2 + 2u_{B0}u_{B1}f_{01}f_{10} + u_{B1}^2f_{11}^2)$. Local stability of these equilibrium states are analysed numerically by using (C 2), (C 4) and (C 5), with subscripts A and B interchanged.

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